Thank you for downloading this document from the RMIT Research Repository.

The RMIT Research Repository is an open access database showcasing the research outputs of RMIT University researchers.


Citation:

See this record in the RMIT Research Repository at:

Version: Published Version

Copyright Statement: © 2010 The Contributors

Link to Published Version:
No group of plants or animals on the planet exhibits the range of morphological diversity seen among the extant Crustacea.' This provocative quote from Martin and Davis (2001) highlights at least one attribute of the group. Nevertheless, the body plan of the Crustacea has a number of unifying characteristics, including a five-segmented head with two pairs of antennae and an elongate body that may be divided into two more-or-less distinct sections – generally the thorax or ‘body’ and the pleon or ‘abdomen’. Each of these sections bears multisegmented appendages (mostly limbs) that are primitively biramous (forked) but some are uniramous in many groups. Brusca and Brusca (2002) gave a succinct summary of the characteristics of the subphylum. In addition to enormous diversity of form, crustaceans exhibit a great range of sizes (exceeded only by molluscs, which can claim the largest individual invertebrate in the form of the colossal squid), from minute interstitial and parasitic forms (e.g. Tantulocarida) measuring as little as a tenth of a millimetre to giant crabs, lobsters, and isopods with a body size of up to half a metre in length or breadth and weighing up to 20 kilograms. By virtue of their edibility, many crustaceans are prized items on restaurant menus around the world.

They are an ancient group, dating from at least the Early Cambrian (Chen et al. 2001), and have diversified abundantly since then. Calculations of the number of named living species of Crustacea range from approximately 50,000 to 67,000. Estimates of the potential number of species range from 10 to 100 times that number. The smaller species, such as those of the Peracarida and Copepoda may eventually be found in numbers comparable to those of the insects on land. By way of an example, the Isopoda currently number approximately 11,000 species, but estimates suggest that as many as 50,000 species of Isopoda could exist on coral-reef habitats alone (Kensley 1988), a figure close to the current total for all Crustacea, while Wilson (2003) estimated a total of 400,000 deep-sea species! Clearly, with thorough documentation, crustacean diversity will be found to be huge.

Five (Brusca & Brusca 2002) or six (Martin & Davis 2001) classes of Crustacea are recognised. Whichever classification is used, only the cave-dwelling
Remipedia have not yet been found in New Zealand waters. As one moves down the taxonomic hierarchy from class to species, the level of endemism increases. The New Zealand fauna currently stands at 2974 known species, of which at least 485 have not yet been named or described. This number is very conservative, and more than a thousand additional species will surely be discovered. Most major groups of Crustacea (orders) are to be found in New Zealand waters, though many families and genera will be found to be absent, particularly among those groups with strong warm-water representation, such as the commercially and gastronomically desirable ‘prawns’. Prawns of the family Penaeidae (notably Penaeus and Metapenaeus) and portunid crabs of the genera Portunus and Scylla are rare or absent.

Class Branchiopoda: Fairy shrimps, water fleas, and kin

The approximately 1000 species of branchiopods (‘gill feet’) mostly inhabit fresh water (Dumont & Negrea 2002). They cover a wide range of body form from many-segmented, ancient-looking taxa – generally the larger-bodied forms such as Anostraca (fairy shrimps), Notostraca (tadpole shrimps), and ‘Conchostraca’ (clam shrimps) – to more-modified short-bodied taxa like the Cladocera (water fleas). The larger Branchiopoda do not collectively form a natural, evolutionary group but have a general similarity (many segments and same structure of trunk limbs) and are almost all adapted to a short life-span in temporary pools.

There are more than 250 species of Anostraca (fairy shrimps) worldwide (Dumont & Negrea 2002), none of which is naturally represented in New Zealand (Chapman & Lewis 1976) although the brine shrimp Artemia franciscana has apparently been introduced into saline Lake Grassmere near Blenheim. They are all relatively slow and graceful forms that swim with the back facing the bottom (opposite to most other crustacea) while they use their 11 pairs of trunk limbs, beating in metachronal (wave-like) fashion, for both swimming and filtration.

The Notostraca (tadpole shrimps) comprises about 10 species worldwide, one of which (Lepidurus apus viridis) is found in New Zealand. One of the most striking features of notostracans is the large, flattened dorsal carapace that originates immediately behind the head and overhangs a part of the body. Behind the carapace is a relatively long (sometimes very long), flexible and limbless abdomen that ends in a pair of superficially segmented tail-like processes. At the front end, the carapace has a conspicuous so-called ‘dorsal organ’ (used for osmoregulation). The first and second antennae – which often have sensory functions in the Crustacea – are much reduced in size in the adult, and the sensory function has been taken over by the very long endites (innermost branches) of the first pair of biramous trunk limbs. All notostracans have basically the same lifestyle. In contrast to most other branchiopods, notostracans are not filter-feeders, but remain near the bottom, where they use the heavily chitinised parts of the anterior trunk limbs to handle detritus and small organisms (Fryer 1988).

It has recently been shown that the former order ‘Conchostraca’ is most likely to be paraphyletic, having given rise to descendant evolutionary lineages (Braband et al. 2002; Olesen 1998, 2000; Spears & Abele 2000; Richter et al. 2007). The taxonomic rearrangement of Martin and Davis (2001) recognises the order Diplostraca, with four suborders – Laevicaudata, Spinicaudata, Cyclodida, and Cladocera – of which only the Cladocera and Spinicaudata are represented in New Zealand, the latter by a species of Eulimnadia. All diplostracans have the body and legs enclosed between a large, sometimes bivalved carapace. The biramous second antennae are used for swimming, while the phyllopodous (leaf-like), often serially similar, trunk limbs are used for filtration. The most speciose group in New Zealand is the Cladocera, discussed below.
**Summary of New Zealand crustacean diversity**

A query (?) following an entry for alien species indicates that alien status is suspected for some but not confirmed.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Described living species + subspecies</th>
<th>Known undescribed/ undetermined species</th>
<th>Estimated unknown species</th>
<th>Adventive species named + unnamed</th>
<th>Endemic species</th>
<th>Endemic genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branchiopoda</td>
<td>44</td>
<td>5</td>
<td>7</td>
<td>3?</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Anostraca</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1?</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Notostraca</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Diplostraca</td>
<td>42</td>
<td>5</td>
<td>7</td>
<td>2?</td>
<td>5</td>
<td>0</td>
</tr>
<tr>
<td>Cephalocarida</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>1</td>
</tr>
<tr>
<td>Maxilopoda</td>
<td>661+2</td>
<td>139</td>
<td>2,067</td>
<td>16?</td>
<td>153</td>
<td>5</td>
</tr>
<tr>
<td>Ascothoracica</td>
<td>2</td>
<td>1</td>
<td>7</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Acrothoracica</td>
<td>1</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Rhizocephala</td>
<td>8</td>
<td>3</td>
<td>30</td>
<td>0</td>
<td>4</td>
<td>0</td>
</tr>
<tr>
<td>Thoracica</td>
<td>77</td>
<td>6</td>
<td>20</td>
<td>3</td>
<td>34</td>
<td>2*</td>
</tr>
<tr>
<td>Tantulocarida</td>
<td>3</td>
<td>0</td>
<td>8</td>
<td>0</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Branchiura</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Pentatostomida</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Copepoda</td>
<td>568</td>
<td>129</td>
<td>2,000</td>
<td>11?</td>
<td>111</td>
<td>3</td>
</tr>
<tr>
<td>Calanoida</td>
<td>252+1</td>
<td>9</td>
<td>290</td>
<td>6?</td>
<td>10</td>
<td>0</td>
</tr>
<tr>
<td>Cyclopoida</td>
<td>100</td>
<td>4</td>
<td>500</td>
<td>5?</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Mormoniloida</td>
<td>1</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>130</td>
<td>99</td>
<td>850</td>
<td>0</td>
<td>63</td>
<td>3***</td>
</tr>
<tr>
<td>Siphonostomatoida</td>
<td>85+1</td>
<td>16</td>
<td>330</td>
<td>0</td>
<td>30</td>
<td>0</td>
</tr>
<tr>
<td>Monstriloida</td>
<td>0</td>
<td>1</td>
<td>27</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>356</td>
<td>86</td>
<td>320</td>
<td>3</td>
<td>89</td>
<td>7</td>
</tr>
<tr>
<td>Palaeocopida</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Podocopida</td>
<td>275</td>
<td>82</td>
<td>200</td>
<td>3</td>
<td>61</td>
<td>6</td>
</tr>
<tr>
<td>Myodocopida</td>
<td>78</td>
<td>4</td>
<td>120</td>
<td>0</td>
<td>24</td>
<td>1</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>1,425+1</td>
<td>255</td>
<td>2,665</td>
<td>23</td>
<td>850</td>
<td>85+10</td>
</tr>
<tr>
<td>Leptostraca</td>
<td>3</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Stomatopoda</td>
<td>8</td>
<td>0</td>
<td>20</td>
<td>1</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Anaspidacea</td>
<td>2</td>
<td>4</td>
<td>5</td>
<td>0</td>
<td>5</td>
<td>1</td>
</tr>
<tr>
<td>Bathynellacea</td>
<td>5</td>
<td>3</td>
<td>5</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Lophogastrida</td>
<td>5</td>
<td>1</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mysida</td>
<td>17</td>
<td>1</td>
<td>50</td>
<td>0</td>
<td>11</td>
<td>0</td>
</tr>
<tr>
<td>Thermosbaenacea</td>
<td>0</td>
<td>0</td>
<td>5</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>439</td>
<td>64</td>
<td>800</td>
<td>11</td>
<td>268</td>
<td>48+10</td>
</tr>
<tr>
<td>Isopoda</td>
<td>358</td>
<td>67</td>
<td>1,000</td>
<td>7</td>
<td>331</td>
<td>19**</td>
</tr>
<tr>
<td>Tanaidacea</td>
<td>40</td>
<td>77</td>
<td>300</td>
<td>0</td>
<td>12</td>
<td>0</td>
</tr>
<tr>
<td>Curnaceae</td>
<td>51</td>
<td>24</td>
<td>110</td>
<td>17</td>
<td>66</td>
<td>7*</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td>19+1</td>
<td>0</td>
<td>15</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Decapoda</td>
<td>480</td>
<td>12</td>
<td>150</td>
<td>4</td>
<td>147</td>
<td>10</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td>2,488+3</td>
<td>485</td>
<td>~5,060</td>
<td>46?</td>
<td>1,097</td>
<td>98+10</td>
</tr>
</tbody>
</table>

* including one new undescribed genus
** including two new undescribed genera
*** including three new undescribed genera
Order Diplostraca: Suborder Cladocera – water fleas

The Cladocera is generally believed to be a monophyletic group within the Branchiopoda (Martin & Cash-Clark 1995; Olesen 1998; Taylor et al. 1999; Spears & Abele 2000; Martin & Davis 2001), a notion that was called into question by Fryer (1987) when providing detailed diagnoses for all branchiopod ‘orders’ (the rank was changed by Martin & Davis 2001). The Cladocera is by far the most diverse and speciose group within the Branchiopoda, with approximately 640 species worldwide (Korovchinsky 2000), which is more than half of all branchiopod species described.

Historically, Sars (1865) had recognised four tribes within the Cladocera – the Haplopoda, Ctenopoda, Anomopoda, and Onychopoda – which are basically still accepted as monophyletic groups; these groups are now treated as infraorders (Martin & Davis 2001). The Anomopoda is the most species-rich, with at least five families (the number varies depending on the author), 75 genera (Dumont & Negrea 2002), and approximately 560 species (Korovchinsky 2000); the Ctenopoda has eight genera and 47 species (Korovchinsky 2000), the Onychopoda 10 genera with 34 species (Rivier 1998), and the Haplopoda is monotypic with only one species (Leptodora kindtii – not represented in New Zealand).

The four infraorders are rather different in their general morphology, which means that cladocerans are difficult to characterise overall. They are in general small, free-living crustaceans ranging from about 0.2–5.0 millimetres in length (with the exception of Leptodora kindtii, which is a giant at one centimetre long). Most are somewhat compact in appearance (except for L. kindtii and some Cercopagidae, an onychopod family not represented in New Zealand). They have a bivalved carapace (sometimes modified) with one compound eye, small tubular unsegmented antennules (Ilyocryptus excepted), large branching antennae, and a distinctive pair of so-called ‘postabdominal setae’ (similar setae are seen in other branchiopods). They swim using their antennae. The Ctenopoda and Anomopoda are somewhat alike and both have a bivalved carapace that covers the body (but not the head), a pair of curved caudal claws, and five to six (Anomopoda) or always six (Ctenopoda) flattened leaf-like trunk limbs that are used to filter food particles from the water. In the Ctenopoda the six trunk limbs show serial similarity (as in the ‘large’ branchiopods), while the trunk limbs of the Anomopoda have undergone remarkable evolutionary modifications in relation to food selection, with each limb in many cases being different from its neighbour limb (Fryer 1963, 1968, 1974, 1991). The remaining two groups, the Haplopoda and Onychopoda, are also somewhat alike, having, in contrast to all other branchiopods, narrow-footed segmented trunk limbs – four pairs in the Onychopoda and six pairs in the Haplopoda, used for predation or at least for selective feeding. Olesen et al. (2001) have shown how the segmented trunk limbs of the Haplopoda (Leptodora kindtii) have been derived secondarily from the typical phyllopodous limbs of other branchiopods. Both the Haplopoda and the Onychopoda have a relatively small carapace that does not cover the trunk limbs.

In New Zealand, as elsewhere, freshwater cladocerans (water fleas) can often be found in great abundance in open water or at the weedy edges and bottom deposits of lakes, ponds, and stream backwaters (Chapman & Lewis 1976). A child with a scoop-net can easily capture a good supply for a home aquarium. A few species are known from brackish and nearshore ocean environments (Rivier 1998). Among the freshwater species, some are strictly planktonic, others are bottom–dwelling, and Scapholeberis (Daphniidae) lives against the surface film. Simocephalus (Daphniidae) has the distinctive habit of interrupting its swimming and hanging down from algal filaments by a hooked bristle on one of the swimming antennae (e.g. Fryer 1991). Daphniids are specialist filter-feeders, while chydorids and many macrothricids feed by scraping particles off substrata.
using their trunk limbs. Genera in the infraorders Onychopoda and Haplopoda are predaceous or at least raptorial feeders (Rivier 1998).

Cladocerans are able to produce non-fertilised (parthenogenetic) eggs that develop in a brood-pouch under the carapace and hatch as miniature adults. Females may continue to moult and grow after reaching sexual maturity, unlike copepods and ostracods. Cladocerans reproduce sexually as well as asexually and produce resting eggs after males have appeared in the population; these eggs undergo a period of dormancy before development begins. In the case of the Anomopoda, resting eggs are protected by a part of the mother’s carapace, which is shed together with the eggs as an ephippium. The appearance of males is probably triggered by environmental conditions.

Summary of New Zealand crustacean diversity by environment

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Terrestrial species</th>
<th>Fully freshwater species</th>
<th>Marine/estuarine species</th>
</tr>
</thead>
<tbody>
<tr>
<td>Branchiopoda</td>
<td>0</td>
<td>41</td>
<td>8</td>
</tr>
<tr>
<td>Anostraca</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Notostraca</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Diplostraca</td>
<td>0</td>
<td>40</td>
<td>7</td>
</tr>
<tr>
<td>Cephalocarida</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Maxillopoda</td>
<td>2</td>
<td>68</td>
<td>730</td>
</tr>
<tr>
<td>Ascothoracida</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Acrothoracica</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Rhizocephala</td>
<td>0</td>
<td>0</td>
<td>11</td>
</tr>
<tr>
<td>Thoracica</td>
<td>0</td>
<td>0</td>
<td>83</td>
</tr>
<tr>
<td>Tantulocarida</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Branchiura</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Pentastomida</td>
<td>1*</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Copepoda</td>
<td>1</td>
<td>67</td>
<td>629</td>
</tr>
<tr>
<td>Calanoida</td>
<td>0</td>
<td>11</td>
<td>250</td>
</tr>
<tr>
<td>Cyclopoida</td>
<td>0</td>
<td>21</td>
<td>83</td>
</tr>
<tr>
<td>Mormonilloida</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Harpacticoida</td>
<td>1**</td>
<td>35</td>
<td>193</td>
</tr>
<tr>
<td>Siphonostomatoida</td>
<td>0</td>
<td>0</td>
<td>101</td>
</tr>
<tr>
<td>Monstrilloida</td>
<td>0</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td>Ostracoda</td>
<td>1</td>
<td>37</td>
<td>404</td>
</tr>
<tr>
<td>Palaecopida</td>
<td>0</td>
<td>0</td>
<td>3</td>
</tr>
<tr>
<td>Podocopida</td>
<td>1**</td>
<td>37</td>
<td>319</td>
</tr>
<tr>
<td>Myodocopida</td>
<td>0</td>
<td>0</td>
<td>82</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>120</td>
<td>90</td>
<td>1,470</td>
</tr>
<tr>
<td>Leptostraca</td>
<td>0</td>
<td>0</td>
<td>5</td>
</tr>
<tr>
<td>Stomatopoda</td>
<td>0</td>
<td>0</td>
<td>8</td>
</tr>
<tr>
<td>Anaspidaceae</td>
<td>0</td>
<td>6</td>
<td>0</td>
</tr>
<tr>
<td>Bathynellacea</td>
<td>0</td>
<td>8</td>
<td>0</td>
</tr>
<tr>
<td>Lophogastrida</td>
<td>0</td>
<td>0</td>
<td>6</td>
</tr>
<tr>
<td>Mysida</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>Amphipoda</td>
<td>47***</td>
<td>54</td>
<td>402</td>
</tr>
<tr>
<td>Isopoda</td>
<td>72</td>
<td>17</td>
<td>336</td>
</tr>
<tr>
<td>Tanaidacea</td>
<td>0</td>
<td>1</td>
<td>116</td>
</tr>
<tr>
<td>Cumacea</td>
<td>0</td>
<td>0</td>
<td>75</td>
</tr>
<tr>
<td>Euphausiacea</td>
<td>0</td>
<td>0</td>
<td>19</td>
</tr>
<tr>
<td>Decapoda</td>
<td>1</td>
<td>4</td>
<td>487</td>
</tr>
</tbody>
</table>

Totals: 123 236 2,614

* internal parasite of mammal
** damp forest litter
*** including 11 supralittoral species

- Water flea
  *Ilyocryptus sordidus* (Cladocera).
  From Chapman & Lewis 1976
Summary of New Zealand fossil crustacean diversity

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Described fossil species + subspecies</th>
<th>Known undescribed/undetermined species</th>
<th>Endemic species</th>
<th>Endemic genera</th>
</tr>
</thead>
<tbody>
<tr>
<td>Maxillopoda</td>
<td>61</td>
<td>19</td>
<td>60</td>
<td>2</td>
</tr>
<tr>
<td>Acrothoracica</td>
<td>0</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Rhizocephala</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Thoracica</td>
<td>61+3</td>
<td>14</td>
<td>59</td>
<td>2**</td>
</tr>
<tr>
<td>Ostracoda*</td>
<td>284</td>
<td>127</td>
<td>22</td>
<td>5</td>
</tr>
<tr>
<td>Archaeocopida</td>
<td>0</td>
<td>2</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Palaeocopida</td>
<td>1</td>
<td>0</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>Podocopida</td>
<td>283</td>
<td>124</td>
<td>21</td>
<td>5</td>
</tr>
<tr>
<td>Myodocopida</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Malacostraca</td>
<td>67</td>
<td>44</td>
<td>61</td>
<td>8</td>
</tr>
<tr>
<td>Phyllocarida</td>
<td>7+1</td>
<td>1</td>
<td>7</td>
<td>0</td>
</tr>
<tr>
<td>Eumalacostraca</td>
<td>60</td>
<td>43</td>
<td>54</td>
<td>8</td>
</tr>
<tr>
<td>Isopoda</td>
<td>4</td>
<td>0</td>
<td>4</td>
<td>1</td>
</tr>
<tr>
<td>Decapoda</td>
<td>56</td>
<td>43</td>
<td>50</td>
<td>7</td>
</tr>
<tr>
<td>Totals</td>
<td>412</td>
<td>190</td>
<td>143</td>
<td>15</td>
</tr>
</tbody>
</table>

* Several species range to the present day; these are also in the Recent checklist.  
** undescribed new genera

The end-chapter list of New Zealand Cladocera is based on the work of Chapman and Lewis (1976) for freshwater species and the records of Krämer (1895) and Jillett (1971) for marine species. The marine forms particularly need revising, as most of Krämer’s species are not well known. The zoogeography of freshwater zooplankton in Australasia (Bayly 1995 and references therein) suggests that the New Zealand cladoceran fauna reflects the fact that New Zealand split from Antarctica during the Late Cretaceous. New Zealand, Australia, and South America completely lack the predaceous-raptorial families Polyphemidae and Cercopagididae (Onychopoda), the Leptodoridae (Haplopoda), and the Holopediidae (Ctenopoda). It seems likely that these families evolved in Laurasia after splitting from Pangaea (Bayly 1995). On the other hand, the Anomopoda, well-represented in New Zealand, are a very ancient group (from at least 130 million years ago) that was probably distributed over Pangaea.

Class Cephalocarida

The Cephalocarida was introduced as a new crustacean subclass by Sanders (1955) for a tiny, primitive-looking species taken off the Atlantic coast of North America. Since then, very few additional species have been discovered, and the most recent treatments recognise only one family with five genera and 10 species worldwide (Hessler & Wakabara 2000; Martin & Davis 2001). All are very small, measuring only 2–4 millimetres in length. The swimming limbs barely differ from one another, with the endemic New Zealand genus *Chiltoniella* being the least modified. The class is generally regarded as one of the more primitive of the living Crustacea.

Most species have been recorded from silty seafloors. In general, their biology is poorly known. New Zealand’s sole species, endemic *Chiltoniella elongata*, is known from the Hawke’s Bay region (Knox & Fenwick 1977).
Class Maxillopoda

Barnacles, seed shrimps, oar-footed bugs (copepods), and related parasitic groups – these are all examples of maxillopod crustaceans. They are a disparate lot, and carcinologists (crustacean specialists) are still arguing over whether or not they are a single evolutionary lineage (monophyletic). Apart from some barnacles, most species are small or minute. Most feed by means of mouthparts called maxillae (instead of using trunk limbs as filtration devices), barnacles again being a notable exception. Other characteristics of maxillopods include a basic body plan of five head and 10 trunk segments followed by a terminal telson. Abdominal segments usually lack appendages; elsewhere on the body, appendages are usually branched (biramous). As a group, maxillopod crustaceans are very important – economically, as in the case of many marine-fouling barnacle species, and more especially ecologically because of their sheer abundance. Copepods, for example, are the most numerous crustaceans in open-ocean waters.

Subclass Thecostraca

This subclass comprises representatives of two infraclasses in New Zealand – the Ascothoracica and Cirripedia (‘curly footed’). The latter includes barnacles, sessile crustaceans that use their trunk limbs to catch food particles. Most New Zealanders will be familiar with the acorn barnacles that carpet the upper zones of rocky seashores or, annoyingly, boat hulls, and perhaps the stalked goose barnacles that attach to floats and other buoyant objects, but few will know of the tiny burrowing and parasitic thecostracans.

Minute borings in mollusc shells, attributed to barnacles, have been well documented since Darwin (1854a) collected and described specimens during his voyage on HMS Beagle. Originally a number of parasitic organisms were included within this group of ‘burrowing barnacles’, e.g. the Ascothoracica and Rhizocephala (Newman et al. 1969), but these latter two taxa have been subsequently shown to possess spermatozoa, nauplius larvae, and newly settled cypris stages that are very different from barnacles. Following the re-evaluation of the Cirripedia by Newman (1987, 1996), the Ascothoracica and Rhizocephala are no longer considered as barnacles by some specialists; on the other hand, Martin and Davis (2001), Buckeridge and Newman (2006), and Lützen et al. (2009) treat the Rhizocephala as a superorder of Cirripedia. Ascothoracicans are represented in New Zealand by two species of starfish parasites (Palmer 1997); living rhizocephalans, virtually unknown in New Zealand until very recently, comprise 11 species (Brockerhoff et al. 2006; Lörz et al. 2008; Lützen et al. 2009).

The burrowing acrothoracicans possess a soft carapace, with calcareous plates reduced or absent. There are about 40 known species worldwide, including one endemic New Zealand species. All live buried in calcareous shells of a wide range of marine invertebrates, including molluscs, echinoderms, corals, bryozoans, and other barnacles. The group has a fossil record extending back to the Devonian (Tomlinson 1987), although no pre-Mesozoic taxa are known from New Zealand. As the fossil record of acrothoracicans is based solely upon burrows, two distinct acrothoracican nomenclatures have developed, one ichnomorphic, the other biological. This may lead to some confusion, as trace-fossil names such as Zapfella have equivalents such as Australophialus. Both systems are used in this review of the New Zealand fauna because the relationship between fossils and living species is unclear.

The familiar thoracican barnacles are classified into four orders with 81 living species in New Zealand – the stalked (pedunculate) Ibliformes, Lepadiformes, and Scalpelliformes, and the generally squat, nonstalked Sessilia, comprising the acorn (balanomorph) barnacles, wart (verrucomorph) barnacles, and the
Brachylepadomorpha (confined to deep-ocean hydrothermal vents and not yet known from New Zealand).

Most barnacles are hermaphrodites, although in some species the ‘typical’ hermaphroditic form may also carry minute or dwarf males within the capitulum (see below). These dwarf males possess either reduced or no appendages and capitular plates, being essentially packages of male gonads. Sexual differentiation does occur in some species, e.g. endemic *Idioibla idiotica*, (Ibliformes).

The pedunculate forms are the most ancient of the barnacles. They are characterised by a stalk (peduncle), by which they attach themselves to the substratum. A series of calcareous plates, together forming a capitulum, are found on top of the peduncle of most species, enclosing most of the soft tissue of the animal. A careful examination of this area verifies the evolutionary placement of the barnacles within the crustaceans, as the animal is effectively arranged head down, with its jointed limbs (cirri) extending out through a slit (orifice) in the capitulum wall. When the barnacle is submerged, the cirri extend into the surrounding water, netting planktonic food.

As the number and arrangement of capitular plates varies considerably between taxa, they are of considerable value in classification. In the goose barnacle *Lepas* (Lepadiformes) there are five plates: paired terga and scuta with a single carina, arranged in a single whorl. However, in species like *Calanctica spinosa* (Scalpelliformes) the number of capitular plates varies from 11 to more than 50, and these are arranged in two or more whorls. In taxa like *Calanctica* and *Angulocalpellum*, the peduncle is armoured with small overlapping plates or scales. In contrast, there are no plates or overlapping scales on the peduncle in *Lepadiformes*. The most primitive order of living thoracicans is the Ibliformes, with predominantly chitinous rather than calcareous plates. Of the five living genera, three of them are found in New Zealand, including the endemic genus *Chitinolepas* from Spirits Bay (Buckeridge & Newman 2006).

The Verrucomorpha are a group of barnacles that, because of their asymmetry, have intrigued cirripede workers since Darwin (1854b). Although they are amongst the most primitive Sessilia that are likely to be encountered as fossils, they are as yet unconfirmed from the New Zealand Mesozoic. They are, however, known from the Cretaceous of Australia (Buckeridge 1983). The Verrucidae are represented in New Zealand waters by species of *Altiverruca* and *Metaverruca*, both of which possess six calcareous plates. The lid (operculum) comprises just two articulating plates, the shell wall being made up of the remaining four: a fixed tergum and fixed scutum, plus rostrum and carina. Unlike other Sessilia, each plate in verrucids joins with its adjacent plate by interlocking ribs. The distribution of verrucid genera tends to conform to depth, with *Verruca* species characteristic of shallow coastal waters, *Metaverruca* to midshelf environments, and *Altiverruca* to the continental slope and deeper. Some verrucid species also have symbiotic or commensal relationships with other invertebrates, and these may be host-specific, e.g. *Brochiverruca* on cnidarians and *Rostratoverruca* on cidaroid urchins (Buckeridge 1997). This appears to be the situation with an as-yet-undescribed verrucid from northern New Zealand waters that inhabits the coral *Ellanopsammia rostrata*.

When one considers balanomorph or acorn barnacles, the image many people have is of a limpet-like creature commonly attached to vessel hulls. Although barnacle fouling on ships is well known, it represents only a small proportion of their distribution. They are best seen as ubiquitous opportunists of the marine environment attached to a great variety of living and inanimate objects. Barnacles include species specialised for attachment to whales, sea snakes, turtles, corals, sponges, and other crustaceans.

Many shallow-water acorn barnacles are known to have variable tolerances to both high temperatures and desiccation. Because of this, species in the intertidal zone may be found distributed in distinctive bands, e.g. on exposed
rocks, where *Chamaesipho brunnea* forms bands in the uppermost intertidal and *Eopella plicata* at mid- to low tide.

The balanomorph shell is made up of two parts: a rigid calcareous wall comprising four or more parietal plates, and an operculum or lid generally made up of paired scuta and terga. The opercular plates articulate to permit extension of the cirri between them during feeding. They also enable the animal to seal itself off from the environment in times of stress (e.g. predation, desiccation). As with the stalked barnacles, the plates are very important in identifying species. Parietal plates may be solidly calcified (e.g. *Austrominius*), calcareous with internal chitinous laminae (e.g. *Eopella*), calcareous with one row of vertical tubes (e.g. *Balanus*), or calcareous with chitin, arranged in multiple rows of tubes as in *Tetraclitella* (Buckeridge 2008). The number of parietal plates is also significant, with four in *Austrominius*, *Eopella*, and *Tetraclitella* and six in *Austromegabalanus*, *Balanus*, *Chamaesipho*, *Coronula*, *Megabalanus*, and *Notobalanus*.

The elements of barnacle anatomy and morphology, forming the basis of our modern classification and understanding, were elucidated by none other than Charles Darwin. His outstanding work on these creatures had a very strong influence on the ideas that eventually led to his revolutionary book *On the Origin of Species*. Indeed, Darwin was so amazed by the profusion and ubiquity of barnacles in the Cenozoic that he described Tertiary seas as ‘abounding with species of *Balanus* to an extent now quite unparalleled in any quarter of the world’. (In Darwin’s time, although most sessile cirripedes were ascribed to the genus *Balanus*, he was able to demonstrate groupings of similar taxa through the use of ‘varieties’.)

That Darwin was infatuated with barnacles is clear, and he put much else aside to work on them: ‘I have for the present given up Geology, and am hard at work at pure Zoology and am dissecting various genera of Cirripedia, and am extremely interested in the subject.’ [Letter to Dieffenbach, February 1847]. But it was not always an agreeable infatuation: ‘I have now for a long time been at work on the fossil cirripedes, which take up more time than the recent: confound and exterminate the whole tribe; I can see no end to my work.’ [Letter to Hooker, 1850]. Darwin did persist, both with his monographs on fossil and living cirripedes (Darwin 1851a,b, 1854a,b) and his *Origin of Species*. Darwin’s second cirripede volume was dated 1851 but came out quite late in 1852. His works endure as a monument to scholarship, and remarkably, one and a half centuries later, still provide the intellectual platform from which we are able to develop our present-day understanding of Earth’s biodiversity.

**Infraclasse Ascothoracica**

These curious creatures are primitive among the coxostreps, ectoparasitic on feather stars and sea urchins, and endoparasitic within some corals and sea stars. Females have a much-reduced thorax and abdomen and a simplification or loss of limbs. The carapace is enlarged and grossly distorted, being much-branched and unrecognisable as belonging to a crustacean. Males are tiny and more recognisably crustacean in form, resembling larvae. They have a well-segmented body enclosed in a carapace and greatly elongated testes and are found within the mantle cavity of females.

Ascothoracicans were unknown in New Zealand until Palmer (1997) found two species inhabiting sea stars off the Otago coast. *Dendrogaster otagensis* was described as a new species, infesting *Asterodon miliaris*. Of a collection of 159 sea stars taken from the coast over an 11-month period, 124 (78%) were infested with the parasite. Found inside the arms and disc of the sea star, there can be as many as 15 female parasites, with their convoluted carapaces over 20 millimetres across, causing some atrophy of the sea-star’s digestive caecae and gonads. Up to 19 creamy-white males 2.9–3.5 millimetres long occur inside the female parasite.

A second species, *Dendrogaster argentinensis*, was also found off Otago, infesting 96% of 152 specimens of the sea star *Allostichaster insignis* quite severely.
This particular parasite, previously known from southern South America and the Falkland Islands, can fill much of the sea-star’s body cavity, comprising up to 28% of the wet weight. Gonads in such specimens are absent, and digestive caeca are severely atrophied. Curiously, specimens of *A. insignis* in other parts of its range (Cook Strait to the Auckland Islands) have never been noted as having such parasites, so it would be interesting to know what conditions promote such infestations in Otago waters.

Dendrogaster belongs to one of three families in the ascothoracian order Dendrogastrida. Palmer (1997) also mentioned an unpublished Te Papa (Museum of New Zealand) record of an undescribed member of the Synagogidae, one of three families in the only other ascothoracian order, Laurida.

**Infraclass Cirripedia: Barnacles**

**Superorder Acrothoracica**

Apart from the study by Batham and Tomlinson (1965) on *Australophialus melampygos*, there has been little work done on New Zealand acrothoracicans. They are a very difficult group to work with, particularly as most occurrences are known only by their tiny borings. *Australophialus melampygos* is often found infesting paua (*Haliotis iris*) and mussel (*Perna canaliculus*) shells, commonly in very large numbers (up to 3350 borings noted in a single paua shell. The family Cryptophilidae was revised by Tomlinson (1969), who introduced *Australophialus* to incorporate the austral members (including *A. melampygos*) of *Cryptophialus* that possessed four rather than three pairs of terminal cirri (feeding appendages).

Existing literature infers that acrothoracicans have very low diversity in the New Zealand region. Further, they appear to be somewhat host-specific, and whilst this is not generally a problem where a host is a common marine invertebrate, there is cause for concern if the host is over-fished. Both *Haliotis iris* (paua) and *Perna canaliculus* (green-lipped mussel) are extensively harvested as a food source, and although they are now widely cultured in marine farms, the new aquacultural environment does not appear to provide the habitat so favoured by *Australophialus melampygos* in nature. The likelihood that the shell-infesting population represents more than one species should not be overlooked, especially in light of acrothoracicans’ poorly mobile larval phase (which may account for its absence from the Chatham Islands). The distribution of these molluscs extends from Northland to Stewart Island; although both species range well into the subtidal, *A. melampygos* is not known much below low tide, its preferred habitat.

*Australophialus melampygos* falls within a group of southern acrothoracicans including *A. tomlinsoni* from the Antarctic and *A. turbonis* from South Africa. Newman and Ross (1971) considered the cirral arrangement of these taxa to be more generalised (and therefore phylogenetically older) than other Cryptophilidae, inferring a Southern Hemisphere origin for the family. However, rather than a South African centre of cryptophilid diversification, abundant cryptophilids in some turritellid gastropods within the Pakaurangi Formation (Early Miocene), Kaipara Harbour, should not rule out the New Zealand region as a potential centre of dispersal.

**Superorder Rhizocephala**

Rhizocephalans are wholly parasitic. They have little similarity with other cirripedes, or indeed other crustacean adults, as there are neither appendages nor segmentation (e.g. Høeg & Lützen 1995, 1996). A rhizocephalan consists of a sac-shaped body, the externa, which is mainly involved in reproduction and is attached to the outside of the host’s abdomen. The host is always another crustacean, in most instances an anamuran or brachyuran crab. A mouth and a digestive tract are absent and nutrients are taken up from the host’s interior by an internal trophic root system (or interna) which is distributed
within the haemolymph of the host (Høeg & Lützen 1995). The externae are most often attached singly or a few together to the host’s abdomen, but some rhizocephalans are colonial and in such species many small externae may attach to the abdomen, appendages, or other parts of the host body (Høeg & Lützen 1993, 1996). Despite their bizarre appearance, rhizocephalans are related to the non-parasitic barnacles, which they resemble in reproducing via short-lived planktonic nauplii and/or cypris larvae (Høeg & Lützen 1993).

Apart from sparse records in the literature, rhizocephalans were almost unknown in New Zealand until the 2000s; there are now at least 10 genera and 11 species (Brockerhoff et al. 2006; Lötz et al. 2008; Lützen et al. 2009). Decapod host species belong to the families Paguridae, Lithodidae, Galatheidae, Chiromactidae, and Callianassidae. Parthenopea vulcanophila (Lützen et al. 2009), is the first rhizocephalan recorded from the vicinity of active cold seeps.

The recently discovered New Zealand rhizocephalans are registered in the invertebrate collections of the National Institute of Water and Atmospheric Research (NIWA) and the National Museum of New Zealand Te Papa Tongarewa, Wellington (NMNZ). Some of the specimens could not be identified because they were in turn infected by species of Cryptoniscinae, a subfamily of hyperparasitic isopods. In the final stage of this relationship of a parasite on a parasite the rhizocephalan host is no longer recognisable (Øksnebjerg 2000).

Recent gene-sequencing studies on the Rhizocephala have indicated that the conventional grouping of its members is in need of rearrangement (Glenner et al. 2003; Glenner & Hebsgaard 2006). Since these findings have not yet resulted in a taxonomic revision, the traditional division of the Rhizocephala into the orders Kentrogonida and Akentrogonida is followed in the end-chapter checklist; as a consequence of the study by Glenner and Hebsgaard (2006), however, Parthenopea is included in the Akentrogonida.

Superorder Thoracica

On 3 October 1769, in calm seas some 300 kilometres off what is now known as Mahia Peninsula, HM Bark Endeavour, under the command of James Cook, retrieved ‘one peice of wood coverd with Striated Barnacles Lepas Anserina?’ (Banks 1962). This was not only the first record of barnacles from New Zealand seas, but also one of the first records of marine life from the region. In an editorial footnote to Banks’s journal, J. C. Beaglehole stated that Daniel Solander (the naturalist who accompanied Banks) considered the species to be Lepas anserifera. The next major scientific expedition to New Zealand was in 1827, when the Astrolabe collected extensive natural history material, including barnacles. The barnacles were subsequently described by Quoy and Gaimard (1834) as Anatifera spinosa, Anatifera elongata, and Anatifera tubulosa (now respectively known as Calantica spinosa (Quoy & Gaimard), Lepas testudinata Aurivillius, and Heteralepas quadrata (Aurivillius)). The first endemic New Zealand barnacle to be described was, therefore, C. spinosa.

In 1839 the New Zealand Company appointed Ernst Dieffenbach as surgeon and naturalist on the Tory. Dieffenbach made extensive biological collections during his time in New Zealand, and included in these were barnacles. These were later compiled by J. E. Gray into a Fauna of New Zealand and listed as an appendix to Dieffenbach’s Travels in New Zealand (Gray 1843). Gray recorded nine thoracicans, now known as C. spinosa, L. testudinata, H. quadrata, Coronula diadema, Epophella plicata, Tetractitella depressa, Tubinicella major, and two unidentified species of Balanus.

Shortly after this, Darwin’s four comprehensive monographs on living and fossil cirripedes were published. Darwin had collected New Zealand barnacles from the Bay of Islands during the voyage of HMS Beagle, which, along with British institutional material, resulted in 14 species being listed from the New Zealand region. Ten were new to science, of which Austrominius modestus,
Notobalanus vestitus, and Notomegabalanus decorus are endemic to New Zealand. Darwin included a complete description of the endemic species Chamaesipho columna, which had previously been described from material supposedly collected from Tahiti (Spengler 1790). Spengler’s original description was, however, incomplete, as the shells he possessed were without opercula or soft tissue. In Foster and Anderson (1986), the status of C. columna was reviewed and it was concluded that Spengler’s material came from New Zealand, where it is endemic. (They renamed the Australian species previously attributed to C. columna as Chamaesipho tasmanica.)

The last major systematic work of the 19th century that dealt with New Zealand barnacles was based upon specimens obtained during the 1873–76 HMS Challenger expedition. In an expedition report, Hoek (1883) described five new species, now known as Amigdoscalpellum costellatum, Anguloscalpellum pedunculatum, Gymnoscalpellum intermedium, Smilium acutum, and Verum novaerzelandiae. During the early to mid-20th century, numerous descriptions of new records for the region, generally for single species, were published and a full list of these was given by Foster (1979). The latter work is the most comprehensive study ever written on living New Zealand Thoracica. In it, Foster listed a fauna of 61 species, nine (including a new subspecies) of which were new, one was a new name, and 15 species were recorded for the first time from New Zealand waters. Foster also made valuable observations on the geographic distribution, zonation, and ecology of barnacle species. In the 14 years following his 1979 monograph, Foster described a further two new species and add records of eight taxa not previously known from New Zealand waters (Foster & Willan 1979; Foster 1980, 1981; Foster & Anderson 1986). Brian Foster died suddenly in 1992, tragically cutting short what was, up to that time, a prolific and invaluable career in barnacle systematics and biology. Since then, J. S. Buckeridge, a student of Foster, has continued study of the New Zealand fauna, frequently in collaboration with W. Newman. The systematics of barnacles was reviewed by Buckeridge and Newman (2006), in which the Iblidae was identified as the most ancient family of Thoracica. Significantly, it was the discovery of an extraordinary but minute new species from New Zealand, Chitinolepas spiritsensis, that provided the impetus for this work, which demonstrated that the New Zealand region not only has a diverse living thoracican fauna but also one of the most primitive.

Although not specifically focussing on the New Zealand fauna, Newman’s (1979) publication is an inspired revision of the phylogenetic and biogeographic relationships between barnacles of the Southern Ocean. His work led to a reappraisal of the entire fauna, with many of the proposed taxonomic concepts incorporated in Buckeridge (1983). The evolving nature of systematic biology results from an ongoing reappraisal of relationships between taxa. As our understanding of barnacle phylogeny becomes more sophisticated, this often creates the need to provide new names for species. The overview herein is based upon the comprehensive review of Cirripedia by Newman (1996), in which subgenera are elevated to full generic status. Consequently, species like Elminius modestus and Austromegabalanus decorus are now listed as Austrominius modestus and Notomegabalanus decorus respectively. A recent publication reviews the status of the Elmininia and identifies Austrominius as a tetractiloid, returning it closer to Eoppella, where Darwin (1854) had originally perceived it to be (Buckeridge & Newman 2010).

There are 81 species of Recent thoracican cirripedes known from the New Zealand EEZ. Of these, six are currently undescribed. Four are stalked barnacles, comprising two species of Scillaelepas (Calanticidae) one of which conforms to a southern group of primitive scalpellids, and two species of Scalpellidae; an unusual undescribed verrucid is likely to represent a new genus; and a possible new species of Acasta (Archaeobalanidae) remains to be determined (J. Buckeridge is currently reviewing this genus of sponge-inhabiting barnacles). All
species referred to as new in the end-chapter checklist are held in the collections of the NIWA Invertebrate Collection, Wellington.

The vertical zonation of thoracican barnacles on New Zealand surf shores has been well documented (e.g. Morton & Miller 1968). The zonation is not always consistent, however, with ranges expanding/contracting in the absence/presence of other taxa (Foster 1979). Nevertheless, there are generalisations that can be made, and these provide useful ecological benchmarks: chthamalids are found higher on the shore than all other thoracicans; below them, and overlapping somewhat, are the tetractilids; further down the shore the lower range of the tetractilids overlaps the balanids. This chthamalid-tetractilid-balanid arrangement appears to be fairly uniform on both temperate and tropical shores (Foster 1974, 1979). *Cantellius septimus*, a widespread Indo-Pacific species, has been found in *Montipora* coral off Raoul Island (Kermadec Ridge), representing the most southerly record of a coral-inhabiting barnacle (Achituv 2004).

Some species are epizoic on cetaceans. *Conchoderma auritum*, *C. virgatum*, and *Coronula* species attach to whales and three species of the latter genus are found in the New Zealand fossil record.

The isolation of New Zealand since the late Mesozoic has led to high regional endemism in taxa that evolved during the Late Cretaceous–Early Cenozoic. This is no more evident than in the thoracican barnacles (Buckeridge 1996a,b, 1999a). Although 40% of the Recent species listed are endemic, the figure is a little misleading, as the current distribution of New Zealand species such as *Austrominius modestus* to include Australia and Europe has almost certainly been achieved via shipping. What is particularly significant about the New Zealand region is the high proportion of endemics that are phylogenetically primitive. The percentage of balanomorph and verrucid taxa that have their earliest (fossil) records in New Zealand is impressive, with 73% of all primitive sessilians with a generic age earlier than the Miocene being first recorded here (Buckeridge 1996a).

There are several species of thoracian barnacles that may be termed ‘living fossils’, i.e. they have fossil records extending back at least to the Early Miocene. Two of these, *Chionelasmus darwini* and *Notobalanus vestitus* extend back to the Eocene and Oligocene, respectively; two others, *Metaverruca recta* and *Chamaesipho brunnea*, to the earliest Miocene. The order Ibliformes extends back to the Permian and the Neolepadinae to the Jurassic.

Sampling of deep-sea cirripedes from the New Zealand EEZ is far from comprehensive, but 13 species are known from depths greater than 1500 m, the deepest of which are *Gymnoscalpellum intermedium* (to 2505 m) *Amygdoscalpellum costellatum* (to 3120 m), and *Verum raccidium* (to 4405 m) according to NIWA database records. Specimens have often been made available as bycatch from the fishing industry or from research cruises. Recent discoveries include the neolepadine *Vulcanolepas osheai* from ca. 1500 metres depth in the volcanically active Brothers Caldera (in the Havre Trough northeast of the Bay of Plenty) and a related taxon, *Ashinkailepas kermadecensis* (Buckeridge 2009), from a cold-water seep at 1165 m on the western flank of the Kermadec Ridge. Both of these taxa have specialisations, like long filamentous cirri, that permit them to feed on bacteria, the most abundant food source in the area, living on the barnacle exteriors and around the vents and seeps (Suzuki et al. 2009). Bathylasmatids such as *Tetrachaelasma tasmanicum*, although not yet formally recorded from within the New Zealand EEZ, almost certainly occur here. This taxon was recently described from 3600 metres on the southeastern Tasman Rise (Buckeridge 1999b) where it is widely distributed as disassociated shells that are very similar to isolated plates collected from New Zealand waters; in the absence of living tissue the latter material has not been placed to species.

Although the total number of thoracican barnacle species from New Zealand is not high compared with the numbers of species of taxa such as the Bryozoa and Mollusca, it is high compared with cirripede faunas from other regions. In particular there is a broader representation of known cirripede taxa (especially
phylogenetically primitive taxa) than in any region of comparable size, and there is a disproportionately large number of species, both living and fossil, that have their earliest records in New Zealand (Buckeridge 1996a).

**Palaeontology and paleoecology**

**Acrothoracica**

Acrothoracian burrows are known to occur in thick-shelled bivalves (e.g. trigoniids) of Late Triassic age from Nelson and Southland (H. J. Campbell pers. comm.) and belemnite guards (e.g. Belemnopsis alfurica) of Late Jurassic age from Kawhia. These can be attributed to the ichnogenus Zapfella, to which the burrow shapes generally conform; however, their true biological relationships remain unclear and, as such, no move is made to classify them at ordinal level or below. The Triassic record extends the range of Zapfella from that provided in Häntzschel (1975) of ‘Jurassic to Tertiary’. Burrows are also known in Early Miocene deposits from the Auckland region, e.g. Waiheke Island (J. A. Grant-Mackie pers. comm.), and in turritellid gastropods from the Pakaurangi Formation, Kaipara Harbour. The later burrows appear indistinguishable from modern Australophialus borings, to which genus they are tentatively assigned.

**Rhizocephala**

Perhaps surprisingly, given their parasitic lifestyle, rhizocephalans are detectable in the fossil record and are known from the New Zealand Miocene. Feldmann (1998) studied a large number of beautifully preserved specimens of the large xanthoid crab *Tumidocarcinus giganteus*. Several males had abnormally broad abdomens, which is normally attributable to the parasitic castration induced by the parasite.

**Thoracica**

Thoracican barnacles have a fossil record extending back to the Paleozoic, but not in New Zealand. The pedunculate order Cyprilepadiformes is known from the Silurian, attached to a eurypterid, and other thoracicans are known from the Early Devonian and the Pennsylvanian (upper Carboniferous) (Newman et al. 1969; Buckeridge 1983; Foster & Buckeridge 1987; Newman 1996; Buckeridge & Newman 2006). There is no record of Paleozoic cirripedes from the entire New Zealand–Australian–Antarctic region, the first such record being *Eolepas? novaezelandiae* from Middle Triassic strata of Southland (Buckeridge 1983). Although there are rare scalpellomorphs of Jurassic age, it is not until the Cretaceous that significant records are known – locally abundant, as-yet-undescribed remains of *Cretiscalpellum?* are known from Middle Cretaceous rocks in the Coverham area. These scalpellomorphs are preserved in association with species of the large bivalve *Inoceramus*, upon which they appear to have been growing. Hence, apart from a new verrucid from the Cretaceous of the Waipara River in central Canterbury, the only barnacles known from the New Zealand Mesozoic are stalked ones. Surprisingly, even though there are barnacle-rich horizons in the Paleocene of the Chatham Islands, there are no barnacles of Mesozoic age known from there. This is not likely to have resulted from a paucity of appropriate facies, as there are some excellent Late Cretaceous fossiliferous horizons present on Pitt Island that could have been expected to have provided an appropriate environment for scalpellomorphs. At present, it must be concluded that the absence of a Cretaceous barnacle fauna reflects incomplete paleontological knowledge, and this provides an impetus for further fieldwork on the islands.

**Cenozoic barnacles**

The New Zealand Cenozoic barnacle fauna is dominated by balanomorphs. The first fossil cirripede to be described from New Zealand strata was the giant

---

Reconstruction of the fossil barnacle *Anguloscalpellum euglyphum* (Oligocene). John Buckeridge
balanomorph *Bathylasma aucklandicum*, from Early Miocene strata near Auckland. The locally abundant, but generally disarticulated plates of this sessile barnacle were however, initially described as a pedunculate (Hector 1888). A quarter of a century was to pass before the true nature of the remains was established, in a paper wherein the author also described two new endemic species now known as *Anguloscalpellum angulatum* and *Smilium subplanum* (Withers 1913) (see Jones 1992). In the early 1920s, Withers, working from the British Museum, was commissioned by the then Geological Survey of New Zealand to produce a monograph of the fossil cirripedes of New Zealand (Withers 1924). This listed 18 species, of which only 15 were truly fossil, and seven of these were both new and endemic to New Zealand. In 1953, he published his last major work that dealt specifically with cirripedes from New Zealand (Withers 1953). This included a revised list of the New Zealand fossil fauna, arranged according to stratigraphic horizons. He listed 15 species, none of which was new. Interestingly, he omitted the record for ‘Balanus amphitrite’ that he included in his 1924 monograph, but added the record for what is now *Pristinolepas harringtoni*. No reason is given for his omission of ‘Balanus amphitrite’, which is now recognised in the New Zealand fossil record as *Amphibalanus variegatus*. In all, Withers described nine fossil cirripedes from the region, all of which are endemic.

Many limestones are so enriched with balanomorph remains that they may justifiably be termed ‘barnacle coquinas’. The first horizons with locally abundant balanomorphs are of late Paleocene age, occurring as lenses in the Red Bluff Tuff of the Chatham Islands. In some of these lenses, the barnacle *Pachylasma veteranum* is also the dominant macrofossil, with the other macrofauna primarily being teeth of the elasmobranch fish *Isurus* sp. plus brachiopod and bivalve shells. Although barnacle-rich horizons are also recorded in the Early Oligocene (Cobden Limestone, West Coast), and Early Miocene (basal Cape Rodney Formation, Auckland), it is the Pliocene coquina limestones of the North Island East Coast that are singularly spectacular, e.g. the Pukenui and Castlepoint Limestones, which contain extensive horizons dominated by *Fosterella tubulatus* and *Notobalanus vestitus*. These coquinas outcrop at Rangitumau and Castle-point respectively (both in the Wairarapa), and have extensive beds in which *F. tubulatus* comprises more than 50% of the total mass. There are no modern equivalents of these deposits, although lesser shell banks of *N. vestitus* and *Notomegabalanus decorus* are today accumulating in the outer Hauraki Gulf near the Mokohinau Islands. It is inferred by Beu et al. (1980) that these deposits originated in subtidal settings dominated by strong currents, in a Pliocene sea occupying the East Coast Inland Depression. These Pliocene ‘barnacle coquinas’ are not only impressive from a cirripedological perspective, they are also the greatest accumulation of fossil crustaceans known!

Because barnacle species tend to be distributed along clearly delineated depth, salinity, and temperature zones, their presence as fossils can be most useful in paleoecological reconstruction. There are, however, some trends in the ‘preferred’ environments of some taxa over time, e.g. species of the genus *Pachylasma* are currently restricted to deep water, with the shallowest living species of the group not known from less than 55 metres. In the Paleocene, however, *Pachylasma veteranum* is known to have lived in very shallow water, along with a diverse fauna of bryozoans, molluscs, and cnidarians, well within the photic zone (Buckeridge 1983, 1999a). A similar pattern can be observed with species of *Bathylasma*, which also occupied upper subtidal environments in the Paleogene, but are now exclusively mid- to outer-shelf species. Indeed, this change, which was interpreted by Buckeridge (1983) as ‘migratory’, is now viewed more as a result of having been excluded (or outcompeted) from the shallower-water environments by ‘modern’ balanomorphs. Modern taxa such as *Austrominius modestus* have a higher metabolism and an earlier onset of sexual maturity, which has permitted the species to aggressively exploit desirable shallow-water niches. This has left refugial chthamalids (such as *Chamaesipho*...
columna and Chamaesipho brunnea) occupying upper littoral niches, and pachylasmatines (such as Pachylasma scutistriata and Bathylasma alearum) mid-to outer-shelf environments (Buckeridge 1999a).

By the Late Miocene, it appears that thoracican barnacles occupied much the same habitats as their modern counterparts (including as epibionts on other crustaceans – Glassner 1960, 1969). As a consequence, the zonation of modern balanomorphs is useful in the reconstruction of the fossil depositional environments that existed in the Late Cenozoic, e.g. in the barnacle-rich Titio-kura Limestone of the eastern North Island Te Aute Limestone Complex. The Titio-kura Limestone (Beu 1995), outcropping in the northwest of Hawke’s Bay, is characterised by a mixed assemblage of barnacles, including Pachylasma sp., Notomegabalanus miodecorus, and the inferred intertidal taxon Epopella cf. plicata. The depositional environment at that time is, however, considered to have been at more than 100 metres depth. The geological processes operating at the time resulted in the build-up of shallow-water sediments on the upper shelf to a point at which the accumulation became unstable. Sediments and faunas were then mobilised, to be transported and deposited alongside deeper-water elements as a mixed thanatocoenosis (death assemblage).

The sessile Balanomorpha are not known from strata older than the Paleocene, with the first of these, Bathylasma rangatira and Pachylasma veteranum, being recorded from the Chatham Islands (Buckeridge 1983). There has been considerable conjecture concerning the origins of the balanomorphs, which diversified and spread very rapidly in the Early Cenozoic. Buckeridge (1996a, 1999a) proposed that the Chatham Islands was a centre of sessilian diversification during the Paleogene, with taxa evolving in the warm shallow seas that characterised the environmental conditions for strata like the Red Bluff Tuff. New Zealand has a remarkable fossil cirripede fauna, with the phylogenetically early taxa Eolasma, Chionelasmus, Waikalasma, Pachylasma, Bathylasma, Tetractitella, Palaeobalanus, Notobalanus, Chamaesipho, and Notomegabalanus having their earliest records here.

As with the Recent fauna, there are a number of publications describing single new species of New Zealand fossil Thoracica. These are listed in the historical review provided in Buckeridge (1983), which also revised and improved current knowledge of the New Zealand and Australian fossil cirripede faunas. Buckeridge listed 69 fossil taxa from New Zealand, of which 36 were new. Of these, 94% (i.e. all but two) are endemic to New Zealand. Since 1983, Buckeridge has described a further six species of fossil cirripedes (Buckeridge 1984a,b, 1991, 1999a, 2008), and in addition has a further four new taxa awaiting formal description.

Economic aspects of barnacles

Marine fouling

The first ‘close encounter’ some New Zealanders may have with barnacles is when they need to remove fouling organisms from the hulls of their recreational or fishing vessels. Barnacles are opportunistic organisms that colonise almost any available surface in the marine environment. Boats and ships provide excellent surfaces for suspension-feeders – a platform within the upper subtidal zone that generally coincides with oxygenated, predator-poor, plankton-rich waters. In addition, the mobile substratum facilitates dispersal.

Exotic fouling species in the New Zealand environment are generally introduced through commercial shipping. It is in this way that the widespread species Amphibalanus amphitrite, A. variegatus, and Lepas anatifera were introduced many decades ago. Lepas anserifera, Fistulobalanus albicostatus, Amphibalanus reticulatus, Megabalanus rosa, M. volcano, and Tetractitella squamosa japonica were introduced on oil-drilling platforms (Foster & Willan 1979) but none appears to have become naturalised in New Zealand waters. Hosie and Ahyong (2008)
reported the establishment of the Australian species *Austromegabalanus nigrescens* and its South American congener *A. psittacus* at Taharoa and Wellington respectively.

Research into the development of antifouling systems has intensified as a result of a greater understanding of the deleterious ecological impact of traditional antifouling paints such as tributyltin (Buckeridge 1998). Preliminary results indicate that low-level ultrasonic transmitters have the potential to restrict organic accumulation on certain hulls.

**Barnacles as a food source**

Although balanomorph barnacles such as the very large South American *Austromegabalanus psittacus* are considered a delicacy, they do not occupy a similar place in modern New Zealand cuisine. There is evidence, however, that barnacles were once eaten by Maori, as they are often found in middens (Foster 1986). In most cases, it appears that this was not through deliberate harvesting; rather it was incidental to the harvesting of other seafood such as *Perna canaliculus* (green-lipped mussel). This is no doubt a reflection of the small size of most shallow-water New Zealand barnacles – many hundreds of *Austrominius modestus* would need to be collected to make even a small meal. Nevertheless, somewhat larger species such as *Notomegabalanus decorus* and *Epopella plicata* may occasionally have been deliberately collected as a dietary supplement (Foster 1986).

**Environmental monitoring**

Thoracican barnacles have a number of properties that may prove to be invaluable to humans. One that is currently under development is their use as environmental indicators. Common shallow-water fouling species such as *Austrominius modestus* and *Epopella plicata* are invaluable in monitoring environmental changes to marine systems during urbanisation (e.g. at Auckland’s Long Bay–Okura Marine Reserve). A high metabolic rate, rapid onset of maturity, and frequent spawning make *Austrominius modestus* an excellent species for gauging the impact of human activities.

**Biotechnology**

Another feature of thoracican barnacles that has intrigued scientists is the means by which they attach themselves to surfaces. Barnacles are known to grow on a very wide range of materials, both natural and synthetic. Their ability to successfully adhere to flexible and elastic materials like plastic sheeting and fibreglass is of specific interest, for if the nature of this ‘organic adhesive’ is determined and commercially manufactured, it will have obvious use in fields such as dentistry.

Barnacles that are commensal or symbiotic with other marine organisms may need to produce chemicals to prevent the host overgrowing them. This is particularly the case with sponge-inhabiting taxa like *Acasta* and coral-inhabiting taxa like *Brochiverruca*. Isolation of chemical deterrents may be invaluable in the design of new drugs for restricting or reducing cell growth in other species, including humans.

**Subclass Tantulocarida: Tantulocarids**

Nearly 30 years ago, a new maxillopodan subclass was created by Boxshall and Lincoln (1983) to accommodate, amongst others, three tiny parasitic crustaceans discovered in the New Zealand region (Bradford & Hewitt 1980; Boxshall & Lincoln 1983; Lincoln & Boxshall 1983). They infect benthic and hyperbenthic crustaceans such as amphipods. Tantulocarids are minute ectoparasites, not exceeding half a millimetre (0.04–0.40 millimetre) in length, with a unique dual life cycle that is completed, without moulting, on a crustacean host (Huys et al.
There are now five recognised families with more than 20 genera and about 30 species worldwide (Ohtsuka & Boxshall 1998), notably with several taxa being recently documented from Japan (Huys et al. 1992; Huys et al. 1994; Ohtsuka & Boxshall 1998).

While there have been no further records of tantulocarids from New Zealand, it is very likely that more species of this subclass will be discovered as the benthic and benthopelagic fauna of the New Zealand region becomes better studied.

### Subclass Branchiura: Branchiurans

Branchiurans are parasitic on marine and freshwater fishes. They resemble copepods in many respects but differ in some important features. Unlike copepods, they have compound eyes and lateral head lobes, the opening of the genital ducts lies between the fourth pair of thoracic limbs, and they have a proximal extension to some of the exopodites (outer branch) of the thoracic limbs. They are good swimmers and females deposit their eggs on stones and other objects. The larvae differ little from the adult. *Argulus* has a pair of suckers on the maxillae and a poison spine in front of the proboscis. One introduced species has been recorded from goldfish in New Zealand (Hine et al. 2000). It is likely that more species will be discovered.

### Subclass Pentastomida: Tongue worms

Tongue worms are obligatory parasites of reptiles, mammals, and birds, inhabiting their respiratory tracts (nasal passages and lungs). Particularly prevalent in the tropics, there are no native species in New Zealand, but one introduced species has been reported (Tenquist & Charleston 2001). This is *Linguatula serrata*, whose most regular host is the dog. It is rare in New Zealand, but developmental stages have also been reported from the brown hare, European rabbit, house cat, and sheep (Thomson 1922; Gurr 1953; Sweatman 1962).

Globally, there are about 130 species, ranging in length from about 3 to 150 millimetres or more and generally transparent or yellow to red-coloured. Like most parasites, their body form is simple and wormlike. Blood is their only food. The jawless mouth (sometimes protruding) and two pairs of lobe-like appendages with claws give the appearance of five orifices, hence, *penta-* (five) *stomida* (mouths). Long treated as a separate phylum of invertebrates, tongue worms are now regarded as highly modified crustaceans, based on sperm and larval morphology, the nervous system, and DNA studies. Some very convincing fossils of apparent larval pentastomids from the Late Cambrian give no evidence of a crustacean relationship, leading Maas and Waloszek (2001) to question it. On the other hand, recent mitochondrial DNA sequencing supports the evidence from sperm that pentastomids are most closely related to the Branchiura (Lavrov et al. 2004).

### Subclass Copepoda: Copepods

Copepods (oar-footed bugs) are small crustaceans that are common in aquatic and semi-aquatic environments, both marine and freshwater. Zoogeographical data indicate that copepods are ancient arthropods (Dussart & Defaye 1995) and fossils are known from the lower Cretaceous (Huys & Boxshall 1991). They have undergone extensive adaptive radiation and include a wide variety of open-water, bottom-dwelling, herbivorous, predatory, and parasitic forms. Copepods can often be extremely abundant and have been estimated to be among the most numerous animals on earth, mostly because of their dominance in the plankton of oceans and lakes. There are a number of excellent accounts that give general information on copepods. The comprehensive monograph by Huys and Boxshall (1991) deals especially with morphology and evolution, while Williamson...
(1991) and Dussart and Defaye (1995) concentrate on the structure, function, and taxonomy of freshwater species. Coull and Hicks (1983) and Mauchline (1998) provide detailed information on the biology of harpacticoid and calanoid copepods, respectively, especially the marine species. These references are the main sources of the following notes.

The name ‘Copepoda’ is derived from two Greek words (kope, oar, and podos, foot), hence oar-footed. Copepods are typically small, mostly in the range 0.5–5.0 millimetres. Free-swimming forms may achieve a minimum size of only 0.2 millimetres (some Oncaea) or a remarkable 18 millimetres (a Valdiviella species), but some parasites are even larger. The body is usually approximately cylindrical and segmented, and divided into three parts—cephalosome, metasome, and urosome (equivalent to head, trunk, and abdomen). There are 10 pairs of appendages on both the cephalosome and metasome, used for both feeding and locomotion (some of these appendages also have a sensory function), and the urosome ends in two bristle-bearing caudal rami. Uniquely among crustaceans, copepods have a flat plate that connects the basal segments of each pair of swimming legs. This plate is probably why copepods can have a rapid jumping mode of movement. In all copepods the first thoracic segment (bearing the maxillipeds) is incorporated in the cephalosome, unlike other maxillopods.

The presence of a uniramous (unbranched) antennule is also a fairly reliable copepod characteristic. In male copepods the first antennae can be typically geniculate (with a prominent elbow), and are used to grasp the female during mating. The antennae, mandibles, maxillules, maxillae and maxillipeds are used in feeding. A wide variety of food types are utilised, including detritus, bacteria, algae, rotifers, nematodes, naidid oligochaete worms, crustaceans, and larval fish, and the structure of the feeding appendages varies in association with diet. The mechanics of feeding are complex, although copepods are probably fundamentally raptorial and use their mouthparts to grasp food particles. Many species, however, especially calanoids, are suspension-feeders and use the mouthparts to create water currents that bring food particles towards the copepod. Smaller particles are then captured passively and directed towards the mouth by bristles on the maxillipeds, maxillae, and maxillules, while larger particles are individually grasped by ‘fling and clap’ movements of the maxillae that grasp both the particle and a packet of water surrounding it and remove the water by an inward squeeze.

Reproduction is usually sexual, and sperm are transferred from male to female in a sac-like spermatophore (a few harpacticoids can reproduce parthenogenetically). Egg sacs are probably not an ancestral condition of Copepoda as many groups lack true egg sacs. Nevertheless, in many copepods the eggs are carried in one or two egg masses, sacs, or strings until hatching. Under favourable conditions, multiple clutches of eggs can be produced, at intervals of a few days or weeks, so that each female may produce tens to hundreds of eggs in a lifetime. The egg hatches into a nauplius larva and the life-cycle typically includes six naupliar stages and six copepodite stages, the last of which is the adult stage. There is a marked metamorphosis between the last nauplius and the first copepodite stage. Development may sometimes be abbreviated, especially in parasites. Copepods are relatively long-lived compared to other microcrustaceans. Development times from egg to adult are typically in the order of 1–6 weeks, but may take several months, and the lifespan of adults may be from one to several months. Developmental times are markedly affected by temperature and food levels. Some copepods have resting stages that enable avoidance of detrimental environmental conditions and dispersal. Calanoids and harpacticoids produce resting eggs that have a thick shell and which can survive extended periods of dormancy and dryness. In cyclopoids and some harpacticoids, copepodites may enter diapause and encyst in bottom sediments.

There are 11 orders, approximately 213 families, 1763 genera, and 11,956 species worldwide (Humes 1994; Ho 2003). The Harpacticoida alone comprises

---

Calocalanus pavo.  
After Giesbrecht 1893
PHYLUM ARTHROPODA CRUSTACEA

54 families, about 599 genera, and about 4400 species (J. Wells, unpublished data updating Wells 2007). The Calanoidea has 42 families with about 2000 species (Boltovskoy et al. 1999); in the Poecilostomatoida there are 55 families, 359 genera, and about 1770 species (Ho 2003); and in the Siphonostomatoida there are 45 families, 377 genera, and about 1840 species (Ho 2003). The known New Zealand copepod fauna comprises 698 species, of which the Calanoidea is the best known with 261 species, nine of which are undescribed. There are only 230 species of Harpacticoida, with about 99 of them undescribed; the remaining orders are also very poorly known.

Copepods live in a remarkable number of environments. These include not only marine and freshwater planktonic realms but in or on aquatic sediments, in association with plants, forest litter, and damp moss, in subterranean habitats or anchialine (isolated-marine) caves, and deep-sea hydrothermal-vent settings, but also in association with other animals as commensals or parasites.

In the marine plankton, calanoid copepods (‘insects’ of the sea) are extremely abundant. Some typical New Zealand examples are Acartia ensifera, Calanus australis, Centropages aucklandicus, and Paracalanus indicus. They are adapted to swimming in the water column and are fine-particle feeders in near-surface waters, eating mainly phytoplankton and protozoans. Carnivorous or detritivorous forms occupy deeper water-layers down to the deepest trenches. In the water column we also find forms that are not strictly free-living but live associated in some way with surfaces – the sea floor, the underside of sea ice, or on other planktonic animals.

The freshwater plankton in New Zealand is dominated by calanoid copepods of the family Centropagidae, which are widespread and very abundant in lakes, ponds, and the lower reaches of larger rivers. Many of the species also occur in Australia, although there are at least three endemic species. Calamoecia lucasi and Boeckella dilatata are typical lake dwellers while B. triarticulata is found in ponds. As in marine habitats, the freshwater calanoids are suspension-feeders on algae and protozoans, although at least some of the boeckellids are also predatory on small zooplankters such as rotifers and nauplii. A few cyclopoid copepods also live in fresh water, although they are usually sparser than the calanoids. They are probably mostly omnivores, consuming both animals and algae. Some are found mainly in the bottom waters and are probably strays from the benthic and littoral areas.

In aquatic sediments, copepods (mainly harpacticoids) live either permanently within the sediment or alternate between the sediment and its surface, browsing on the microflora associated with the sediment particles or with the accompanying detritus. In well-oxygenated coarse-grained sediments such as beach sand, specialised copepods (again, mainly harpacticoids) are part of the ‘interstitial fauna’ that lives within the interstices of this habitat. This habitat is commoner in marine sediments than in freshwater sediments, although it does exist in river systems and their ground waters where a strong intra-sediment water flow occurs. Most families of Harpacticoida have representatives in all of the above habitats, with specialisations for the interstitial habitat having evolved many times in different lineages. These trends exist among the New Zealand fauna to the same extent as they do elsewhere and are represented by numerous endemic and non-endemic species. An extremely important characteristic of this fauna is that, with very few exceptions, the entire life-cycle is benthic and the larvae are not dispersed large distances by water movements. This not only must affect their ecology but must also impact on population genetics and eventually on phylogeny. As a result we should expect a high level of endemism.

Many copepods are associates of plants. In the marine intertidal zone many harpacticoids live in association with seaweeds and sea grasses and are highly specialised for life on the surface of the fronds. Members of the Porcellidiidae, Peltidiidae, and Tegastidae, for example, are especially adapted to this environment; each family is well represented in New Zealand.
littoral areas of freshwater lakes, ponds, and running waters, cyclopoids and harpacticoids are abundant on and amongst macrophytes. Damp terrestrial situations are exploited by cyclopoid and harpacticoid copepods. These include damp soil, forest litter, sphagnum bogs, liverwort and moss clumps, and the pools between the leaves of bromeliads. Only the harpacticoids from this cryptic fauna have been extensively studied in New Zealand, and in these the same trends exist as elsewhere in the world; most species belong to cosmopolitan genera in the predominantly freshwater family Canthocamptidae, and most are endemic.

Copepods live in groundwater and can be caught in springs, wells, and pools in caves. In New Zealand these habitats have not been extensively surveyed (Chapman & Lewis 1976) and nothing is known about the copepods except that parastenocaridids have not been found, despite extensive searching (Schminke 1981a). Overseas, the Parastenocarididae (Harpacticoidea) is a large family of ca. 270 species (190 of them currently placed in the genus *Parastenocaris*) that mostly inhabit the interstices of groundwater. These habitats range from the water table beneath beaches and sand banks, including a few fully marine beaches, to brackish systems such as the Baltic Sea, and riverine and lacustrine inland systems, above and below ground.

Recently the study of deep-sea hydrothermal vents and marine caves has revealed many interesting copepods of great importance to the study of evolutionary relationships between the various groups of copepods, as they are amongst the most primitive forms. Because isolated marine caves are not yet known in New Zealand and the microscopic fauna of New Zealand hydrothermal vents has not yet been studied, these types of copepods have not been recorded here.

In thermal waters of the central North Island only one copepod, the endemic cyclopoid *Paracyclops waiariki*, is known. It is restricted to Lake Rotowhero, which has seasonal temperatures varying between 29.5° and 37.5° C and an average pH of 3.1.

Nearly half of all known copepod species live in symbiotic relationships with other organisms. It is evident that commensalism and parasitism have evolved independently several times in the class, even within an order. Copepods parasitise virtually every phylum of animals from sponges and cnidarians to vertebrates including mammals. They also have a range of associations from external and internal parasitism to varied forms of commensalism. For example, two species of endemic New Zealand harpacticoids are associated with macroinvertebrates — *Porcellidium tapui* on hermit crabs and *Alteuthoides kootare* on sponges. It is interesting to note that these genera are highly adapted for clinging to a substratum and are genuinely ‘phytal’ in this respect. This particular association with macroinvertebrates is almost certainly of the same type as with marine plants, i.e., using them as a substratum on which bacteria, fungi, and microalgae grow abundantly. Similarly, *Paramphiascopsis waihonu* is known only from a sample of spent elasmobranch embryo cases (taken at 1116 m), where many specimens occurred along with a gastropod mollusc; an association with the gastropod is unlikely and it is most probable that both are feeding on detritus and decay products within the case. *Paramphiascopsis* comprises several other species that have been taken in association with ascidians, polychaetes, gorgonians, and decapod crustaceans but many species are also known from algae and sediments.

Harpacticoids are also found in burrows in wood inhabited by the gribble (*Limnoria* spp.), where the nature of the association is unclear (Hicks 1988a), with some authors arguing for an obligate commensal relationship and others believing the attraction for the copepod is the microhabitat created by the gribble. Evidence for the latter is the presence of copepods in decaying wood no longer occupied by *Limnoria*, but the fact remains that the copepod species have never been found in habitats that have not been associated with the gribble. Five species, of which four are endemic, occupy this habitat in New Zealand waters.
Importance of copepods

In both marine and fresh waters worldwide, abundant copepods form a vital link in the food web that leads from minute algal cells or phytoplankton and small protozoans (e.g. Chapman & Green 1987; Bradford-Grieve et al. 1998) to the largest fishes, and some whales in the oceans. Many commercial and non-commercial marine fish (and some crustaceans) are utterly dependent on copepods as a food source during a portion of their larval life. For example, in New Zealand it has been shown that the larvae of hoki (Macruronus novaezelandiae), which forms the basis of the largest New Zealand fishery, feed on copepod adults (e.g. Calocalanus) and copepodites almost exclusively (Murdoch 1990). With their large mouth size, hoki larvae actively select copepods such as Calocalanus and Paracalanus (Murdoch & Quigley 1994). For inshore benthos and for migratory fish, estuaries and lagoons are typically the critical location for this life-history phase. In a New Zealand estuary, Parastenhelia megarostrum is a principal prey item for young post-metamorphic flatfish during the first six months of their lives (Hicks 1984). The very smallest fish feed on the naupliar stages while larger specimens have an increasing proportion of older copepods in their guts. In lakes, copepods are an important part of the diet of smelt (e.g. Stephens 1984, Chapman & Green 1987), which in turn form a major part of the diet of rainbow trout. Copepods can be so abundant that their faecal pellets, produced at a rate of several per hour, are an important source of food for detritus feeders. Copepod grazing can significantly reduce the densities of at least some algal species (e.g. Edgar & Green 1994) and it has been suggested that they may have potential in the biomanipulation of the effects of eutrophication in lakes (Edgar 1993). Copepods are increasingly being used as test organisms in ecotoxicological testing. In New Zealand, the freshwater species Calamoecia lucasi, Boeckella delicata, and Mesocyclops sp. have been shown to be very sensitive to pentachlorophenol (Willis 1998) and the latter two species have been recommended as suitable candidates for the development of routine testing protocols involving acute and chronic endpoints (Willis 1999).

Copepods can be important economic pests when they parasitise commercial species. This is especially the case overseas, where ectoparasitic copepods of the families Ergasilidae and Caligidae (‘sealice’) infect salmonids reared in sea cages, causing damage and sometimes death of valuable aquacultured product reared in marine areas (Johnston et al. 1997). In New Zealand, copepod ‘sealice’ are not yet a problem in salmon culture (Hine & Jones 1994) but the causative copepod genera are present in the farms (Jones 1988a). Copepods of the family Sphyriidae are also of economic importance in that the anterior portion of the copepod is buried in the musculature of the host fish, while the posterior portion bearing egg strings trails from a hole in the skin. Skinning machines do not remove the ‘head’ from the fillet causing wastage and customer complaints.

In freshwaters, the ergasilid Abergasilus amplexus infests a wide variety of fish including longfinned and shortfinned eels, smelt, inanga, goldfish, and perch (e.g. Jones 1981). Two other parasitic copepods, Thersitina inopinata and Paeanodes nemaformis, are rather enigmatic (McDowall 1990). Thersitina inopinata is known only from its free-swimming males, while P. nemaformis, although endemic, is known to parasitise only introduced brown trout and salmon. The exotic copepod Lernaea cyprinacea has been recorded from introduced goldfish. Free-living copepods are also known to be intermediate hosts in the life-cycles of tapeworms of freshwater fish. The initial stages of Amurotaenia decidua, which parasitises bullies, occur in Macrocyclops albidus (Weekes 1986) and planktonic copepods are secondary hosts in the life-cycle of Ligula intestinalis, the pleurocercoid of which infests both rainbow trout and bullies (Weekes & Penlington 1986).

Copepods can be disease vectors for human parasites in tropical climates. But conversely they can also carry the fungi or sporozoans that parasitise...
malarial mosquitoes. Copepods have been implicated in the spread of viruses through fish populations (Mulcahy et al. 1990). Freshwater copepods of the genera *Mesocyclops* and *Macrocyclops* have been used for control of the container-breeding mosquito species of *Aedes*, *Anopheles*, and *Culex*. So far, no examples of these kinds of relationships have been noted in New Zealand.

### Zoogeography of the New Zealand copepod fauna

#### Marine plankton

Very few marine planktonic copepods are endemic to the New Zealand region. The distribution of pelagic Copepoda (Bradford & Jillett 1980; Bradford et al. 1983; Bradford-Grieve 1994, 1999a) in the region appears to be maintained by a combination of factors probably related to their occurrence in water masses in some way or other. The physiological requirements of a species (temperature tolerances, ability to breed in differing temperature regimes, nutritional requirements for growth and breeding) and their behaviour (vertical migration in relation to particular water masses or physical-oceanographic phenomena) all contribute to the patterns we observe. An additional factor (plate tectonics) was probably important in the occurrence of some neritic plankton species in the New Zealand region.

Some species have a clearly coastal distribution. Among the New Zealand epipelagic calanoids, only species of *Acartiidae*, *Calanidae*, *Centropagidae*, *Clausocalanidae*, *Paracalanidae*, *Pontellidae*, and *Temoridae* contain coastal forms that are rarely encountered in oceanic waters. Endemic coastal species such as the calanoids *Acartia ensifera*, *A. jillettii*, *A. simplex*, and *Centropages aucklandicus* and the pereiopod *Corycaeus aucklandicus* are confined to New Zealand waters, whereas *Gladioferens pectinatus*, *Labodocera cervi*, and *Sulcanus conflictus* are confined to Australia and New Zealand. *Calanus australis* is found in at least New Zealand and southeastern Australian coastal waters, where it is essentially restricted to the mid-shelf (Bradford 1985). It seems possible that many of these species had common ancestors with close relatives in other temperate neritic parts of the world as far back as the Oligocene, when equatorial sea temperatures were low (Bradford 1979). *Paracalanus indicus* is restricted to coastal waters, with maximum concentrations occurring close to shore (Bradford 1985), although this species possibly has a broad tropical/subtropical distribution. *Clausocalanus jobei* and *Temora turbinata* also have a tropical/subtropical distribution whereas *Drepanopus pectinatus* has a coastal distribution around subantarctic islands.

Relationships to water masses are most clearly seen among oceanic epipelagic species. Nevertheless, in the New Zealand region some oceanic species are capable of responding rapidly to the heightened productivity of coastal waters and may attain maximum numbers close to the coast, obscuring their oceanic affinities. Examples of this type of distribution are seen in the calanoids *Nannocalanus minor* and *Clausocalanus ingens* and the cyclopoid *Oithona similis*.

Warm-water (tropical) oceanic epipelagic species usually have a cosmopolitan distribution if they are able to breed at a range of latitudes extending to 40°S, whereas those with breeding ranges restricted to lower latitudes (e.g. *Euchaeta rimana*) are not circumglobal in their distribution because of the geographical barriers (South America and Africa) presented to their distribution. In tropical or subtropical waters, epipelagic calanoid species with distributions extending to 40°S and sometimes as far as the Subtropical Front are *Aetideus giesbrechti*, many *Calocalanus* species, *Clausocalanus arculicornis*, *C. lividus*, *C. parapergens*, *C. paululus*, *C. pergens*, *Eucalanus hyalinus*, *Mecynocera clausi*, *Nannocalanus minor*, *Neocalanus gracilis*, *Pareucalanus sewelli*, *Pareuchaeta acuta*, *P. media*, *Rhincalanus nasutus*, and *Subeucalanus crassus*. Species with a warm-temperature (transition zone) Southern Hemisphere distribution include *Aetideus pseudarmatus*, *Clausocalanus ingens*, *Pareucalanus langae*, and possibly *Neocalanus tonsus* and *Calanoides macracarinatus*. Species with subantarctic distributions include *Calan-
**PHYLUM ARTHROPODA CRUSTACEA**

*Neocalanus simillimus, Clausocalanus brevipes, Neocalanus tonsus,* and *Subeucalanus longiceps.* Species with Antarctic–subantarctic distributions include *Aetideus australis, Clausocalanus laticeps,* and *Rhincalanus gigas.*

**Marine sediments**

Throughout the world the copepod fauna of marine sediments (predominantly harpacticoids) is well known only for the intertidal and shallow sea areas. Detailed data are available for only a few sites of more than a few metres in depth, mostly in Europe, although scattered information is known for all depths down to almost the bottom of the deepest trenches. Even for intertidal and sublittoral areas, most of the world outside Atlantic Europe, the western Mediterranean, and a few locations on the eastern coast of the Americas is poorly known or even totally unknown. A reasonably comprehensive survey of the North and South Islands of New Zealand has been carried out, but the results have yet to be fully published and many species remain unnamed. Furthermore, assessment of the zoogeographic relationships of the New Zealand fauna is made impossible by the almost complete absence of information from Australia and New Caledonia. All that can be said at this time is that it seems unlikely that New Zealand will harbour many endemic genera (though that will depend on the attitude of future taxonomists towards taxon definitions).

**Freshwater plankton**

In New Zealand, most freshwater calanoids (eight species of! *Boeckella* and one of *Calamoecia*) belong to the family Centropagidae, the non-marine members of which are mainly confined to Australasia, the subantarctic, the Antarctic Peninsula, and parts of South America (Bayly 1992). Only three of these species are found only in New Zealand (Jamieson 1998); the others also occur in Australia. A further four species are considered to be resident natives (*Boeckella dilatata, B. propinqua, B. triarticulata,* and *Calamoecia lucasi*) whereas *B. minuta* and *B. symmetrica* may have invaded New Zealand since European colonisation (Banks & Duggan 2009). Recently, the diaptomid cross-hemisphere invaders *Skistodiaptomus pallidus* and *Sinodiaptomus valkanovi* have been recorded in constructed water bodies (Duggan et al. 2006; Banks & Duggan 2009; Makino et al. 2009).

Bayly (1995 and references therein) concluded that the present-day distribution of freshwater and brackish Centropagidae can be interpreted as being a result of the colonisation of southern-hemisphere inland waters from marine and then brackish-water ancestors at a time when Australia, New Zealand, and South America were still linked to Antarctica, and Africa, Madagascar, and India had already drifted northwards. The absence of the Diaptomidae from New Zealand, most of Australia, and all of Antarctica also appears to be related to the timing of the separation of these landmasses from Pangaea in relation to the evolution of this family.

The distribution of calanoids in the major lakes is probably well known (Chapman & Green 1987; Jamieson 1988, 1998; Bayly 1992; Banks & Duggan 2009) but has yet to be fully examined in smaller habitats, especially ephemeral pools and the less-accessible high-country tarns. Most species show relatively clear habitat segregation. *Calamoecia lucasi* is widespread in northern, central, and western parts of the North Island, where it is found in streams, ponds, and large rivers. It also lives in a few small lakes in Northern Nelson. *Calamoecia ampulla,* a widespread species in Australia, is known only from one unverified South Island record (Bayly pers. comm.). Of the *Boeckella* species, *B. minuta, B. symmetrica,* and *B. tanea* have restricted distributions in the North Island. *Boeckella tanea* is found only in Northland, *B. symmetrica* in a pond near Auckland, and *B. minuta* in the Waikato River hydroelectric reservoirs and water-supply reservoirs in Wellington. It has been suggested that *B. symmetrica* and *B. minuta* may be
recent immigrants from Australia (Chapman & Green 1987) and this may apply to *C. ampulla* too. *Boeckella propinqua* occurs mainly in central and northern areas of the North Island but, like *C. lucasi*, its distribution also extends to the tip of the South Island. *Boeckella hamata* occurs throughout the southeastern part of the North Island, the eastern part of the South Island, and southern Westland, mainly in reservoirs and coastal lakes. *Boeckella triarticulata* has a similar distribution but apparently does not co-occur with *B. hamata*. It is found mainly in ponds and reservoirs in eastern parts of the South Island from Canterbury to Otago, with one record from Hawke's Bay in the North Island. *Boeckella delicata* has a disjunct distribution, occurring in Northland and the Waikato region of the North Island and also on the west coast of the South Island. *Boeckella dilatata* occurs only in the South Island, mainly in glacial lakes and in associated reservoirs. It also has a disjunct distribution and is found only in northern and southern areas of this island. Unlike the usual situation elsewhere in the world, co-occurrences of two or more species of calanoids in one lake are rare, and most lakes have only one calanoid. In the North Island, there are a few co-occurrences of *C. lucasi* and *B. delicata*, *C. lucasi* and *B. propinqua*, and *C. lucasi* and *B. minuta*, and in the South Island *B. triarticulata* and *B. dilatata*, *B. triarticulata* and *B. hamata*, and *C. lucasi* and *B. propinqua* in a few habitats (Chapman & Green 1987; Jamieson 1998; Banks & Duggan 2009).

Various attempts have been made to explain the distributional patterns of the New Zealand freshwater calanoids (summarised by Jamieson 1998) and, until recently, most of these used dispersalist biogeographical ideas. Banks and Duggan (2009) have highlighted the role of constructed lakes and ponds in facilitating inter-and intracontinental invasions of calanoid species. Maly (1984) suggested that distributions resulted from probabilities of immigration and extinction that were assessed from clutch sizes and the likelihood of predation by fish. Maly (1991) modified these ideas to include the number of existing populations and concluded that dispersal was probably not important over long distances but may be important at local scales. Jamieson (1988) explained the distribution of *Boeckella dilatata*, *B. hamata*, and *B. triarticulata* by relating differences in their ecological requirements and dispersal abilities to vicariant events. More recently, Jamieson (1998) has provided a convincing explanation for the distribution of these three species and *B. delicata* based on panbiogeographic methods. She showed that their distributions are correlated with the three principal pre-Late Cretaceous technostratigraphic terranes that, over the last 150–200 million years, have come together to make up New Zealand. *Boeckella dilatata* and *B. delicata* occur in lakes and ponds on the Tuhua and Caples Terranes and *B. hamata* and *B. triarticulata* on the Torlesse Terrane. The species overlap at the terrane margins. The present-day disjunct distributions of *B. dilatata* and *B. delicata* are thus thought to result from tracks arcing out to sea.

The species pairs on the different terrane groups are thought to differ in ecology; in particular *B. delicata* and *B. hamata* are suggested to have a higher salt tolerance than either *B. dilatata* or *B. triarticulata*, thus enabling sympatry. Localised dispersal presumably explains the overlap of species at the terrane margins. Jamieson’s panbiogeographic approach would seem to have considerable potential for explaining distributions of the remaining calanoids. It is clear, however, that ecological information remains important for explaining distributions of sympatric species. Ecological studies of life-histories and food requirements have been made of some species (e.g. Green 1975; Forsyth & James 1984; Jamieson 1986; Chapman & Green 1987; Burns 1988; Jamieson & Burns 1988; Xu & Burns 1991; Burns & Xu 1990; Twombly et al. 1998; Couch et al. 1999), but much more remains to be done. The effects of post-European colonisation, with altered fish communities and changing trophic status of lakes, on distributional patterns are not known.

The cyclopoid copepod fauna is very poorly known taxonomically and ecologically. A few cyclooids are found in the lake plankton, but their
populations are usually either sparse or seasonal and little is known about them. There are no equivalents of the large-bodied *Cyclops* (in the strict sense) of many Northern Hemisphere lakes.

*Mesocyclops leuckarti* has been recorded from various North Island lakes (Green 1974, 1976; Jamieson 1977; Chapman & Green 1987; Greenwood et al. 1999), but it is likely that these records were not of the nominate species as *M. leuckarti* does not occur in the Southern Hemisphere (Kiefer 1981). Bayly (1995) has suggested that its correct identity is possibly *M. australiensis*. *Macrocyclops albitalius* occurs in low numbers in the Rotorua and Taupo lakes (e.g. Chapman 1973; Forsyth & McCallum 1980), in the lakes of the Waitaki River system, and in other South Island lakes (Stout 1978; Burns & Mitchell 1980). *Eucyclops serrulatus* is found in the plankton of Lakes Hayes and Johnson (Burns & Mitchell 1980) and *Acanthocyclops robustus* in the plankton of Lake Mahinerangi (Mitchell 1975). It still can be concluded that, until a revision is made of the freshwater cyclopoids, no valid assessments of biogeographical relationships can be made. Nevertheless, Karanovic (2005) held it to be highly likely that the cosmopolitan cyclopoids *Acanthocyclops robustus*, *Dicyclops bisetosus*, *Eucyclops serrulatus*, and *Paracyclops fimbriatus* were accidentally introduced to New Zealand by early European settlers in barrels of fresh water. Jamieson (1980a, b) conducted experimental studies of predatory feeding and development rates of *Mesocyclops* sp.

**Plant associates**

In marine systems the term ‘plant associates’ means the fauna associated with macroalgae and sea grasses and is usually called the phytal habitat. In addition, a few species have been found associated only with decaying wood (from wharf piles to driftwood dredged from depths of 1100 metres). These perhaps should be included in the phytal fauna as it is most probable that the role of the living or dead plant is primarily as a substratum for the copepods’ food supply, namely bacteria, fungi, and microalgae attached to the plant. However, in this regard the phytal fauna is little different from the true benthos, which relies on these food sources attached to particles of the sediment.

Most of the species do not show obvious morphological adaptations to the phytal habitat. In those that do, the adaptations are usually to enable the animal to attach itself more effectively to the plant. Very few species seem actually to damage the plant or to be directly feeding on its tissues. Many genera that contain species found among algae have other species living on or in the adjacent benthic sediment. Many species are found equally often among algae and in sediments without associated plant growth. Also, it is known that many of the species washed from samples of macroalgae and sea grasses are actually associated with the sediment and detritus that becomes trapped in the interstices of the plant and thus are really part of the sediment fauna. Even many of the truly phytal species that do show adaptations to that environment have been shown to leave the plant for mating; this may partially explain the relative rarity of males in collections of these species.

In the marine system, about 45% of the described phytal species are endemic. Only a few undescribed species currently exist in collections, which may partly be a consequence of inadequate collecting and cataloguing. Notwithstanding, the phytal fauna is quite well known ecologically (e.g. Hicks 1977, 1988b) and, while it is very probable that many species remain to be discovered, the main outlines of the fauna are well known. Unfortunately, the phytal fauna of adjacent marine regions is as poorly known as their sediment fauna and similar remarks about understanding zoogeographical relationships apply. The comments below on endemism in the sediment fauna apply equally to the phytal but the lack of regional collecting makes it futile to try to estimate the true level of endemism.

The situation in freshwater and terrestrial systems is much the same. Some copepods (cyclopoids and harpacticoids) probably use plants mainly as the substratum on which their food grows, but much less is known about
their ecology. Certain copepods are found associated with aquatic vegetation in lakes and ponds, and with mosses (Harding 1958; Chapman & Lewis 1976). In semiterrestrial situations such as mossy banks and the edges of waterfalls or in damp forest litter and decaying wood, some copepods (such as Goniocyclops silvestris and a variety of harpacticoids) are found; most are apparently endemic but this fauna has still to be properly examined (Chapman & Lewis 1976).

Animal associates
It is difficult to make any definitive statement about the zoogeography of animal associates because the commensal and parasitic copepod fauna of marine invertebrates in New Zealand and neighbouring seas is very poorly known. For example, known New Zealand siphonostomatoid species diversity is only 29% of that in European seas, and even less for cyclopoids and harpacticoids, whereas, based on what is known for well-studied high-level Animalia taxa in both regions, New Zealand species diversity matches or exceeds that in European waters (Gordon et al. in press). The end-chapter checklist of New Zealand species in these copepod orders is annotated to indicate the type of relationship and host.

Species identifications of parasitic copepods from fishes of neighbouring seas are, in many cases, awaiting critical review. For example, Trifur lotellae in New Zealand would appear to be identical to Trifur physiciuli from Australia. There are many other such examples. Also, the parasitic copepod fauna of marine invertebrates in New Zealand and neighbouring seas is almost totally unknown. Nevertheless, Jones (1988b) examined the then known parasitic copepod fauna and concluded that endemism on teleosts at the generic level was very low (2%) and there were no endemic genera on elasmobranchs (sharks).

The freshwater parasitic copepod fauna consists of only three species – Abergasilus amplexus and two very rare or extinct species, Thersitina inopinata and Paeonodes nemaformis. Abergasilus is an endemic estuarine genus common in, and known only from, Lake Ellesmere and the Chatham Islands lagoon. It has close affinities with South American genera. Thersitina has been found only once, in a plankton sample from Lake Poerua (Percival 1937). Paeonodes nemaformis has been found only twice, both times in South Westland on introduced salmonids (Hewitt 1969). The genus has also been found in Africa and is apparently closely related to Mugilicola, found in South Africa, India, and Australia (Boxshall 1986). The native hosts of Thersitina and Paeonodes are unknown, despite extensive searching. It is concluded that the parasitic copepod fauna of marine vertebrates is derived from the wandering of host fishes and reflects the strong links with Australia and the island chains to the north (Jones 1988a,b).

Endemism
One key element in the occurrence of endemism in New Zealand is the paleogeography of the region. The freshwater, brackish, and inshore copepod faunas illustrate the key elements of such reconstructions (Lewis 1984; Bayly 1995). The absence of the calanoid family Diaptomidae and presence of freshwater species of Centropagidae in Australia, New Zealand, South America, and Antarctica indicates that the period when these land masses were still linked but already separated from Africa, Madagascar, and India (120–80 million years ago) is crucial in reconstructing the evolution of Boeckella, Calamoecia, and Gladioferens in New Zealand and other southern hemisphere regions. These events, and the subsequent submergence of New Zealand in the Oligocene (35 million years ago) were probably responsible for speciation and the currently observed endemism (Bayly 1995).

The connection between New Zealand and Antarctica was broken during the Late Cretaceous. Three of eight New Zealand species of Boeckella are endemic to New Zealand (Maly & Bayly 1991) and it is likely that this genus inhabited the fresh waters of the ancestral landmass when it separated from Antarctica.
By the Late Oligocene, nearly all of the New Zealand landmass (possibly all of it according to Landis et al. 2008) was submerged. Significant extinctions will have occurred at this time, accounting for the relatively impoverished fauna of New Zealand compared with that of Tasmania. On the other hand, the multiple vicariant events associated with the production of a diminishing New Zealand archipelago in the Oligocene might have been expected to result in some speciation and the currently observed endemism if not all of the landmass was in fact submerged.

We predict that a higher degree of endemism than is currently recorded will be discovered amongst freshwater and benthic copepods when the less well-known groups are revised. But we need to introduce here a note of caution in this discussion of endemism. While the number of endemic species indeed reflects the evolutionary history of a particular fauna, in practice the number of such species recognised by past and present taxonomists depends on the interpretation of morphological variability within a species, especially where there is discontinuous distribution and not enough morphomolecular information for phylogenetic analysis.

**Marine plankton**

Very few marine planktonic species are endemic to New Zealand. The main reason for this is that most species are oceanic and are relatively widespread in a global sense, ranging from circumglobal subantarctic and Indo-Pacific to distributions encompassing all the world’s oceans. Only a few coastal calanoid or cyclopoid species are endemic to New Zealand waters (*Acartia ensifera*, *A. jilletti*, *A. simplex*, *Centropages aucklandicus*, and *Corycaeus aucklandicus*). The cyclopoid *Corycaeus aucklandicus* is endemic to coastal waters of northern New Zealand.

**Freshwater plankton and benthos**

Only three freshwater calanoid species are endemic – *Boeckella dilatata*, *B. hamata*, and *B. tanea*; the other seven species also occur in Australia. Only two (*Metacyclops monacanthus*, *Paracyclops waiariki*) of the 19 cyclopoid species are known to be endemic to New Zealand. All others are supposedly cosmopolitan or Australasian. Notably, several genera recorded from Australia, some with multiple species (*Apocyclops*, *Australocyclops*, *Ectocyclops*, *Mixocyclops*, *Neocyclops*, *Thermocyclops*), have not yet been recorded from New Zealand. Some studies (see Bayly 1995) have shown much greater degrees of differentiation and endemicity than previously recognised in microcrustaceans, and it is evident that more stringent resolution of morphotypic variation of the New Zealand freshwater cyclopoids is required before their status can be assessed. Presumed ‘cosmopolitan’ species may be so only because of widespread and indiscriminate misuse of authoritative (northern hemisphere) taxonomic references. As noted earlier for *Mesocyclops leuckarti* (discovered to be a species complex by Kiefer (1981) and not represented by the nominate species in the Southern Hemisphere), comparable species groups may be found in other ‘cosmopolitan’ species. An on-going global revision of the Cyclopoida (e.g. Dussart & Defaye 1995; Einsle 1996) will help resolve some of the problems. This series should be consulted as a guide to the global literature on cyclopoid genera and families, and in particular for the accepted modern level of taxonomic discrimination.

**Marine sediments**

Approximately 50% of the described harpacticoid species are endemic, but at least three times as many species remain undescribed in collections, and it is reasonable to estimate that at least 75% of these will prove to be endemic new species. It would seem, therefore, that the rate of endemism in New Zealand is high compared, for example, to the British Isles (as an example of another island group of comparable size), where probably it is less than 10%. But this comparison is meaningless. The British fauna has been investigated for much
longer and at much greater intensity. As a result, it is known to contain at least four times as many species. Further, and very importantly, the British Isles are close to the shores of northwestern Europe, where the fauna is also very well known and shares many species with Britain. New Zealand is distant from its nearest neighbours. This, and its geological history since separation from the rest of Gondwana, may well have increased the level of endemism, but the lack of data from Australia (where the fauna is very poorly known) undoubtedly inflates the current estimates.

The limited amount that is known about the benthopelagic calanoid fauna indicates that there may be some degree of endemism (e.g. Bradford 1969; Bradford-Grieve 1999b) in the New Zealand region. Nevertheless, in the deep sea the perception of endemicity may reflect the paucity of sampling of near-bottom faunas worldwide.

Cryptic habitats

Freshwater harpacticoids in New Zealand have been collected mainly from clumps of moss or liverworts or similar vegetation in streams, the littoral of ponds and lakes, or from wet banks close to water bodies and in damp forest in leaf litter. Of the 19 named species in the end-chapter checklist, 17 are endemic, but relatively little collecting has been carried out and large areas of the country remain unexplored. The total fauna is likely to be many times the recorded number of species, but it is probable that a very high level of endemism, and of localised distribution of species, may be found. It will be interesting to see if their distribution supports the panbiogeographic explanation for the distribution of freshwater planktonic Calanoida (Jamieson 1998). The presence of small cyclopoid species has also been noted, but only one has been identified to species and the true extent of this fauna cannot be estimated at this time (Chapman & Lewis 1976).

Gaps in taxonomic knowledge of copepods and scope for future research

Platycopioida

This order is not known in the New Zealand region. It is possible that platycopioids will be found when the benthopelagic realm is properly sampled, because they have been found in other temperate, shallow-water, near-bottom habitats. Other genera have been found in marine caves in Bermuda so their relatives might not be expected to occur in New Zealand.

Calanoida

The marine pelagic calanoid copepod fauna of New Zealand is fairly well known, mainly from the work of Janet Bradford-Grieve. The end-chapter crustacean species list incorporates results from Bradford and Jillett (1980), Bradford et al. (1983), and Bradford-Grieve (1994, 1999a,b). Their data are augmented by information in the revisions of the Aetiidae (Markhaseva 1996) and Euchaetidae (Park 1995). All these works incorporate other records of 19th- and 20th-century workers.

A number of calanoid families have not been recorded in the New Zealand region. This may partly reflect lack of extensive sampling. For example, the poor sampling of benthopelagic habitats at all depths is probably responsible for the absence of the Diaixidae, Discoidae, Hyperbionychidae, Mesaiokeratidae, Parkiidae, Pseudocyclopiidae, Ridgewayiidae, and Ryocalanidae, although it is likely that the New Zealand fauna does include some species from a number of these families. The apparent absence of isolated marine (anchialine) caves in New Zealand probably explains the absence of the Boholinidae, Epacteriscidae, and Fosshageniidae.

Species of Parapontellidae have been recorded only from the North Atlantic

![Metridia lucens (Calanoida)](From Bradford-Grieve 1999)
Ocean and from deep waters of the Malay Archipelago, so this rare family may not occur in the New Zealand region.

Other families are absent from the New Zealand fauna for paleogeographic reasons. The Diaptomidae are known from fresh waters in most of the world apart from New Zealand, most of Australia, and all of Antarctica (Bayly 1995). Pseudodiaptomids are brackish to marine species, widespread in other parts of the world but present in the Australasian region only in northern Australia.

The taxonomy of the freshwater planktonic calanoids is reasonably well known (Chapman & Green 1987), although genetic studies using modern techniques are required to assess whether there has been cryptic speciation in any of the geographically widespread and disjunct species and in those shared with Australia (cf. Boileau 1991). Ecological studies are still in their infancy, and for all species much more needs to be known about autecology (e.g. growth and reproduction, feeding rates, behaviour, life-history strategies, population dynamics, etc.), and contributions to community and ecosystem dynamics (e.g. competitive interactions, predation effects, production rates, contribution to food chains, nutrient cycling, etc.).

Misophrioida
Members of this order have not been recorded from New Zealand. It is possible that they might be found when marine benthopelagic habitats are more extensively sampled.

Cyclopoidea
This order now includes the Poecilostomatoida (Boxshall & Halsey 2004). Cyclopoids have been relatively little studied in New Zealand – knowledge of the marine, freshwater, and brackish non-parasitic Cyclopoida is very scattered and inadequate.

Early records of freshwater Cyclopoida were summarised by Hutton (1904) and amplified by Chapman and Lewis (1976). The synonymies and taxonomic arrangement given by Dussart and Defaye (1985) in their checklist of the world free-living Cyclopoida were taken into account in compiling the New Zealand list. In addition, the revision of the Paracyclops fimbriatus complex (Karaytug & Boxshall 1998) and the records of Roper et al. (1983) were noted. The commoner New Zealand taxa in ponds and lakes are known but both their generic and species status need re-examination in view of the recent taxonomic revisions of supposedly cosmopolitan genera (Morton 1985; Dussart & Defaye 1995). The underground and cryptic fauna is unknown taxonomically apart from Goniocyclops silvestris in forest litter (Harding 1958), and genera and species described by Karanovic (2005), but other undescribed species are known. Entries in the end-chapter checklist accompanied by a question mark are doubtful old records that need further investigation.

Checklists entries of the free-living marine planktonic families Oithonidae, Corycaeidae, and Sapphirinidae of the New Zealand region are based on the unpublished records of Janet Bradford-Grieve; the identities of the species need more detailed study. The species of Oncaeidae are known from the work of Heron and Bradford-Grieve (1995).

Another group of families comprises mainly marine parasites or associates of other animals. For example, Hemicyclops (a near relative has been discovered in New Zealand but is undescribed) has a typical cyclopoid body form and lives in loose associations with other marine organisms (e.g. polychaetes), sharing their burrows. There has been some work on fish parasites in New Zealand but the fauna is essentially unknown or undescribed – an extensive collection of Sarcotaces spp., made by Jones in the 1980s and 1990s from around New Zealand, remains in the Auckland Museum collection awaiting description.

The parasitic families Archinotodelphyidae, Chordeumiidae, Cucumari-colidae, Mantridae, Ozmanidae, and Thespesiopsyllidae and the marine benthic
family Cyclopinidae are not known from New Zealand. The freshwater parasitic family Lernaeidae is represented by only Lernaea cyprinacea, which was introduced with ornamental fish (Boustead 1982). The commensal Ascidiolidae and Notodelfphidae, living in association with tunicates, are known from only two collections (Schellenberg 1922a, b; Jones 1974, 1979). It is certain that many more cyclopid associates of marine invertebrates remain to be found and described.

Data on the occurrence of commensal and parasitic forms have been collated here using the works of Thomson, Hewitt, Jones, Pilgrim, and Ho as described above. In general, we can say that the symbiotic copepods of New Zealand are very poorly known, particularly those occurring in association with marine invertebrates. Certainly, those parasitic on marine fishes are better known than those parasitic or commensal on/in other hosts, but we still cannot say that fish copepods are well known in New Zealand. There is currently nobody working on symbiotic copepods in New Zealand.

**Gelyelloida**

The two known species of this order are found in subterranean waters of France and the order is unlikely to be found in New Zealand.

**Mormonilloida**

This order contains only two species that are usually found at mesopelagic depths. Mormonilla phasma has been recorded off the east coast of northern New Zealand.

**Harpacticoida**

Early contributions to knowledge of New Zealand’s fauna were made by Thomson (1878a,b, 1882), Brady (1899), Sars (1905), Brehm (1928, 1929), Farran (1929), Lang (1934), and Harding (1958). More recent additions to the fauna have been made by Barclay (1969), Hicks (1971, 1976, 1986, 1988a,c), Lewis (1972a,b; 1984), Wells et al. (1982), Hicks and Webber (1983), and a number of other authors. Hicks has also contributed a body of ecological and biological information on the phytal harpacticoid fauna. Included herein are unpublished records of freshwater species from Dr Maureen Lewis, and marine species from Drs John Wells and Geoff Hicks. When the presently undescribed species in existing collections are worked up, our knowledge of the sediment-dwelling harpacticoids of seashores will be reasonably good, but much work still needs to be done on the marine phytal fauna (mainly nationwide collecting to establish distributional patterns). As is common worldwide, there is very little knowledge of the sediment or phytal faunas of the sublittoral and deeper.

Lack of extensive exploration may be responsible for the absence of some families. It is highly probable that Argestidae, Cerviniinae (Aegisthidae), Cletopsyllidae, and Nannopodidae will be found in shelf and deep-water sediments and Longipediidae and Metidae associated with seashore plants and algae. On the other hand, the absence of the Parastenocarididae may be for geological reasons.

Only a fraction of New Zealand’s freshwater and damp terrestrial locations has been surveyed. It is to be expected that the number of species in the fauna will be at least tripled, and New Zealand’s geological history makes it likely that a number of intriguing questions of zoogeography and phylogeny will arise as a result. The harpacticoid fauna of New Zealand’s ground waters is completely unknown, yet cave systems exist that are comparable to the species-rich karst formations of Europe.

Of particular note is the paucity of information on the fauna of the far offshore islands from the Kermadecs to the Chathams and subantarctic islands.

**Siphonostomatoida**

All Siphonostomatoida are parasites or associates of other animals and the order is mainly marine. Most work has been done in New Zealand on the parasites...
of fish, but this work is nowhere near complete. Almost nothing is known of the vast proportion of this order likely to live in association with marine invertebrates. We estimate that there are many species waiting to be discovered in the New Zealand siphonostomatoid fauna. There is currently nobody working on symbiotic copepods in New Zealand.

Commensal and parasitic forms have been collated here using the works of Thomson, whose major work was published in 1890 and whose collection is still housed in the Otago Museum (Thomson 1890). Gordon Hewitt also published extensively in the 1960s (Hewitt 1963, 1967, 1968, 1969) and, later, one of his students, Brian Jones, continued (1979, 1981, 1985, 1988b, 1991); his collection, including many undescribed species, is now in the Auckland Museum. A large collection was amassed at Kaikoura by students of the University of Canterbury under Bob Pilgrim (Pilgrim 1985) and some of that material was worked up by Ju-Shey Ho (Ho 1975, 1991; Ho & Dojiri 1987). The compilation given in the end-chapter crustacean species is based on the parasite list of Hewitt and Hine (1972), Pilgrim (1985), and the unpublished collection records of Jones.

Monstrilloida
All Monstrilloida have internal parasitic naupliar and early postnaupliar stages and free-swimming non-feeding adults. The known hosts are polychaete worms and prosobranch molluscs. Members of this order have been noted in the New Zealand fauna although there are no published records and descriptions.

Conclusions
There are few copepod taxonomists in New Zealand and none is able to work full-time on the subject. The greatest gaps in our knowledge copepod diversity are in the orders Cyclopoida, Harpacticoida, Siphonostomatoida, and Poecilostomatoida, especially concerning copepods as symbionts and parasites. These can be filled only by sampling little-studied environments, namely phytal, freshwater, deep-water, damp-terrestrial groundwater, and offshore islands. Sampling of benthopelagic and deep-sea habitats will yield records of hitherto undiscovered families and orders.

Because copepods are ecologically and economically so important, there is tremendous scope to understand the roles they play in the different ecosystems that they occupy, and to understand their impact on the other organisms with which they live in association, some of which are directly exploited by humans.

Class Ostracoda: Seed shrimps, mussel shrimps
Ostracods are tiny bivalved crustaceans that are widely distributed in the oceans, in fresh waters, and, rarely, in terrestrial situations. Food-mediated seasonal blooms in some freshwater habitats can result temporarily in vast numbers. Their shape confers on them the common name seed shrimps or mussel shrimps. Species sub-class Podocopa range from 0.2 to 1.5 millimetres in length, while modocopids are often much longer, reaching an extreme of 30mm in Gigantocypris. Their shells, strengthened by deposition of calcium carbonate amongst the layers of cuticle, also fossilise well; in fact, ostracods are the most abundant arthropods in the fossil record, with a body plan that has been conserved at least since the Silurian. The shells can be brightly coloured and highly sculptured, making them attractive creatures to study, especially with a scanning electron microscope. They have an indistinctly segmented body like most arthropods, with paired appendages that are adapted for a variety of functions. Their identification is normally a specialist occupation.

They are very useful organisms, as knowledge of their taxonomy and distribution can be applied to studies of ecology and to environmental monitoring in relation to water quality, water depth, salinity levels, and temperature, as well as in stratigraphy. The number of specialists studying this group of animals is declining even though there is great potential for their usefulness. There are
approximately 22,000 living and fossil species in the Catalog of Ostracoda published by the American Museum of Natural History and estimates of likely
global diversity suggest more than 62,000 species in total. Of the described living
species, 7000 belong to subclass Podocopa and 600 to subclass Myodocopa
(Cohen 1998). There are many more species yet to be found in New Zealand,
both living and fossil, in all environments.

Ostracods live in most aquatic environments and even, in the case of one
New Zealand species – the bright yellow *Scottia audax* – in the damp leaf litter
of the forest (Chapman 1961). Freshwater species live for between one season
(as ponds dry) and three years. Marine species similarly live for one season
to two years. Many marine planktonic ostracods constitute food for fish and
species of one family (Entocytheridae, represented in New Zealand by a single
species) are commensal on fish and other arthropods. Some myodocopids are
bioluminescent but none have yet been found in New Zealand.

The first description of an ostracod, by Carl Linnaeus (1746), was very
generalised. A figure was published in 1753, but the ‘father’ of the study of
ostracods is regarded as O. F. Müller who, in a 1785 monograph on Entomostraca
from Denmark and Norway, produced good descriptions and figures of
freshwater ostracods.

**History of study in New Zealand**
Currently, the New Zealand living ostracod fauna stands at 442 species (including
86 undetermined), mostly marine but also comprising 37 freshwater and one
terrestrial species. This tally is the product of many zoological studies since 1843;
actual descriptive taxonomy has proceeded in pulses. The first species to be studied,
by William Baird, was a relatively large (1.94 millimetres body length) freshwater
species (*Candowocypris novaezelandiae*), often found in ponds and drinking
troughs for farm animals (Baird in White & Doubleday 1843). It was collected
by naturalist-explorer Ernst Dieffenbach. Baird (1850) was also responsible for
describing the large (6.5 millimetres) marine species *Leuroleberis zealandica*
sent to him by Rev. Richard Taylor of Waimate, one of the early settlers. George M.
Thomson, teacher, Member of Parliament, and an amateur naturalist, produced
the first locally published paper on ostracods from the Dunedin district in 1879.
The first global oceanographic voyage of HMS *Challenger* (1873–1876) brought
the ship into New Zealand waters and into Wellington Harbour for sampling.
The results were published by Brady (1880). With the general establishment of
the New Zealand colony, there was by the end of the 19th century an exchange of
information between naturalists in New Zealand and Europe who were keen to
document the fauna. So material was sent away for identification. Norwegian G.
O. Sars (1894) published on freshwater species contained in dried mud and Brady
(1898), living in Newcastle, England, received some marine specimens from New
Zealand. Owing to the paucity of New Zealand ostracod taxonomists, this practice
continued well into the 20th century with Brehm (1929) in Austria, Kornicker
(1975) in the USA, and Hartmann (1982) in Germany providing identifications.
One consequence is that many of the type specimens of New Zealand species
reside in overseas institutions.

The freshwater ostracod fauna was reviewed by Chapman (1963) and
Chapman and Lewis (1976), and Scarsbrook et al. (2003) briefly summarised the
ecology of New Zealand groundwaters in which ostracods occur but which are
poorly known.

The podocopids and platycopids from the shallow intertidal to outer shelf
have been the most intensively studied ostracods because they are also the most
accessible (e.g. Morley & Hayward 2007). As mentioned above, ostracods are
useful for environmental monitoring. They are sensitive to small changes in
salinity and water quality and respond negatively to pollution. One study of a
New Zealand waste outfall has shown the effects of sewage on a coastal ostracod
fauna (Eagar 1999).
The planktonic mydociops, which require specialist zoological knowledge, has been treated in monographs by Poulsen (1962, 1965) and Kornicker (1975, 1979) and in research studies by Deevey (1982). The first halocyprids were not recorded until Barney (1929). This group, together with the deep-sea podocypids, had received the least attention, but the recent study by Jellinek and Swanson (2003) has significantly increased knowledge of the latter.

Fossil species have followed a similar pattern of study. The earliest paper was by Jones (1860) on some tertiary species from Orakei. A bulletin by Chapman (1926) was issued by the New Zealand Geological Survey for Cretaceous and Tertiary species, but he used European names. His records are therefore not explicitly included in the following checklist, but the species are probably still represented there as synonyms of other workers’ identifications. Benson (1956) recorded the occurrence of ostracods in late Middle Cambrian rocks from New Zealand, based on F. H. T. Rhodes’s identification of their remains in a limestone. The preservation did not permit accurate identification. Simes (1977) recorded a phosphatic or phosphatised specimen from the limestone of the Upper Cambrian Anatoki Formation, and silicified ostracods were recorded by Marden et al. (1987) from the Triassic (Norian age). No other records whatsoever are available for any specimens from the Ordovician to the Jurassic.

Good fossil faunas are now known from sediments of Cretaceous age at several localities and these have been published recently (Dingle 2009). There have been a large number of papers on the systematics and palaeoecology of New Zealand region Tertiary Ostracoda from the mid-1950s onwards (Swanson, 1969; Ayress 1990, 1991, 1993a, b, c, 1995, 1996; Ayress & Warne 1993; Ayress et al. 1994, 1995, 1997, 1999; Ayress & Drapala 1996). These faunas are rich, easily obtained, and interesting as they can be tied into other palaeontological work. Most of the ostracod species in the end-chapter fossil checklist are therefore Tertiary species. The first publications to illustrate New Zealand ostracods using scanning electron microscopy came later (Swanson 1979a, b, 1980). The end-chapter checklist following builds on the one published by Eagar (1971).

Features of the New Zealand ostracod fauna
Many Cenozoic marine species are endemic, long-ranging, and even still living. Presuming that they have not evolved a tolerance to changed ecological conditions, it can be assumed that the paleoeviromental conditions in which they lived were the same as now. Of particular interest are species of the endemic living-fossil genera Manawa and Puncia (Punciidae). Similar in shape and ornamentation to some Paleozoic genera, they are found living in shallow water off the north and east coasts of New Zealand. They provide insight into the soft-part anatomy of a group of ostracods (order Palaeocopida) that has otherwise been extinct for a long time (Hornibrook 1963; Swanson 1990; Horne et al. 2005).

Freshwater species are rare as fossils. Many species are swamp- or pond-dwellers and are not found on lake margins; inasmuch as ostracod shells are very soluble in the acid conditions of swamp deposits, their chances of preservation there are small. Further, most of New Zealand was submerged by the Late Oligocene and there were relatively few lakes, along with limited means of dispersal, available in the geological past (Hornibrook 1955; Eagar 1995a). Once colonisation from Europe was established, trout, salmon, and carp were introduced from Europe via Australia and it is likely that ostracod eggs travelled as hitchhikers to New Zealand on the damp media used to transport the fish (Eagar 1994). There is one non-marine saline species – Diaecypris thomsonii (see Bayly & Williams 1973) – from Sutton, Otago, in salinity conditions of up to 15 parts per thousand. Guise (2001) discovered in the Avon-Heathcote Estuary, Christchurch, a new endemic genus of brackish-water ostracod (Swansonella) that tolerates higher salinities.
There are now more opportunities for introducing ostracods into New Zealand. Resting eggs that can withstand desiccation may even be transported by aircraft on footwear and camping gear. In addition to European freshwater species, several other species have an Australasian distribution. One marine species discovered close to shipping ports in the North and South Islands may have been brought in ballast water (Eagar 1999).

Few studies have been made of the anatomy of New Zealand ostracods. These were mostly on myodocopids (Poulsen 1962, 1965, Kornicker 1975, 1979) and to a lesser extent to the freshwater species (Podocopida: Cyprididae) (Chapman 1963; Eagar 1995b; Rosetti et al. 1998), with a few ventures into the marine podocopids (e.g. Brady 1902; Swanson & Ayress 1999).

Class Malacostraca

This class contains more than half of all known species of crustaceans, including the aristocrats – the giant spider crabs of Japan with their 3-metre leg span (vying with fossil eurypterids as the largest of all arthropods) and the New Zealand packhorse rock-lobster (*Sagmariasus verreauxi*) at 20 kilograms – and krill, one of the most ecologically critical malacostracans in marine food webs, slaters, and tiny sand-hoppers. Malacostracans are very unevenly divided into three subclasses – Phyllocarida, Hoplocarida, and Eumalacostraca.

Subclass Phyllocarida: Phyllocarids

Order Leptostraca

The Leptostraca is the sole living order of the Phyllocarida, a group of Crustacea with a long geological history (Rolfe 1969), possibly extending back as far as the Cambrian, some 600 million years ago (Briggs 1992). Despite new conclusions from DNA analyses as to their place in crustacean evolution (Spears & Abele 1999), the Leptostraca may still be regarded as ‘living fossils’ indicative of the times and conditions in which the so-called primitive arthropods lived (Hessler & Schram 1984; Dawson 2003b). They are known from the New Zealand Ordovician (Chapman 1934), and the presence of several living species of Leptostraca in the region is of considerable interest. Using the small-subunit 18S ribosomal-DNA gene of 10 representative foliaceous-limbed Crustacea, Spears and Abele (1999) concluded that the Phyllocarida are true malacostracans, which diverged fairly early from the main lineage. This result is consistent with the pioneer work of Claus (1888) and Calman (1909) and with Manton’s (1934) study of embryology, and also corroborates the views of Dahl (1987, 1991) of the Leptostraca as an early offshoot.

The late British zoologist Sir Alistair Hardy (1956) vividly recalled the excitement of his first encounter with one of the little crustaceans, *Nebaliopsis typica*, found in great depths but rarely collected, and then usually dead and very damaged. It had only ever been seen alive on one occasion – on the Swedish Antarctic Expedition in 1904 – until a second specimen was collected from the *Discovery II* fifty years later. The Leptostraca, wherever they have been found subsequently, have continued to excite and interest zoologists and paleontologists alike.

A paleontological summary of the Phyllocarida was made by Rolfe (1969). Monographs on the Leptostraca as a whole have been made by Claus (1888) and Cannon (1960), and these still have their usefulness, but a new and compact text has been produced (Dahl & Wägele 1996). More recently, the relationships of the leptostracan genera were examined by Olesen (1999) and by Walker-Smith and Poore (2001), who revised the families and genera. The latter authors also provided a complete listing of all species of Leptostraca together with keys to the families and genera. Some 42 species of living Leptostraca are recognised.
at present, divided into three families – Nebaliopsidae (genera *Nebaliopsis*, *Pseudonebaliopsis*), Paranebalidae (named only in 2001, containing *Paranebalia*, *Levinebalia*, and *Saronebalia*), and Nebaliidae (with five other genera). Many species of *Nebalia* and *Paranebalia* remain undescribed as yet (Dahl & Wägele 1996).

Leptostracans are small, usually 4–12 millimetres in length although one species, *Nebaliopsis typica*, can exceed 35 millimetres. They are characterised by the possession of a relatively large, bivalved carapace, hinged on the midline and held together by an adductor muscle. The carapace loosely covers the abdomen and part of the thorax, and is attached by a hinged rostral plate covering the head and closing the anterior gap of the carapace itself. Long anteriorly projecting antennae are used for swimming, the antennal flagellum in males being as long as the body. There are eight pairs of foliaceous, leaf-like thoracic limbs that also provide a feeding mechanism and may be modified in the female in the form of a fan of plumose setae forming a basket-like chamber for brooding eggs between the ventral regions of the valves of the carapace. The first four pairs of pleopods are well developed and biramous whereas the 5th and 6th pairs are small and uniramous. The abdomen ends in two characteristic long and articulated tail spines or furci. In contrast with all the six abdominal segments possessed by all other Malacostraca, the Leptostraca have a 7th segment and this lacks any appendages. The telson may be considered an 8th segment.

Relatively little is known of the life-history, growth rates, or physiology of most leptostracans. Useful observations have been made by Cannon (1927), Rowett (1943, 1946), Martin et al. (1996), Vetter (1996a), and Wägele (1983). Manton (1934) worked on the embryology of *Nebalia bipes*, helping to elucidate phylogenetic relationships of the Phyllocarida (Dahl 1987; Spears & Abele 1999). Linder (1943) described some larval stages, which could be useful for recognition in sorting plankton samples. Leptostracans play a significant role in benthic production (Rainer & Unsworth 1991; Vetter 1996a,b; MacLeod et al. 2007). The unusual marine rotifer *Seison* is often found epizoic on leptostracans. None has yet been discovered in New Zealand but it would be worth checking local *Nebalia* to ascertain their presence or absence.

Leptostracans are widely distributed as a group. Individual species may be limited or widespread in depth range and geographically, but taxonomic caution needs to be observed in the case of the purportedly wide-ranging species. Dahl’s (1990) analysis of the *Nebalia longicornis* complex showed that it comprised at least 10 different species. Walker-Smith (1998) reviewed the genus *Nebaliella*, describing the first known Australian species. In her unpublished Honours thesis, she recognised six new species and a new genus of Leptostraca from Australia (Walker-Smith pers. comm. 2000).

Present-day leptostracans live in a variety of habitats, including under intertidal stones, with decaying seaweed or dead shell, in crab pots, on mangrove shores and coral reefs, and in subtidal sandy plains or muddy sand. A non-New Zealand species, *Speonebalia cannoni*, is the only leptostracan to be recorded from a groundwater habitat. *Nebalia hessleri* lives in enriched sediments and detrital mats with low oxygen levels in submarine canyons off southern California. Here they form the highest density ever reported for a macrofaunal assemblage, namely 1.5 million per square metre. In northwestern Spain, Moreira et al. (2009) reported six species of leptostracans in subtidal sediments, the largest number of species recorded in a single area. *Dahlella caldariensis* occurs among mussels and vestimentiferan worm tubes, swimming above clumps of animals at hydrothermal vents.

The New Zealand leptostracan fauna

The New Zealand fauna currently consists of five species in four of the 10 known genera. Unfortunately, little is known of the true numbers of taxa represented in
The first to be recorded and named in New Zealand was *Nebalia longicornis*, based on a single mature male collected in Otago Harbour (Thomson 1879a). It was subsequently described in more detail, based on records from 8–10 metres depth in Dunedin Harbour and 20 metres at Stewart Island (Thomson 1881). This later paper by Thomson (with its slightly different figure) appears to have been overlooked by all subsequent authors. *Nebalia longicornis* was inadequately described and illustrated according to Dahl (1990), and great taxonomic confusion subsequently resulted from attempts to apply this name to later records of *Nebalia* from other parts of the world. Since Thomson's type specimen could no longer be found, Dahl redescribed the species based on a female collected from Otago Harbour in 1965, thereby fixing *Nebalia longicornis* Thomson, 1879a as a member of the New Zealand fauna. Thomson (1913) noted his *Nebalia longicornis* as found in Otago Harbour and frequently taken outside the Otago Heads in trawl-nets.

Thiele (1904) reported a specimen of what he considered to be *Nebalia longicornis* from Akaroa Harbour. Dahl (1990) examined this specimen and found it to be a species of *Nebalia* (then in his genus *Sarsinebalia*) but in too damaged a condition to be able to describe further. Thiele had also recorded juvenile *Nebaliella antarctica* from Akaroa Harbour but apparently this specimen has not been re-examined.

In 1907, W. Benham collected a juvenile *Nebalia* from Musgrave Harbour on the Auckland Islands that Chilton (1909) attributed to *N. longicornis* as then understood. Another specimen was taken at Port Ross, Auckland Island, in 1914 during the Mortensen Expedition (Stephensen 1927). Calman (1917) reported two immature specimens of Leptostracá collected in 1911 at Terra Nova Stations 130 and 135 off Three Kings Islands and in Spirits Bay [given incorrectly by Dahl (1990) as Stns 10 and 15]. Dahl (1990) has since examined these specimens, concluding that one is a *Nebalia* and the other a *Sarsinebalia*.

Morton and Miller (1968) described a *Nebalia* as a member of the protected sandy-beach fauna, one of the small filter-feeding Crustacea that live in the fine sands of the lower beach. They also illustrated it as the prey of the small shallow-water cephalopod *Sepioloida pacifica*.

The only other work on New Zealand leptostracans has been the description of *Levinebalia fortunata* (Wakabara 1976, as *Paranebalia*) based on 16 females collected by trawl nets at 420–660 metres depth in canyons off Otago Peninsula, representing a marked extension to the known bathymetric range of the genus. Apart from Prof. John Jillett at Otago (see Dahl 1990) no-one has conscientiously searched New Zealand habitats for leptostracans. It is likely that deliberately intensive collecting will reveal not only great extensions of the range of the already listed forms but undescribed species as well. Morton (2004) suggested searching for leptostracans in black anaerobic sediments with decaying algae and carrion-baited traps may also be useful (Lee & Morton 2005), especially for assessing population densities.

Chapman (1934) described several species from Ordovician rocks in Fiordland, based on numerous specimens. They have never been studied since and are listed in the end-chapter checklist of fossil New Zealand Crustacea under the generic names recommended by Rolfe (1969).

### Subclass Hoplocarida

#### Order Stomatopoda: Mantis shrimps

Mantis shrimps are among the most aggressive and behaviourally complex crustaceans. All are active predators and mark one of the very few radiations of obligate carnivores within the Crustacea. The general morphology of mantis
shrimps has been described by Holthuis and Manning (1969), and characteristic features are the triflagellate antennules, well-developed stalked eyes, and the greatly enlarged, raptorial second maxillipeds. The name mantis shrimp stems from these large and powerful raptorial claws. Prey is captured by ‘spearing’ or ‘smashing’, depending on whether the dactyl of the raptorial claw is extended or kept folded during the strike. (Think of the dactyl as a finger, opposing the thicker ‘thumb’ of the claw.) Hence the two modes of prey-capture define the ‘smashers’ and the ‘spearsers’ among mantis shrimps (Caldwell & Dingle 1976). The strike of the raptorial claw is among the fastest known of animal movements, being completed in 3–5 milliseconds, and the strike of large species of ‘smashers’ may break aquarium glass.

Vision in mantis shrimps is strongly developed. In most species, the cornea is divided into two halves by a midband of ommatidia, enabling binocular vision with each eye. Additionally, the midband ommatidia in many families enable colour vision and detection of polarised light (Marshall 1988).

Most stomatopods live in temperate or tropical shallow marine habitats, but several species also range into subantarctic waters, and a few tropical species may occur in brackish water. Seven superfamilies are recognised: Bathysquilloidea, Erythrosquilloidea, Eurysquilloidea, Gonodactyloidea, Parasquilloidea, Lysiosquilloidea, and Squilloidea. Most members of the Gonodactyloidea occur on coral reefs where they shelter in or under boulders and coral. The bathysquilloids are known only from deep outer-shelf waters. Members of other superfamilies generally burrow in flat sandy and muddy harbour bottoms and sea-floors.

The Stomatopoda comprises the only living order of Hoplocarida, two other orders (Aeschronectida and Palaeostomatopoda) being known only as fossils. Compared with other major crustacean groups such as the Decapoda, the fossil record of the Hoplocarida is relatively poor but it appears that the hoplocarids originated in the Devonian and the Stomatopoda proper first appeared during the Carboniferous. Recognisably modern stomatopods, with well-developed raptorial claws, did not appear until the Mesozoic (Holthuis & Manning 1969; Hof 1998; Hof & Schram 1998).

Over the past three decades, the taxonomy of the Stomatopoda has been extensively revised, largely through the work of the late R. B. Manning, who recognised five living superfamilies (Manning 1995). Ahyong and Harling (2000) provided the most recent phylogenetic study. At present, more than 450 species in more than 100 genera, 19 families, and 7 superfamilies are recognised.

The stomatopods of the Atlantic have been monographed and are well known (Manning 1969, 1977), while those of the eastern Pacific were treated relatively comprehensively by Schmitt (1940) and Hendrickx and Salgado-Barragán (1991). Stomatopod diversity in the Indo-West Pacific region, however, is more poorly known. The most important major works for this region are those of Kemp (1913) on the Indian fauna, Manning (1995) on the Vietnamese fauna, and Ahyong (2001) on the Australian fauna. The Indo-West Pacific fauna has been extensively studied in the past decade (e.g. Ahyong 2002a,b,c; Ahyong & Naiyanetr 2002; Ahyong et al. 2008).

The New Zealand fauna

New Zealand’s mantis shrimps are known from only a few studies, the most important of which are those of Miers (1876), Chilton (1891, 1911a) and Manning (1966). Manning (1966) recognised three species from New Zealand and its offshore islands: *Pterygosquilla schizodontia*, *Heterosquilla tricarinata*, and *Acaenosquilla brazieri* (as *Heterosquilla brazieri*). He also remarked that *Squilla tridentata* Thomson, 1882, synonymised with *H. tricarinata* by Chilton (1891), was probably a distinct species. Ahyong (2001) recognised Thomson’s species as distinct under the combination *Heterosquilla tricarinata*. Other additions to the...
New Zealand stomatopod fauna are *Hemisquilla australiensis* (Stephenson 1967), *Odontodactylus brevirostris* (Manning 1991), and the striking 30-centimetre-long, scarlet deep-sea species *Bathysquilla microps* (O’Shea et al. 2000). Therefore, seven species are presently recorded from New Zealand.

The commonest species are *Heterosquilla tricarinata* (known around both main islands and Chatham, Stewart, Campbell, and Auckland Islands, generally in intertidal sand or mudflat burrows) and *Pterygosquilla schizodontia* (central New Zealand to the Auckland Islands, burrowing in subtidal sand and mud). Their biology has received little scientific study. Larval development of *Pterygosquilla schizodontia* was studied by Pyne (1972). Several studies have been conducted on *H. tricarinata* including those of Fussell (1979), Greenwood and Williams (1984), and Williams et al. (1985).

The New Zealand stomatopod fauna is relatively small, and this is consistent with the primarily tropical distribution of most species. Nevertheless, low diversity may also reflect low collecting effort. Study of collections from northern island groups in New Zealand territorial waters should reveal numerous additional faunal records. The Japanese mantis shrimp *Oratosquilla oratoria* has become established in some North Island estuaries and is the first exotic species of Stomatopoda to be detected in New Zealand waters. New species and numerous additional distribution records will be reported in a forthcoming review of the New Zealand Stomatopoda by Shane Ahyong.

**Subclass Eumalacostraca**

**Superorder Syncarida**

*Orders Anaspidacea, Bathynellacea*

The Syncarida constitutes a group of tiny crustaceans that may be regarded as living fossils, with a geological history extending as far back as the Carboniferous (Dover 1953; Drummond 1959; Brooks 1969; Schram & Hessler 1984; Uhl 1999, 2002; Jarman & Elliott 2000; Dawson 2003a). They are little known to most biologists, the exception being the large-sized *Anaspides*, found in Tasmania, which has attracted much interest and attention largely because of its accessibility in open waters rather than the subterranean habitat in which most syncarids live.

The Syncarida were first made known to science by the report of a fossil species, *Uronectes fimbriatus*, in Europe. Their relationships and place in the crustacean hierarchy remained a matter of contention until Packard (1885, 1886) gave them separate status as the Syncarida. Much later, Brooks (1962, 1969) finally settled the status of the fossil as one of three orders constituting the superorder Syncarida, and Schminke (1975) related them to the living orders. Schram (1984) subsequently reviewed and revised the fossil species, which range in time from the Early Carboniferous (Uhl 2002) to the Early Permian in Europe and North America, the Late Permian of Brazil, and the Triassic of Australia, corresponding to the former landmass of Laurentia prior to the formation of Pangaea.

New Zealander George Malcolm Thomson, a noted amateur scientist, teacher, and politician, is generally credited with the discovery and description of the first living syncarid—*Anaspides tasmaniae*, which he discovered when visiting Tasmania in January 1892. He was of the opinion that his discovery was a schizopod shrimp (Thomson 1894). However, Calman (1896) said this new crustacean was no schizopod and supplemented Thomson’s description in some detail, comparing *Anaspides* with fossils from Illinois and Germany that Packard (1885) had already placed in his new group, Syncarida. Calman concluded that *Anaspides* was, in fact, a living representative of primitive malacostracans that had flourished widely in Paleozoic times.

Ironically, however, living syncarids had in fact been discovered some years previously when Vejdovský (1882, 1889) published a description of the tiny *Bathynella* that he had found two years earlier in a well in Prague. Calman (1899)
subsequently recognised *Bathynella* as a syncarid, but little more was known until 1913 when Chappuis (1915) found more specimens in a well near Basle. He placed them in a new taxon, Bathynellacea. Syncarids were soon found to occur in many places throughout Europe, in wells, springs, or streams in caves (Chappuis 1939) as well as in Australia, New Zealand, Japan, North and South America, and elsewhere.

Although Thomson turned out not to be the first discoverer of a living syncarid, the finding of such an ancient form of crustacean living in Tasmania did excite many subsequent workers (up to the present day), resulting in a substantial number of publications on aspects of their morphology, development, ecology, and relationships – and even a poem in the style of Longfellow dedicated to *Anaspides* (Mesibov 2000). In essence, there have been two approaches to the study of the Syncarida, one concentrating on the relatively tiny subterranean and interstitial forms (basically the order Bathynellacea), and the larger, open-water taxa of Australia (order Anaspidacea, which also includes the subterranean Stygocarididae). General accounts of the Syncarida can be found in Siewing (1959), Noodt (1964), McLaughlin (1980), Schminke (1982), Schram (1986), and Coineau (1996, 1998).

Within the Eumalacostraca, the Syncarida are distinguished by the absence of a carapace, an elongate body form (more or less cylindrical in the subterranean forms), with a thorax consisting of seven or eight segments, the first segment being fused to the head in some groups. The abdomen consists of six segments and a telson, or five segments followed by a pleotelson formed from the fusion of the 6th segment with the telson.

The order Anaspidacea contains four families: Anaspididae, Kooningidae, Psammaspididae, and Stygocarididae. Only the last of these has been found in New Zealand. They include the largest of the syncarids, with a body length ranging from about 1 to 50 millimetres. The Bathynellacea contains two families, the Bathynellidae and the Parabathynellidae, which are both represented in the New Zealand fauna as it is presently known. They are very much smaller in size than the anaspidaceans, ranging from about 0.4 to 3.5 millimetres.

The body form of syncarids is reflected in the habitats in which they are found: the tiny forms, with slender, cylindrical bodies, devoid of pigment and eyes, are found in caves and underground waters, whereas the much larger forms, such as *Anaspides*, found in surface waters are shrimp-like.

Living syncarids comprise more than 200 species worldwide (Camacho & Valdecasas 2008), although fresh explorations and more refined collecting techniques are already increasing this number. There are many species of syncarids collected from eastern Australian caves and karst areas awaiting identification and description (Thurgate et al. 2001) and such may be the case for New Zealand.

Syncarids have the reputation of being rare animals, although the pioneer investigations by Chappuis (1943) on *Bathynella* in Hungary showed that numerically rich collections could be made at individual sites. Much of the alleged rarity is a consequence of their small size (which is why early investigators in New Zealand such as Chilton did not find them) and their largely subterranean habits. Schminke (1986) has said that those who know how to sample their habitats ‘today have lost the impression of dealing with rare animals.’ Syncarids are globally widespread; Schminke (1986) listed all the species then known, with their locations. New taxa continue to be described Camacho 2005a,b; Cho 2005; Cho et al. 2005, 2006; Camacho et al. 2006; Cho & Schminke 2006).

While some Syncarida inhabit open- and surface-water habitats (Camacho & Valdecasas 2008), it is acceptable to say that syncarids are characteristic of subterranean habits throughout the world, whether groundwater (as revealed by sampling wells, springs, and gravel river margins), or caves with streams and sandbanks providing living space in the interstitial spaces between sediment grains.

Syncarids have been recorded from springs in Australia (Knott & Lake

---

*Stygocaris townsendi.*

From Scanbrook et al. 2003
(1980), and in New Zealand they occur in similar situations as well as from groundwater in wells (Scarsbrook et al. 2003), just as did the first-discovered European living syncarids. Many syncarids have been collected from caves, although in New Zealand only *Stygocaris townsendi* has been described from such a habitat (Morimoto 1977). Karst landscapes throughout the world provide habitats for syncarids.

Information on the development, life-history, and habits of syncarids is still quite limited. So far as the Anaspidacea are concerned, most of the developmental studies have been done on *Anaspides tasmaniae*, by Hickman (1937), with other aspects covered in other studies, for instance Dohle (2000). The biology of bathyneillaceans is less well known, but what is known has been summarised by Coineau (1996). In feeding, *Anaspides* has a filtering mechanism, used in conjunction with collecting particles by scraping detritus with its limbs. Smith (1908) noted that *Anaspides* was an omnivorous feeder, eating dead insects as well as each other, but mainly feeding on algal slime and submerged mosses and liverworts. The habitat of Tasmanian anaspidaceans, notably *Allanaspides hickmani* and *A. helonomus*, is under continuing threat (Driessen et al. 2006).

Compared to the amount of information regarding the general biology and ecology of the anaspidacean syncarids, there is virtually nothing recorded about the lifestyle and habits of the bathynellaceae. What is known has been summarised by Coineau (1996), and Camacho (1992) has outlined the abiotic characters of the subterranean environment in which most of bathynellaceans live.

Camacho (2006) noted 256 species and subspecies of extant Syncarida, 95% of which are subterranean in habitat. In addition to the two living orders is the order Palaecaridacea, which is entirely fossil.

The order Anaspidacea comprises five families, of which three are confined to Australia. These include: Anaspididae, with five genera – *Allanaspides*, *Anaspides*, *Paranasaspides*, *Anaspides* (Triassic, Australia), *Koonaspides* (Lower Cretaceous, Australia); Koonungidae, with two genera – *Koonunga*, *Micraspides*; Psammaspididae, with two genera – *Eucrenonaspides*, *Psammaspides*; and Stygocarididae, with four genera – *Oncostygocaris* (Chile), *Parastygocaris* (Argentina), *Stygocarella* (New Zealand), and *Stygocaris* (Australia, New Zealand, Chile). The 21 living species of Anaspidacea are confined to the Southern Hemisphere. *Anaspides tasmaniae* is of particular interest in the context of mitochondrial DNA studies, in which it has been demonstrated that there may be at least three cryptic species (Jarman & Elliott 2000).

The order Bathynellacea comprises two families, both distributed widely throughout the world, totaling 66 genera an 219 species: Bathynellidae, with more than 20 genera (including *Bathynella*, of which there are New Zealand representatives) and more than 80 described species, and Parabathynellidae, with about 32 genera and more than 90 species (also recorded from New Zealand in the genera *Atopobathynella*, *Hexabathynella*, and *Notobathynella*). As discussed by Camacho et al. (2002), there have been two contrasting views as to the systematic position of the bathynellids as being either within the superorder Syncarida or as a separate suborder Podophallocarida in infraorder Eomalacostraca. These Spanish researchers’ molecular studies in Spain on a cave-dwelling bathynellid, *Iberobathynella* (*Espanobathynella*) *magna*, have now provided a nucleotide sequence that supports a basal position for the Bathynellacea with a clear distinction from the Syncarida, placing them in the Podophallocarida but retained in the Eumalacostraca.

Schminke (1986) postulated that the Syncarida originated in the marine environment from whence they invaded freshwater by two independent lines, living first in surface waters and then invading the groundwater habitat. He developed the ‘zoea’ theory (Schminke 1981b) in which it was suggested that the Syncarida originally passed through a series of larval stages and through neoteny reached sexual maturity at a stage corresponding to the zoea larva of...
the penaeid prawns (Decapoda). Schminke (1972) had previously demonstrated, by a study of all the then-known species of *Hexabathyrella* (but which did not include the subsequently discovered *H. aotearoae* of New Zealand), all of which were known to occur close to the sea, that syncarids did not invade the freshwater interstitial habitat from sandy marine beaches. Presumably, some of the more recently discovered occurrences of *Hexabathyrella aotearoae* indicate secondarily derived habitats. This species is closest evolutionarily to Australian *H. halophila* (Camacho 2003).

Biogeographically, the breakup of the ancient supercontinent Gondwana has been invoked to explain some of the distributions between northern and southern hemispheres and within the austral landmasses (Schminke 1973, 1974, 1975, 1980, 1981a; Williams 1986). Subsequent information about the distribution and phylogeny of the various syncarid groups can be found in Coineau (1996), Camacho and Coineau (1989), Camacho et al. (2000), and Guil and Comacho (2001).

The New Zealand fauna
In 1967 and 1968, visiting German scientist Kurt Schminke searched for syncarids quite widely throughout New Zealand, taking almost 200 samples from interstitial freshwaters at 11 different localities (Schminke & Noodt 1968; Schminke 1973). Of these, 36 yielded syncarids in the families Bathynellidae, Parabathynellidae, and Stygocarididae. In his unpublished thesis, Schminke (1971) included two new forms of *Bathynella*, a species and its subspecies (as yet not formally described), collected from the Tauherenikau River in the Wairarapa and from the Orari River in South Canterbury. In his major work on the evolution, taxonomy and biogeography of the world fauna of the Parabathynellidae, Schminke (1973) listed his collecting locations in New Zealand with descriptions and distribution maps of four new species from New Zealand: *Atopobathyrella compagana*, *Hexabathyrella aotearoae*, *Notobathyrella chiltoni*, and *N. hineoneae*.

Schminke (1978) subsequently reported on a collection, made by by G. Kuschel of the former DSIR Entomology Division, which included a female bathynellid from a bore in Nelson, and two females of *Notobathyrella*. He also noted two more specimens of *Atopobathyrella compagana* and described *Notobathyrella longipes* from wells at Motueka. In the Anaspidacea, Schminke (1973) mentioned at least three unidentified New Zealand species of Stygocarididae in one new genus, later describing *Stygocarella pleotelson* (Schminke 1980) and noting 16 localities from which other unidentified specimens had been collected. During a brief trip to New Zealand in 1975, Morimoto (1977) collected syncarids at four South Island locations, finding three species of *Stygocaris*, of which *S. townsendi* was described as new. More recently, in a NIWA study of the New Zealand groundwater fauna (Scarsbrook et al. 2000), syncarids appeared to be widespread in interstitial habitats in alluvial groundwaters in Hawkes Bay and Canterbury, both within the margins of gravel riverbeds and in the deeper (10–20 metres) ground water.

Thus, the New Zealand syncarid fauna, as presently known from limited sampling, consists of at least four species of Anaspidacea – *Stygocaris*, and one or possibly more species of *Stygocarella*. The Bathynellacea is represented by what appear to be quite abundant and widespread species of Bathynellidae (*Bathynella*), none formally described, and three genera of the Parabathynellidae – *Atopobathyrella* and *Hexabathyrella* (each with one described species), and *Notobathyrella* (at least four species, three of them named). It is highly likely that the New Zealand syncarid fauna will be found to be much more extensive, if only in terms of the distribution of the already described species, all of which are endemic.

Gaps in knowledge of Syncarida
Not only is taxonomic knowledge of the New Zealand Syncarida incomplete; even less is known about their ecology and special adaptations to the several
kinds of habitats in which they occur. It is apparent that a geographically widely distributed syncarid fauna exists in New Zealand’s ground waters. The brief venture into cave collecting by Morimoto (1977), taken with what is known of the distribution of syncarids in Europe and Australia, suggests the prospect of further exciting discoveries locally in this particular habitat. Cave systems and karst-type landscapes with sink holes and sunken streams are common in many parts of New Zealand (Crossley et al. 1981), and there is a very strong fraternity of recreational cavers, some of whom have already contributed to scientific knowledge of cave life. There is a real challenge to use the technical expertise of such people to look for these fascinating ‘living fossils’; a preliminary guide to promote such work was issued by the New Zealand Department of Conservation (Hunt & Millar 2001). The results of a 15-year study of Spanish cave fauna by Camacho (2000) shows what could be achieved by a systematic approach towards elucidating New Zealand’s subterranean syncarid fauna.

There is a growing appreciation worldwide of the importance of groundwater organisms as environmental indicators of water quality, not to mention the scientific interest of these organisms in their own right (Danielopol 1992; Marmonier et al. 1993; Danielopol et al. 2000; Gibert et al. 1994; Jones & Mulholland 2000; Scarsbrook et al. 2000, 2003) and the need to understand karst landscapes and their fauna from a conservation perspective (William & Wilde 1985) and cave life in general (Vandel 1964; Ford & Cullingford 1976; Sasowsky et al. 1997; Culver 1982; Camacho 1992; Juberthie & Decu 1994–2001). ‘Living fossils’ carry appealing overtones in the public imagination (Dawson 2003a), so the demonstration of the existence even of such tiny forms as the syncarids could be another highlight to make known.

Orders Lophogastrida and Mysida (‘Mysidacea’): Opossum shrimps

The Mysidacea are shrimp-like but have a number of characters, including a ‘brood pouch’, that distinguish them from other crustaceans of similar appearance. They are mainly marine, living in all oceans from great depths to brackish coastal waters, and there is a small number of freshwater species. They are of limited commercial importance and therefore not as familiar as the decapod shrimps and prawns. Mysidacea may, however, be very common, particularly in estuaries and coastal waters, where they often congregate in large swarms, and are of considerable importance as primary consumers and as food of fishes.

Historically, the Mysidacea comprised a single order with two suborders – Lophogastrida and Mysida. The two groups differ in important ways and there is now debate over whether they are mono- or polyphyletic (having one, or more than one, ancestor). Some workers question whether the Mysida, which contains the great majority of Mysidacea, even belongs in the large malacostracan superorder Peracarida, with the Lophogastrida; see Martin and Davis (2001) for a discussion of mysid classification. These authors discarded the Mysidacea, raising the two suborders to ordinal status, a decision followed here. Even so, the two groups have many characters in common and, since relatively few species (24) have been recorded from New Zealand waters, are discussed here collectively.

Historical studies

Mysidacea have been recognised since the late 18th century. The taxonomic literature is scattered and deals mostly with northern hemisphere faunas and least with that of the Indian Ocean and Australasia. Major contributors include Tattersall and Tattersall (1951), Gordan (1957), Mauchline and Murano (1977), Mauchline (1980), and Müller (1993).

The history of New Zealand mysidacean taxonomy is brief. The first published record is that of Thomson (1880), who described Siriella denticulata.
Kirk (1881) described *Mysis meinertzhagenii*, but the type and further evidence of its existence have not been found since. Thomson (1900) described *Tenagomysis novazealandiae* from brackish water near Dunedin, and Calman (1908) attributed an immature mysidacean specimen to the genus *Pseudomma*, apparently not identified since. *Tenagomysis tenuipes* Tattersall, 1918, from Carney Harbour, Auckland Islands, brought the early list of mysidaceans known with certainty to occur in New Zealand to three. Next, Walter Tattersall’s (1923) report on the Mysidacea of the 1910 *Terra Nova* Expedition to Antarctica and the Southern Ocean added 12 species. Eight were new, seven of which belonged to *Tenagomysis*, and the remaining species was named *Gastroscus australis*, the first and so far only named species of the genus from New Zealand. New records for New Zealand of previously described species of Mysida included *Euchaetomera oculata, E. typica*, and *Siriella thompsoni*. Chilton (1926) presented an overview of New Zealand Mysidacea to that date. Later, Olive Tattersall (1955) identified *Boromysis rostrata* and *Euchaetomera zurstrasseni* from New Zealand waters and Hodge (1964) redescribed *Tenagomysis chilonti*. The most recent addition to the fauna was that of *Tenagomysis longosquama* (Fukuoka & Bruce 2005).

Walter Tattersall (1923) appears to be the first to have recorded a species of Lophogastrida, *Paralophogaster glaber*, in New Zealand. Apart from a record of *Lophogaster sp.* from Te Papa (Museum of New Zealand) collections, the remaining records are from Fage (1941) reporting on mysidaceans caught by the 1928–30 *Dana* Expedition, all in the family Gnathophausiidae: *Gnathophausia elegans, G. zoa, Neognathophausia ingens*, and *N. gigas*.

Clearly there are more mysidacean species to be described from New Zealand. Small numbers of specimens have been collected, with most material in New Zealand held at the University of Otago and Auckland University of Technology (Jocqué & Blom 2009).

**Morphology, species, and endemism**

The carapace is well developed in Mysidacea and covers the thorax, as it does in euphausiids and decapod shrimps, but is fused with the anterior three or four thoracic segments only; the back of the carapace can simply be lifted to expose the posterior four or five thoracic segments. They have a shrimp-like abdomen with fully developed or reduced pleopods, and the telson and paired uropods form a tail fan. Mysidacean eyes are compound and stalked although in a few deep-water species they are reduced to immovable plates. The antennules are always biramous and most have an antennal scale. Of the eight pairs of thoracic appendages, the first one or two are modified as maxillipeds. The remaining six or seven pairs form legs and generally bear swimming exopods. A feature of female mysidaceans is their large leaf-like oostegites, on the inner side of some or all of the legs, which overlap to form a brood chamber or marsupium (recalling the name opossum shrimp) beneath the thorax, in which eggs are laid and the young develop. Both orders have all these characters in common.

In the Lophogastrida, however, gills are present on some or all of the legs, pleura (‘side plates’) are present on the abdominal segments, and the pleopods are well developed and usually unmodified in both sexes. Lophogastrids also have seven pairs of oostegites but lack statocysts in the endopods of the uropods. All species of Lophogastrida live offshore in meso- and bathypelagic habitats, with many being hyperbenthic (living close to the bottom) in deep water. The largest mysidaceans belong to this order and most occur throughout the world’s oceans but are less often seen than species of Mysida, because of their oceanic existence.

A characteristic of the Mysida (excluding all 33 species of the Petalophthalmidae) is the presence of a pair of balancing organs or statocysts, in the telson. Situated near the base of each uropodal endopod, statocysts are an obvious feature, distinguishing mysids from similar animals such as euphausiids (krill). Mysids also lack gills and the pleopods of females are reduced or rudimentary;
those of males are variously modified. Like the lophogastrids, many mysids have seven pairs of oostegites, but there are fewer pairs in some subfamilies of the Mysidae, including the Gastroscincinae, Mysinae, and Siriellinae, which between them contain 16 of the 18 species of Mysida recorded from New Zealand. Mysids occur throughout the marine environment to deep oceanic trenches but are particularly concentrated in coastal regions, and 24 species have colonised fresh waters around the world.

Adult Mysidacea range considerably in size from 2–3 to 350 millimetres long. The largest are in the Lophogastrida but most species belong to the Mysida and are appreciably less than 100 millimetres long. The few species recorded from New Zealand almost cover this range, with mature females of Tenagomysis macropsis as small as 3.2 millimetres long (Greenwood et al. 1985) and the largest of all mysideans, Neognathophausia gigas, also being recorded in New Zealand waters (Fage 1941).

Around 1000 species of Mysidacea have been described worldwide, the great majority in the order Mysida, with some 51 in the Lophogastrida. Twenty-four species have been recorded in New Zealand waters, representing both orders (see end-chapter checklist). Of the three lophogastrid families, the Eucopiidae are not yet known here. Of the four families of Mysida, two are found in New Zealand – the Pandalopthalmidae (one unnamed species) and Mysidae (all other species). Globally, this is a very large family, with ca. 870 species. Four of the six subfamilies occur in New Zealand.

As might be expected in a worldwide group inhabiting a wide diversity of habitats, endemism reflects distribution; no species of the oceanic order Lophogastrida is confined to New Zealand whereas endemism is high in species occupying coastal and littoral waters. Twelve of the 18 species (~67%) of New Zealand Mysida are endemic, including all 10 species of Tenagomysis (Müller 1993), but although the genus was first described from Otago (Thomson 1900) it is no longer restricted to New Zealand; five species are known from either Australian or African shores. While Siriella denticulata is endemic, S. thompsoni is cosmopolitan in its distribution, as one of a minority of epipelagic Mysidacea. The five non-endemic New Zealand Mysida are offshore species, the shallowest among them being Euchaetomera typica, another pelagic species, found between the surface and 380 metres. The distributions of the two unnamed species of Mysidacea are not known. Neither Petalophthalmus sp. from deep offshore water nor Lophogaster sp. in a typically oceanic genus is likely to be endemic.

**Ecology and distribution**

Distributional records of named New Zealand Mysidacea are, for the most part, far from comprehensive, although there are probably records of littoral species in unpublished environmental reports from various parts of the country. Apparently the only records of Paralophogaster glaber are those of Tattersall (1923) offshore of Cape Maria van Diemen and the Three Kings Islands in the far north. Te Papa collections indicate that Neognathophausia ingens is common around central New Zealand at least as far south as Banks Peninsula, N. gigas is present off the east coast of the North Island, and Gnathophausia zoea in the Bay of Plenty and on the outer Challenger Plateau west of Cook Strait. The deepest record of any of the mysidean species found in New Zealand waters is that of G. zoea, at 6050 metres (Müller 1993) at a non-New Zealand locality.

The majority of mysidean species are found on the inner shelf and in coastal and littoral areas and form an abundant component of estuary zooplankton. Many have very localised distributions and can form dense concentrations among rocks and algal beds. Ingles (1973) encountered Tenagomysis macropsis in high numbers in association with red algae in Pauatahanui Inlet. All 10 Tenagomysis species in New Zealand are coastal pelagic or littoral, and in some cases freshwater dwellers. Tenagomysis macropsis is widespread around New
Zealand, from Spirits Bay eastwards almost to the Chatham Islands (Tattersall 1923) and south to Foveaux Strait although the maximum recorded depth of the species is only 24 metres (Bary 1956). New Zealand’s southernmost species, *T. tenuipes*, is so far known only from Foveaux Strait and east of Stewart Island (Bary 1956), and from Carnley Harbour, Auckland Islands.

New Zealand has no strictly freshwater species but *Tenagomysis chiltoni* passes through its life-cycle in at least one completely freshwater locality – Lake Oturi, near Waverley, southwestern North Island (Hodge 1964). Thomson (1900) had originally collected *T. chiltoni* from fresh and saline waters in Otago. Jones et al. (1989) confirmed that this species also frequents saline waters in the Avon-Heathcote Estuary (Christchurch) but is an upper estuarine species and was seldom found in salinities greater than 20 parts per million (ppm). Chapman and Lewis (1976) reported *T. chiltoni* and *T. novaezelandiae* as living in brackish water below the *Paratya curvirostris* (Decapoda) zone in streams. Jones et al. (1989) indicated a salinity-correlated ecological separation between *T. chiltoni* and *T. novaezelandiae* in the Avon-Heathcote Estuary with the former in upper reaches and the latter mid- to upper estuarine. In this study and that of Greenwood et al. (1985), *T. macropsis* was found throughout the estuary and had no linear correlation with salinity range along a transect from 4.1 to 30.1 ppm. In his work in Pauatahanui Inlet, Ingles (1973) found distinct differences in distributions between three species in the Horokiwi Stream – *T. macropsis* occurred in the estuary proper, entering only the mouth of the stream, *T. novaezelandiae* centred around the mouth and lower part of the stream, while *Gastrosaccus australis* was highest upstream, not moving as far as the mouth.

*Tenagomysis macropsis*, the most abundant species in the Avon-Heathcote Estuary, occurs in greatest numbers at salinities between 16.9 and 19.2 ppm, but it is clearly euryhaline as Bary (1956) found it in great numbers in Foveaux Strait (ca. 60,000 individuals in one plankton tow). The results from overnight surface samples in a tideway, taken during his survey of mysidaceans and euphausiids east and south of the South Island, indicated daily vertical migrations by *T. macropsis* and *T. tenuipes*. The numbers of both species at the surface (including juvenile *T. macropsis*), peaked around 2 a.m. Bary’s is the only study published to date on vertical distributions of New Zealand Mysidacea.

Swarming is characteristic of mysidaceans (though not as densely as euphausiids) and more complex than it may appear. Mauchline (1980) discussed possible reasons for this behaviour. Concentrations probably result when physical and chemical factors in the water make some areas more habitable than others. Salinity, food availability, light or dark, and age class are all components of swarming behaviour. Conditions change regularly in estuaries and dispersed populations can be forced to aggregate in restricted areas at low tide. Ingle’s (1973) work on *T. macropsis* in Pauatahanui Inlet suggested a relationship between shoaling and the tidal cycle. Breeding aggregations also take place, probably more so in deep-water species because littoral mysidaceans regularly aggregate for other reasons but breed at the same time. Data gathered by Greenwood et al. (1985) suggested that *T. macropsis* may undertake seasonal migrations, in common with littoral mysids in other parts of the world (Mauchline 1980). Mature *T. macropsis* females move up-estuary with the rise of temperature in spring whereas Roper et al. (1983) found them closer to the estuary mouth in winter. Aggregation of females over the summer breeding season suggests that this is for breeding purposes. Swarming in currents can also lead to the segregation of age classes, which have differential swimming rates. Swarms are of all shapes from globular to elongated and can be very extensive horizontally in the water but only a few centimetres thick (Mauchline 1980).

**Reproduction and development**

Mysidacea do not have planktonic larvae as most euphausiids and decapods do. Instead, development of embryos and larvae takes place in the marsupium, from
which they emerge as juveniles. Mating usually, if not always, involves the male using its fourth pleopods to deposit sperm in the female marsupium (Mauchline 1980) and eggs are fertilised as they are laid in the marsupium. The number and size of resulting embryos depends upon the size of the eggs and the female and on water temperature and season. Meso- and bathypelagic species tend to have larger eggs and produce somewhat fewer young than epipelagic and coastal species, relative to body size.

The embryo (developmental stage 1) grows to some extent in the egg membrane, mouls into a stage 2 (eyeless) larva, and passes through a third (eyed) stage to moult into a juvenile ready to emerge from the marsupium. Juveniles grow to become adults without passing through further stages, although the abdomen increases in proportion to the cephalothorax, and the appendages and telson undergo gradual changes as well. Jones et al. (1989) found the sizes of embryos in Avon-Heathcote Estuary species to be in accord with the range generally found for coastal forms. A range of embryo numbers was also carried in the marsupia of the Tenagomysis species: 4–25 in T. macropsis, 6–19 in T. novaezelandiae, and 22–39 in T. chiltoni.

In T. tenuipes from Foveaux Strait, Bary (1956) found that females (up to 19.9 millimetres long) shed juveniles of 4.2 millimetres length. Those of T. macropsis from the same area were about 2.5 millimetres long, mature females of T. macropsis being less than half the length of T. tenuipes. Greenwood et al. (1985) found emerging larvae of T. macropsis to average only 1.47 millimetres in length in the Avon-Heathcote Estuary.

Food and predators
Dietary studies of Mysidacea are limited and none has been carried out on any New Zealand species, although Chapman and Lewis (1976) considered that Tenagomysis chiltoni and T. novaezelandiae might be detritus feeders. Chapman and Thomas (1998) subsequently reported predatory feeding in T. chiltoni. Mouthparts and thoracic appendages are variously modified in relation to diet. Some species are strict filter feeders, some specialise in grazing phytoplankton, and some are carnivores concentrating on certain substrata such as algae, but most are more opportunistic and eat a considerable range of the organic material in their environments. Mauchline (1980) tabulated the diets of 25 species of mainly northern hemisphere mysids. Though by no means comprehensive, his table showed the major importance of organic detritus, significantly supplemented by diatoms, other algae, copepods, and other crustaceans. Probably most New Zealand shallow-water species have similarly generalised diets, but a few specialised feeders are indicated. One of the most extreme modifications of feeding appendages is of the mandibular palp in Petalophthalmus species. It is greatly elongated, projecting well beyond the antennae. Carnivorous Petalophthalmus armiger pierces its prey and sucks out the internal contents (Mauchline 1980). Lophogaster typicus is incapable of filter-feeding, having mouthparts modified to feed on large lumps of food material on the surface of sediments, suggesting that New Zealand Lophogaster sp. could have a similar diet.

Filter-feeding is common in Mysidacea and is accomplished using setose mouthparts and thoracic appendages. The animals ‘stand on their heads’ above soft substrata, creating a current using the thoracic exopods and filtering particles from the stirred-up sediment. In common with euphausiids (see section on Euphausiacea), some Mysidacea employ a ‘food basket’, formed by the mouthparts and anterior thoracic appendages, in which food items collected using the mandibular palps are retained until they are chewed and swallowed.

Some species follow diel feeding rhythms, with certain species feeding by day, others only at night. Gastroscaps australis individuals caught by Jones et al. (1989) were virtually all taken at night in the Avon-Heathcote Estuary, suggesting that they feed nocturnally instead of competing with the three Tenagomysis species by day.
Mysidacea are important links in the food web between primary producers (e.g., bacteria and microalgae) and secondary consumers, especially in coastal waters. They therefore play a critical role in the cycling of energy through the detrital pathway (Jones et al. 1989). Mysids especially are eaten by a very wide variety of fish and also by decapod crustaceans, seabirds, cetaceans, and other predators. Data on predation of lophogastrids is limited because they live offshore but the size and appearance of the largest species facilitates their recognition in stomach contents. Albacore tuna eat Neogamathophausia ingens. Deep-sea hyperbenthic rattails eat mysidaceans including N. gigas, a species also reported in fin whale stomachs (Nemoto 1959 in Mauchline 1980) and N. ingens has been found in the stomachs of pigmy sperm whales stranded in New Zealand (Te Papa data). Weddell seals and gentoo penguins are known to eat the Antarctic mysid Antarctomysis maxima and, intriguingly, yellow-nosed albatross near Tristan da Cunha have been found with N. ingens and N. zoea in their guts (Mauchline 1980). It seems these otherwise extremely deep-living lophogastrids may undertake diel migrations near enough to the surface to be captured by albatrosses. Deep benthic and midwater prawns including Aristaeopsis edwardsiana, Pasiphaea tarda, and Aristaeomorpha foliacea, found in New Zealand waters, have also been found to eat mysidaceans.

Mauchline (1980) cited many studies of the diets of coastal fish that indicated the major significance of mysids as food items. He also noted that mysids tended to be underestimated as prey items because their remains were often mistaken for euphausiids. Little information on mysidaceans in the diets of New Zealand fish is apparent, although Griffiths (1976) reported that introduced European perch in the Selwyn River (Canterbury) eat high numbers of T. novaezealandiae. Estuaries such as Avon–Heathcote and Pauatahanui are important as fish nurseries and there is little doubt that the mysids that concentrate there are an important part of their diets. In lakes of the Waikato district, mysids are an important part of the diet of smelt (Northcote & Chapman 1999). Along the coast, seahorses (Hippocampus abdominalis) ingest Tenagomysis similis along with amphipods and the shrimp Hippolyte bifidirostris (Woods 2002), all found in the subtidal kelp beds in which seahorses live.

Mysidacea employ defensive strategies to avoid being eaten, including, as in shrimps and lobsters, tail flexing. While transparent and virtually invisible when swimming, mysids have chromatophores – pigment cells – that enable them to adopt camouflage colours and blend with algae, rocks, or sand. Lophogastrids are uniformly bright red, so can avoid detection by exploiting the lack of penetration of red light in sea water, as do many meso- and bathypelagic decapods. Swarming may also confer some protection on mysidaceans by reducing the number of targets apparent to their attackers.

A wide range of ecto- and endoparasites have been reported in Mysidacea. Very common endoparasites are ellobiopsid protozoans (phylum Myzozoa) such as Thalassomyces fasciatus, found in N. gigas, N. ingens, and G. zoea. Choniostomatid copepods parasitise mysidaceans, and epicaridean isopods, particularly of the family Dajidae, are common ectoparasites. Juvenile and small male dajids live in the host’s marsupium among the developing larvae.

Economic aspects
Mauchline (1980) reported that thousands of tons of Neomysis intermedia, N. japonica, and Acanthomysis mitsukurii are harvested each year in Japan; N. intermedia from brackish lakes is the most important of these and is cooked, dried, and eaten. There do not appear to be any other major fisheries for Mysidacea but several species are or have been fished in South-east Asia, China, and Korea by local fishers, who net them when they swarm. Some species have been reared successfully in laboratories, and freshwater species have been successfully transferred to other rivers or lakes as food for fish. It is also possible that some Mysidacea have colonised other habitats by transferring there on ships’ hulls or in ballast water.
Future work
There is clearly a need for further taxonomy followed by biological research on the Mysidacea of New Zealand before we can gain a reasonable appreciation of their diversity. Historically, New Zealand has never had the services of a mysidacean specialist but the need for such work is surely increasing given the importance of mysids in the marine economy, particularly as a major food of fish. Once Mysidacea currently held in collections are analysed, further assessment of their diversity, numbers, and roles in the region will require sampling gear and strategies appropriate to the collecting of these generally small and easily damaged animals.

Order Amphipoda: Beach fleas, sand hoppers, and kin
Amphipods are among the most ubiquitous crustaceans, inhabiting diverse environments from the depths of the oceans’ trenches to high altitudes on mountains, living in situations as varied as plankton in the open seas, burrowers in surf beaches, litter-dwellers on forest floors, epizoites on the skin of whales and dolphins, and cryptic inhabitants of subterranean aquifers more than 20 metres below ground level. Amphipods are likely to be found in almost all aquatic habitats, as well as on land wherever water is freely available or humidity is high. In many of these situations, species are numerous and numbers high, frequently overwhelmingly so. It is surprising, therefore, that they have received relatively little scientific attention.

The name of order is derived from two Greek words – amphi, both or of two kinds, alluding to the forward orientation of the anterior legs and the backward and/or lateral orientation of the posterior legs (Stebbing 1888), and podos, foot.

The relative neglect of amphipods as subjects for scientific study in New Zealand may be because of two related attributes – their biodiversity is bewildering and different species are often not easily distinguished by the untrained eye. The trained worker, on the other hand, finds the myriad variations on the basic morphology fascinating, continually generating questions about relationships between taxa and the selective value of the differences in morphological structures.

The basic amphipod body plan is difficult to define because of the group’s diversity. Amphipods are distinguished from other peracarids (malacostracan crustaceans that brood their eggs and young) by the following combination of characteristics: body generally laterally compressed, carapace absent, eyes sessile and usually lacking cuticular facets, pereon (thorax) with seven pairs of unbranched limbs, pereopods (legs) 1–4 orientated anteriorly, pereopods 5–7 directed posteriorly, pereopods 1–2 usually modified as subchelate (grasping) gnathopods, coxal gills present on some pereopods, pleon (abdomen) segments 1–3 with multi-articulate swimming appendages (pleopods), usually biramous, pleon segments 4–6 (urosomites) with stouter, biramous uropods, the final urosomite with a distinct telson.

Some 6000 species in about 120 families are known worldwide (Barnard & Karaman 1991). Estimates suggest that several thousand species await discovery and scientific description, despite more than 100 new species being described annually, on average, during the mid-1980s. The order is divided into three suborders – Ingolfiellidea, Gammaridea, and Hyperiidea; caprellids (formerly Caprellidea) are now regarded as specialised gammarideans.

Historical overview
Knowledge of the New Zealand amphipod fauna began with Dana’s (1852, 1853–55) descriptions of a few species, but accelerated with G. M. Thomson’s and Charles Chilton’s work. Thomson’s (1879b) first paper was followed by 14 more over the next 34 years; that of Chilton (1882a) was succeeded by 52 papers by 1926, although not all dealt with New Zealand species. Thomson and
Chilton’s (1886) ‘Critical list of the Crustacea’ contained 71 amphipod species names: 63 gammarideans, four hyperiids, three caprellids, and one cyamid.

Chilton was the strongest influence on early New Zealand amphipod systematics. He himself was influenced by DellaValle’s (1893) attempt to combine many of the world’s Gammaridea into fewer species and he treated many New Zealand species as variants of extrinsic taxa (Barnard 1972a). This tendency was exacerbated in his later career by his acquaintance with research on phenotypic variation of amphipods at Plymouth (England). This led him to regard many New Zealand species as phenotypes of sub-cosmopolitan species (Barnard 1972a) or as variants of local species (Fenwick 2001a). Significant contributions were also made by Stebbing (1888, 1910) through his work on local collections made by the Challenger and Thetis Expeditions. Also notable are Walker’s (1908) work on subantarctic material, K. H. Barnard’s (1930) studies of Terra Nova Expedition collections from the far north of New Zealand, and Stephensen’s (1927) and Nicholls’s (1938) studies of subantarctic amphipods.

A new phase of New Zealand amphipod systematics began in the 1950s with D. E. Hurley’s detailed papers (1954–75) on gammarideans, hyperiids, and cyamids. Several problems were resolved, new species described, and many previously described species clarified. Extensive collections from New Zealand’s deep waters were made during the Danish Deep-Sea Expedition, 1950–52, on the Galathea. Dahl’s (1959) and Barnard’s (1961) reports on these collections added considerably to knowledge of our fauna. In none of the preceding investigations, however, was there any attempt to collect amphipods widely in New Zealand waters in order to gain understanding of species’ distributions. This, however, was the approach followed by J. L. Barnard during his 1967–68 visit. The resulting monograph (Barnard 1972a) made a preliminary assessment of the biogeography of the New Zealand gammaridean fauna, described numerous new taxa, and provided the most comprehensive guide to date of the fauna (although its focus was algae-living amphipods). Barnard’s visit and monograph stimulated much subsequent local interest in the gammaridean fauna (Cooper 1974; Cooper and Fincham 1974; Hurley and Cooper 1974; Fincham 1974, 1977, 1979, 1981; Lowry 1979, 1981; Fenwick 1976, 1977, 1983; Myers 1981; Fenwick 1982, 1983; Moore 1983a,b, 1985; Lowry and Stoddart 1983a,b, 1984).

New Zealand freshwater amphipods were studied by Hurley (1954a, c, f) over this period, as were terrestrial amphipods (Hurley 1955a, 1957a, c). Bousfield (1964) and Duncan (1968) also investigated the terrestrial amphipods. Subsequently, Duncan (1994) substantially reviewed this group, recognising several new genera and species.

Elements of the New Zealand hyperiid fauna were reported by Stebbing (1888) and K. H. Barnard (1930). After about 1950, hyperiids and caprellids were usually investigated and reported separately from gammarideans, with Fage (1960), Shih (1969), and Hurley (1955b) exploring the fauna more fully. Much of this information is brought together in Vinogradov’s (Vinogradov et al. 1996) substantial review of the world hyperiids, with Zeidler (2003a, b, 2004a, b, 2006, 2009) refining the group’s systematics and adding further new records. The New Zealand caprellids were reviewed by McCain (1969) and he described one new species subsequently (McCain 1979).

Amphipod diversity in New Zealand currently stands at 500 species, of which 64 are undetermined or undescribed.

**Amphipods in the ecology of New Zealand**

The general abundance of amphipods means that, despite their small individual size, collectively they are important in the ecology of many ecosystems, especially as food for larger animals. Huge densities of amphipods are found among New Zealand seaweeds, in which they often dominate the associated fauna (Fenwick 1976; Taylor 1998).

Several studies have demonstrated the importance of gammaridean and
hyperiid amphipods as food for fish and birds in New Zealand. Amphipods were the most frequently utilised food item among 26 species of common northern New Zealand reef fishes (Russell 1983). Indeed, Jones (1988, p. 454) considered ‘the importance of gammaridean amphipods as a food source ... startling’ for juvenile fish. They were the principal food item for adults of several species and formed important secondary foods for the others (Russell 1983). These amphipods were mostly gammarideans and caprellids but some planktivorous fishes ate a few hyperiids. Small fish species were most dependent upon amphipods for food. Amphipods were eaten by 75–90% of specimens and comprised 40–60% of diet by volume in the various triplefin species (Russell 1983). A few large species also fed extensively on amphipods. Over half of all red moki, blue moki, trevally, goatfish, and juvenile snapper ate gammaridean amphipods, which made up 40%, 38%, 51%, 55%, and 62%, respectively, of their food by volume (Chat & Kingett 1982; Russell 1983). A similar study at Kaikoura (Duffy 1989) confirmed the importance of amphipods as food for fishes and showed their increased consumption by fishes inhabiting brown seaweeds of semi-sheltered, southern shores.

Amphipods are important food for some fishes inhabiting soft bottoms and estuaries also. Adults of nine species of fish in the Avon-Heathcote Estuary all ate amphipods, although they were a common (> 10%) food item for three species only – common sole (13%), cockabully (68%), and common bully (74%) (Webb 1973). Although amphipods were scarce in the diets of yellow-bellied and sand flounders in the estuary (Webb 1973), their juveniles fed almost exclusively (92–96% of food items) on the small tube-dwelling amphipod *Paracorophium excavatum* (Nairn 1998). Offshore, however, larger amphipods were common items (33%) in adult yellow-bellied flounders’ diets (Knox & Fenwick 1978).

Fish also eat pelagic hyperiid amphipods. Warehou, banded rattails, javelin fish, black oreos, southern blue whiting, carinate rattails, small-scaled brown slickhead, and small-scaled nototheneids all include amphipods as substantial components of their diets. Many of these fishes fed extensively on amphipods when smaller (up to 37% of food weight and eaten by up to 75% of small fish), with individual fishes taking larger prey as their sizes increased (Gavrilov & Markina 1981; Clark 1985; Rosecchi et al. 1988; Clark et al. 1989). Amphipods were a minor element of the diets of several other deeper-water fishes, notably hoki, smooth oreos, smooth rattails, and orange roughy. Pelagic fishes are the usual predators of these amphipods, but benthic fishes may feed extensively on hyperiids when swarms are carried into shallow water. At The Snares, the demersal telescope fish, as well as spotties, banded wrasse, and benthic nototheneid cod, fed intensively on hyperiids (*Themisto gaudichaudi, Hyperietta luzoni*) and krill swarming close to the surface (Fenwick 1978).

The importance of amphipods in freshwater fishes’ diets varies with species, amphipod abundance, abundance of other prey items, and fish size. Long-finned and short-finned eels, whitebait (*Galaxias maculatus*), mudfish, common smelt, and brown trout all eat small numbers of the common stream amphipod, *Paracalliope fluviatilis* (McDowell 1968; Eldon 1979; Ryan 1986; Jellyman 1989; Sagar & Glova 1995, 1998; Hicks 1997). Typically, amphipods comprise less than 5% of whitebait food, but more are eaten with increasing fish size (McDowell 1968). Amphipods are commoner in the diets of whitebait closer to estuaries than those further upstream and, in some rivers, amphipods comprise up to 45% of the diet (McDowell 1968). Similar variation in the consumption of amphipods occurs in eels. Amphipods (*Paracalliope fluviatilis* and the brackish *Paracorophium excavatum*) may be a major (70%) or minor (< 0.01%) food for short-finned eels, depending upon the specific habitat, season, and eel size, with amphipods being most important for small eels 100–190 millimetres long. Similarly, juvenile brown trout feed preferentially on amphipods, which make up 80% of food items of trout inhabiting tree-lined sections of some rivers.

Birds also feed on marine and estuarine amphipods. A number of oceanic birds typically feed extensively on hyperiid amphipods. Red-billed gulls, cape
pigeons, Buller’s mollymawks, and sooty shearwaters fed on hyperiid swarms at The Snares, with the latter two diving below the surface to catch them at times (Fenwick 1978). Fairy prion chicks are fed a diet comprising 14% amphipods by weight, diving petrels consume 17% by weight of amphipods, and grey-faced storm petrels at the Chatham Islands include four species of amphipods in their diet (Prince & Morgan 1987).

Numerous other New Zealand birds eat amphipods as larger or smaller components of their diets. For example, most penguins are believed to include these crustaceans in their diets (Croxall & Lishman 1987). In North American estuaries, some migratory waders consume 10,000–22,000 corophiid amphipods per day (Wilson 1989). Related species (plovers, dotterels, and wrybills) in New Zealand probably eat appreciable quantities of amphipods. Ground-foraging, insectivorous birds (e.g. robins, fernbirds, tits, and wekas), as well as blackbirds and song thrushes, are almost certain to include land hoppers from among plant litter in their diets. In addition, gulls and other birds probably capture beach-fleas from amongst wrack at times.

Diversity of New Zealand amphipods

**Ingolfiellidea**

Ingolfiellids are highly specialised, mostly small (< 3 but up to 14 millimetres long), worm-like animals adapted to living interstitially in marine and freshwater sediments, as well as in groundwaters. Marine species occur from the intertidal to the deep sea. Widely regarded as very primitive amphipods, over 30 species are known from two families. They are reported from most continents, including Australia, and two species from New Zealand interstitial marine habitats (Schminke & Noodt 1968) remain undescribed.

**Caprellidea**

In a detailed cladistic analysis, Myers and Lowry (2003) demonstrated that caprellids and cyamids are specialised corophiidean amphipods. They are discussed separately here but the end-chapter checklist follows Myers and Lowry. The Caprellidea includes two distinct families, both found worldwide – the skeleton shrimps (Caprellidae) and whale lice (Cyamiidae). Whale lice live ectoparasitically on whales and dolphins, whereas caprellids are benthic and often extremely abundant among algal fronds and on bryozoans, hydroids, and sea stars intertidally and on shallow marine bottoms. Each group’s body form is very different, although both possess rudimentary abdomens and vestigial abdominal limbs. Whale lice have short, flattened bodies with powerful limbs adapted to grasp their hosts’ skin firmly. Caprellids have long slender bodies and their last three pairs of legs, grouped posteriorly, are modified for grasping the substratum, leaving their anterior legs and antennae free for feeding.

Caprellids are quite diverse, with about 85 genera worldwide (McCain & Steinberg 1970; Laubitz 1993). The New Zealand skeleton-shrimp fauna comprises just eight species in six genera, belonging to two subfamilies (McCain 1969, 1979; Guerra-Garcia 2003). Half (four) of these species are endemic. Eight species of whale lice in four genera are known from New Zealand (Hurley 1952; Lincoln & Hurley 1980), whereas the worldwide cyamid fauna comprises 27 described species in six genera (Martin & Heyning 1999). If, however, cyamids known to occur on whale and dolphin species reported from New Zealand waters are considered, the total cyamid fauna may number some 19 species in all six known genera.

**Hyperiidea**

Hyperiid amphipods are purely pelagic, living freely in the ocean or associated with other pelagic invertebrates, from the surface to abyssopelagic depths (> 7000 metres) (Vinogradov et al. 1996). Species living near the surface typically
make diurnal vertical migrations from below 200 metres depth to spend the hours of darkness within the surface 50 metres.

A great variety of body shapes occurs within the hyperiids, making them extremely difficult to characterise. Large eyes and/or an inflated head and variously reduced first thoracic segments or pleon and urosome are common (e.g. Hyperiidae), although the opposite is true in others (e.g. Scinidae). The very compact forms of many surface dwellers (e.g. Platyatidae) contrast with the needle-like shapes of Rhabdosoma species. Lengths also vary widely from 2.5 millimetres (e.g. Hyperietta luzoni) to over 150 millimetres for the extremely elongate Rhabdosoma armatum.

Some hyperiids live on and within one or a few species of jellyfish, siphonophores, and ctenophores. The relationship between host and amphipod seems uncertain, but the consistent pairings of some species (e.g. Hyperia macrocephala is found only on the jellyfish Desmonema gaudichaudi) indicate commensalism. Host tissues and other prey items in the guts of these amphipods suggest that the amphipods behave opportunistically, with no obvious advantage to the host. Species of the family Phronimidae apparently eat the viscera of pelagic tunicates, siphonophores, and heteropods and use the prey’s transparent covers as a refuge against predators and for rearing their eggs.

Over 240 species of hyperiid in more than 72 genera and 23 families are known from the world’s oceans. It is difficult to characterise the New Zealand fauna because of the hyperiid pelagic habitat. Many hyperiids have very wide distributions (Vinogradov et al. 1996), so it seems inevitable that most widely distributed species will be found in local waters eventually (Zeidler 1992), depending upon movements of the specific water masses with which they tend to be associated (Young & Anderson 1987). Thus, New Zealand’s hyperiid fauna probably exceeds the reported 94 species in 49 genera reported from our surrounding seas (Hurley 1955b; Kane 1962; Vinogradov et al. 1996; Zeidler 2003a, b, 2004a, b, 2006, 2009) and a total fauna in excess of 100 species seems probable.

Gammaridea

The Gammaridea is the most abundant, ubiquitous, and diverse of the amphipod suborders. More than 5800 species in about 1100 genera are known, some from hadal depths exceeding 10,000 metres (Dahl 1959) and others higher than 4000 m above sea level (Stebbing 1888). Gammarideans range in length from about 2–3 millimetres to a whopping 340 millimetres for the abyssal Alicella gigantea (Barnard & Ingram 1986). Large size appears to be associated with higher dissolved-oxygen concentrations in cold-water habitats, and warm-water faunas are dominated by very small species. These amphipods also seem most abundant and diverse in temperate to cool climates, with tropical faunas being relatively inconspicuous, although surprisingly diverse (Thomas 1993). Gammarideans are often referred to as the laterally compressed amphipods. Land-hoppers, beach-fleas, and many aquatic amphipods certainly have the typical shape. However, several tube-dwelling and nestling genera have elongated, more vermiform, shapes. Burrowers in surf beaches (urothoids and some phoxocephalids) are wide-bodied, presumably for stability in high-energy habitats. Iphinotus typicus is even more flattened. Its limpet-like shape adapts it for life on the fronds of smooth brown seaweeds on New Zealand’s turbulent rocky shores.

Marine and freshwater gammarideans are predominantly free-living and benthic. A few are planktonic and others form close associations with algae, hydroids, bryozoans, and a variety of other invertebrates. Members of some families build tubes, nests, or columns from strands of material secreted from glands in their anterior legs, variously incorporating mud, sand, shell, bryozoan fragments, and other particles from their habitats. Species of yet other families
characteristically burrow in soft sediments, at times burrowing to more than 200 millimetres beneath the sediment surface. Scavenging, detritivory, and omnivory are the predominant feeding habits, but predation, ectoparasitism on fish, and herbivory also are known (Bousfield 1987; Enequist 1949; Lowry & Stoddart 1983b; Sainte-Marie & Lamarche 1985; Haggitt 1999).

The New Zealand gammaridean fauna (including caprellids and cyamids) comprises 401 species (62 undescribed) in 192 genera (10 unnamed), belonging to 55 families. [Figures below indicate that New Zealand’s total gammaridean amphipod diversity is probably 3–4 times greater than the total reported here.] This equates to about 5.6% of the world’s described species and 15.8% of world genera, representing over a third of all families. Some 74% of the species (296) are endemic, as are ~29% (55) of the genera. The fauna inhabiting each of three major habitats in New Zealand is discussed separately below.

Terrestrial amphipods
All terrestrial species belong to the Talitridae, the only amphipod family to have successfully occupied terrestrial habitats worldwide. These amphipods inhabit gardens, forest floors, and grasslands, where they live in litter, under trees and rocks, or in burrows that they construct themselves. Some 36 species in 10 genera occur in New Zealand (Duncan 1994; Fenwick & Webber 2008). Beach fleas are usually considered with terrestrial species, and 11 species in three genera are known from shore environments, although their revision seems overdue. Most New Zealand talitrids are endemics, but there are at least three aliens. New Zealand species range in length from c. 5–6 to > 50 millimetres for the giant subantarctic Notorchestia aucklandiae. Land hoppers and beach fleas occur throughout New Zealand, including the subantarctic islands, from sea level to over 2000 metres.

Freshwater amphipods
Some 53 species (~30 undescribed) in nine named (and 10 additional unnamed new) genera belonging to eight families are reported from freshwater habitats in New Zealand (Fenwick 2001a,b). Several undescribed species from hypogean water (saturated sediments beneath or beside streams and rivers (hyporheic) and groundwater) are currently under investigation and others from epigean (surface) waters await description (Fenwick 2000). Within these habitats, amphipods are often surprisingly abundant, but have received little attention. This relative neglect probably reflects their small adult sizes (3–6 millimetres body length), although two hypogean species (Phreatogammarus fragilis and Ringaniu toonuiiti) grow to over 20 millimetres long. All New Zealand freshwater species, five named genera, ca. 10 unnamed genera, and three families are endemic.

Marine and estuarine amphipods
The New Zealand marine and estuarine amphipod fauna comprises some 365 species. Amphipods inhabit every conceivable habitat in the sea, although few species live in estuaries. They are predominantly benthic, living in and on mud and sand and rocky bottoms, as well as among other invertebrates and algae. The total diversity of the New Zealand marine amphipod fauna is difficult to estimate, but is likely to comprise at least three times the presently known species. Of the known marine fauna, 194 species (~53%) and 35 genera (19%) are endemic.

Special features of the New Zealand gammaridean fauna
Biodiversity and abundance
Amphipods are frequently a major component of marine benthos, especially in cool-temperate to cold-water environments. New Zealand is no exception in this respect. A study of animals inhabiting the green alga Caulerpa brownii at
Kaikoura on the South Island east coast revealed a fauna dominated by huge numbers of amphipods – up to 12,000 per 200 grams wet weight (handful) of alga (Fenwick 1976). Some 61 species occurred in this specific habitat. Amphipod abundance increased dramatically with increased exposure to wave action, but fewer species predominated. Thus, the fauna at more sheltered sites comprised lower densities, with more species having more equal abundances.

Shallow sand bottoms at Kaikoura illustrate amphipod abundance in another near-shore habitat. Four species of amphipods and a large myodocopid ostracod comprise most of the fauna in this habitat. Amphipod densities average about 6000 per square metre, fluctuating from a winter low of 4000 to a summer high of more than 12,000 per square metre (Fenwick 1985). Crowding of these crustaceans is reduced by each species occupying a different depth in the sediment (Fenwick 1984) – cryptically coloured, surface-skipping Patuki roperi lives in the top 25 millimetres of sand, smaller white Ringaringa littoralis dwells at about 40 millimetres depth, bright red Paracentromedon? whero inhabits mid-depths (50–80 millimetres), and large Protophoxus australis overlaps at mostly 65–85 millimetres. Leuroleberis zealandica, a very large ostracod, is most abundant at 75–100 millimetres depth. Species’ mean depths in the sediment change slightly between sand ripples (150–200 millimetres high) and troughs, as well as with season.

Amphipods are a significant component of surf-zone faunas on New Zealand’s exposed beaches, such as in Pegasus Bay (Fenwick 1999). These small, frail-appearing crustaceans not only survive in these highly turbulent situations, but some species are found nowhere else. Amphipod densities peak just outside the zone of wave break, at about six metres depth in Pegasus Bay. Biodiversity of the amphipod fauna changes markedly with depth and, hence, changes in wave-induced turbulence, with most species abundant in only one depth zone. All but one of the abundant inshore (3–10 metres depth) species are free-living active burrowers of the family Phoxocephalidae.

These three studies demonstrate some key aspects of marine amphipod biodiversity. Perhaps most significantly, amphipods are a very important component of faunas inhabiting many of the shallow marine habitats around New Zealand. Not only are amphipods abundant in many of these habitats, but also their biodiversity is high. Individual species of amphipods are very sensitive to small changes or variations in their environments, resulting in marked changes in faunas within and between habitats. Species within some families exhibit very different tolerances of environmental factors, indicating that species or genus may be more useful levels of taxonomic resolution for amphipods in ecological investigations.

**New Zealand Phoxocephalidae**

Phoxocephalids are the typical amphipods of the surf beaches and sandy shores that make up so much of New Zealand’s coastline. Fifteen (88%) of the 17 phoxocephalid species known from New Zealand are endemic. Eight (53%) of the 15 genera to which these species belong are endemic and monospecific. This generic diversity and endemism is remarkably high. Museum collections indicate that the fauna includes 15 or more undescribed species, indicating over 30 species of phoxocephalids in New Zealand.

The Australian shallow-water phoxocephalid fauna consists of 89 species in 26 genera (comprising 40% of the known phoxocephalid species worldwide), with 23 of these genera endemic (Barnard & Drummond 1978; Barnard & Karaman 1983). Despite the high diversities of both the Australian and the New Zealand phoxocephalid faunas, there is little overlap between the two. Only one shallow-water genus (Booranus?) seems to be shared between New Zealand and Australia, although three deep-water genera (Cephalloxoides, Harpinioptis, Protophoxus) and two of their species are found on both sides of the Tasman Sea.

Australia is regarded as the epicentre of phoxocephalid evolution because
of high diversity of species and genera and high generic endemism (Barnard & Karaman 1983). The subantarctic islands of South America are the only other centre of phoxocephalid radiation, with distinctive attributes present among its species and genera. New Zealand’s location between Australia and South America indicates that the New Zealand phoxocephalid fauna is likely to be both diverse and of special biogeographic interest.

Groundwater amphipods

Late in the 19th century the biological world was intrigued by Chilton’s (1882a,b, 1884, 1894) reports of crustaceans living within aquifers of the Canterbury Plains. Following this initial work, the groundwater received scant attention. Subsequent workers, including Chilton himself (e.g. 1912, 1924), apparently assumed no additional species, assigning specimens to known taxa without critical examination.

During the 1970s Guillermo Kuschel of the former DSIR surveyed groundwater faunas by pumping wells throughout the country. Ten new gastropod mollusc, 71 mite, and two water-beetle species were described from these collections (Scarsbrook et al. 2003). The several amphipods from Kuschel’s collections await full investigation, but preliminary work (Fenwick 2000) revealed several new taxa. Current collecting effort indicates the existence of a further 20–30 species of groundwater amphipods.

The described hypogean (groundwater) amphipod fauna of New Zealand comprises four species in three endemic genera (two of which have epigean representatives) each belonging to quite different families. Two of the hypogean families are endemic. Given the number of species, this fauna seems remarkably diverse at generic and familial levels. Preliminary work indicates that the New Zealand hypogean amphipod fauna appears dominated by paraleptamphopids and is very different to that of Australia, where hadzioids and crangonyctioids predominate (Bradbury & Williams 1997). Taxonomic work on these collections is required to determine the true diversity, to determine relationships with the Australian freshwater amphipod fauna, and to make the fauna accessible to ecologists.

Should we be surprised by a high diversity of groundwater amphipods in New Zealand? Groundwater volumes in New Zealand are huge and probably several times greater than volumes within surface waters (lakes and rivers). For example, the groundwater of the Golden Bay region is estimated to approximate the volume of water in Lake Taupo. There are extensive aquifers beneath most of the Canterbury Plains to depths of 350–550 metres. This is not simply all water, but variably porous gravels with water moving through interstices. Obviously, there is a huge volume of water beneath the plains. Other parts of the country also comprise large plains of porous alluvial gravels (e.g. Waimea Plains around Nelson, the Heretaunga Plains of Hawke’s Bay) containing extensive aquifer systems. Given the very large habitable volumes available and the apparent barriers to dispersion between each groundwater system, a high amphipod biodiversity should not be unexpected.

Investigations at one site in Canterbury indicate that groundwater amphipods help to maintain the quality of Canterbury’s groundwater (Fenwick et al. 2004). The three known amphipod species, as well as a large subterranean isopod (Phreatoicus typicus), congregate at sites of organic enrichment from sewage-oxidation-pond effluent. A series of field and laboratory experiments showed that these animals browse on non-living organic slime layers from sediment and stone surfaces (Fenwick 1987). Extrapolation of experimental results using conservative estimates of crustacean densities indicates that the two dominant amphipods remove large amounts of organic carbon annually in the vicinity of the disposal area.

Further understanding of the biology of these valuable groundwater systems depends on documenting and monitoring their biodiversity to facilitate...
ecological studies for improved policy formulation and management decision-making. Fundamental to this is better taxonomic knowledge of the fauna.

**Biogeography of the freshwater fauna**

Some New Zealand freshwater amphipods have attracted considerable interest from workers seeking to untangle phylogenies and relationships between faunules of Gondwana and other landmasses. Two endemic genera are of special interest. *Phreatogammarus* was seen as ‘an amazing antiboreal morphological counterpart of the Holarctic crangonyctids’ (Barnard & Barnard 1983, p. 51), a group now largely confined to North America. This genus was considered to be ‘perhaps the most primitive [living] gammarid’ (ibid., p. 420) that is ‘now a perfect relict’ (Barnard & Barnard 1982, p. 264). The absence of any significant amphipod fossils increases the significance of *Phreatogammarus* to evolutionary biologists. The morphologies of both *Phreatogammarus* and *Paraleptamphopus*, a modern derivative from a *Phreatogammarus*-like ancestor (Barnard & Barnard 1983), are incompletely known. Thus it is difficult to establish the relationships of these two genera with other genera.

Other New Zealand freshwater amphipod genera are also distinctive and have intriguing faunal relationships. *Paracalliope*, a genus with three New Zealand species and Australian, Philippine, New Caledonian, and Fijian representatives, is calliopiid-like, but sufficiently distinctive to justify placement in a separate family, the Paracalliopiidae, which has one other genus (Barnard & Karaman 1982, 1991). The endemic genus *Chiltonia*, together with the closely related *Afrochiltonia, Austrochiltonia*, and *Phreatochiltonia*, comprise the subfamily Chiltoniinae from New Zealand, Australia, and South Africa (Barnard 1972b). Yet another endemic genus poses biogeographic and phylogenetic problems. Bousfield (1977) moved the genus *Paracrangonyx* into his superfamily Bogidielloidea, re-assigned it to the Crangonyctoidea (Bousfield 1978), thence (Bousfield 1982, 1983), along with three other disparate genera, to the family Paracrangonyctidae within his superfamily Liljeborgioidea. Barnard & Barnard (1983, p. 52) placed *Paracrangonyx* among the bogidiellid gammaroids ‘for the moment’. Following careful analysis, Koenemann and Holsinger (1999) found the genus to be most closely related to three genera from each of Western Australia, Madeira, and East Africa. After reviewing these placements and rediagnosing the genus, Fenwick (2001b) concluded that the relationship of *Paracrangonyx* to other genera remains uncertain, but that it belongs within the crangonycoid cluster and is close to the Paramelitidae, as well as showing relationships to other genera of Australian hypogean amphipods.

Many of these taxa have not been re-examined since their first collection. The original specimens of some species are in very poor condition and the illustrations and descriptions of some are inadequate. Consequently, many older taxa must be revised before descriptions of new taxa can take place.

**Special associations**

The ecology of New Zealand amphipods is generally poorly known and few associations with other invertebrates are reported. Gammaridean amphipod associations with other crustaceans, ascidians, sponges, hydroids, echinoids, molluscs, and other organisms elsewhere are well documented (e.g. Vader 1978, 1984, 1996) and some New Zealand amphipods probably live in similar associations.

The corophioid amphipod *Pagurisaea schembrii* occurs only on the hermit crab *Paguristes pilosus*, where up to 50 at a time live among the dense setae on the host’s chelifeds, walking legs, and carapace (Moore 1983a). The amphipods apparently do not steal their host’s food but use their specially modified antennae to capture food particles from the host’s respiratory current whilst sheltering within the host’s setae and shell.

Some amphipods are found almost exclusively on algae, but the nature of
the relationships between amphipods and the algae is uncertain. Many species are found on more than one species of algae, as well as on foliose invertebrates (hydroids, bryozoa). This suggests that many amphipods use their hosts more as a substratum than as a partner in some interdependent association. Species of the tube-building genus *Notopoma* found at Kaikoura illustrate this apparently non-obligate relationship. *Notopoma fallohidea* lives only on the green alga *Caulerpa brownii* at relatively sheltered sites (Lowry 1981). One of its congeners, *N. harfoota*, is extremely abundant on the same alga in more severe wave action, but lives on other algae also. A third Kaikoura species, *N. stoora*, is most abundant on the foliose bryozoan *Costaticella solidula*, although a few occur on *Caulerpa*.

Another New Zealand amphipod, *Orchomenella aahu*, bores into stipes of the kelp *Ecklonia radiata* to eat up to 22 milligrams per day of the more palatable (low phenolic content) internal tissues (Haggitt 1999). These amphipods remain within the stipe, reproducing several times. Whole families of as many as 300 individuals, comprising several generations, live within most infected plants. This association seems opportunistic because *O. aahu* is also an active scavenger of animal tissue (Lowry & Stoddart 1983b).

The large subantarctic amphipod *Rakiroa rima* appears to live only within empty sponge-covered shells of a large barnacle (*Megabalanus campbellii*) (Lowry & Fenwick 1982). Similarly, some cryptic species such as *Acontioptoma tuberculata*, *Ocosingo fenwicki*, and *Stomacontion* spp. are known only from among collections of subtidal encrusting sponges (Lowry & Stoddart 1983b). It is uncertain whether these are commensal associations or whether the conditions sought by the amphipods are found coincidentally in close proximity to these other organisms. Some have, however, evolved specialised morphological and reproductive adaptations to their inquinulous life-styles. For example, species of *Ocosingo* and *Stomacontion* have specialised piercing mouthparts (Lowry & Stoddart 1984). *Acontioptoma* and some *Stomacontion* species undergo a sex change to ease the problems of finding a mate; small sexually mature males change into reproductive females as they grow larger (Lowry & Stoddart 1983b, 1984, 1986).

The place of some amphipods in various food webs makes them ideal intermediate hosts for parasites. The common freshwater amphipod *Paracalliope fluviatilis* is the intermediate host for a parasitic nematode (*Hedruris spinigera*) commonly found in long-finned and short-finned eels, smelt, brown mudfish (Hine 1978, 1980; Jellyman 1989), and whitebait (McDowall 1968). Infection rates of the nematode in these fishes (up to 38% for short-finned and 70% for long-finned eels) are often directly related to abundances of the amphipod and the incidence of *Paracalliope fluviatilis* or smelt in the fishes’ diets (McDowall 1968; Hine 1978). This amphipod is also the intermediate host for three additional parasites of freshwater fishes – *Acanthocephalus galaxii*, *Coitocaecum anaspides*, and at least one species of hymenolepid cystocercoid (Hine 1978). Similar amphipod–parasite relationships are almost certain to occur among marine species.

These observations show some of the diverse relationships between amphipods and other organisms. Other relationships, notably those between widely distributed hyperiid amphipods and various other planktonic invertebrates (salps, tunicates, medusae), plus those between cyamids and their cetacean hosts, are not considered. Numerous other relationships between New Zealand caprellid and gammaridean amphipods and various parasites, other invertebrates, and algae are likely to be described in the future.

Alien species
Relatively few invasive amphipods (11 species) have been reported in New Zealand. Among the hyperids, the potential for a species to invade seems extremely low; ships’ ballast water seems the only feasible vector, but the likelihood of hyperiids surviving within ballast water for any appreciable time seems remote. Certainly, exotic species may arrive fortuitously as ephemeral
transients within water masses not normally entering our region. Such arrivals seem destined to disappear when their water masses are displaced by the more usual regime.

One New Zealand caprellid, *Caprella mutica*, is a very recent invader (Willis et al. 2009), another species (*Caprella equilibra*) is cosmopolitan, and a third (*Caprellina longicollis*) is widespread in southern waters (McCain 1969, 1979). Caprellids’ usual association with sessile fouling invertebrates at sites of high water movement suggests that the latter two caprellids could arrive on the fouled hulls of ships and, thus, may be invaders. Equally, several additional cyamids may be found in New Zealand in the future. Whale hosts of several more species are known from New Zealand waters, but these small, apparently rare, amphipods are collected infrequently.

One land hopper, *Arcitalitrus sylvaticus*, has been imported from Australia. It is established in urban and disturbed habitats of northern New Zealand, displacing native land hoppers to become the principal land hopper in domestic gardens in Wellington and Auckland (Duncan 1994). The species has failed to become established in Christchurch, despite at least two separate introductions via potted plants.

There is no evidence of any exotic amphipods invading New Zealand’s fresh waters. A few gammarideans have been introduced to harbours, however, via ships. Two corophioids, *Monocorophium acherusicum* and *Apocorophium acutum*, are cosmopolitan and ‘trace out some of the major shipping routes, particularly that from England through the Mediterranean and Suez Canal to South Africa’ (Hurley 1954f), indicating that both are invaders. *Ericthonius pugnax*, another tube-building corophioid, is probably another invader because, although its distribution is less readily explained (New Zealand and Indonesia), the species was not discovered in New Zealand until 1923, some 70 years after its original description.

Two additional corophioids have been reported as invaders in New Zealand. *Paracorophium brisbanensis* and an unidentified species of *Corophium* were found in brackish waters of the upper reaches of Tauranga Harbour. Both were regarded as adventives because neither was reported from New Zealand previously, they were not found at any of 92 similar sites surveyed around the country, both Tauranga populations had ‘remarkably limited genetic variability’, and juveniles dominated their population structures (Stevens et al. 2002).

Another notable alien amphipod, distributed nearly globally, is the wood-boring *Chelura terebrans*. First found in New Zealand in Auckland Harbour (Chilton 1919), this small amphipod bores into most human-made wooden structures around the world (Barnard 1955). *Chelura*, along with *Limnoria* isopods and boring molluscs (*Teredo* species), wreaks havoc on wharf piles, rapidly boring into the timber and weakening any wooden structures. Apart from Chilton’s (1919) original records, there appear to be no other reports of this species from New Zealand, although it is certain to be more widespread.

Three additional aliens were found in the sea chest (a large recess in a ship’s hull for seawater intake pipes) of a vessel from the tropical Pacific that was slipped at Nelson in September 1999. These were *Stenothoe gallensis* and *Elasmopus rapax*, two known tropicopolitan species, and an unidentified species belonging to the cosmopolitan genus *Podocerus*. The first two species were abundant and included mature males, gravid females, and juveniles. There is no information on whether any of these species has become established in Nelson or elsewhere in New Zealand, despite repeat surveys.

In general, it seems extremely difficult to determine whether marine species with wide distributions are invaders (become established on new shores through dispersal by human activities) or simply arrived by natural dispersal. Several other New Zealand species have variably wide extrinsic distributions, but the ecologies of only a few seem likely to equip them for dispersal on the hulls of ships. Tube-builders and nestlers, especially corophioids, are the most likely candidates. For
example, *Gammaropsis crassipes* was described from shallow bays and harbours in eastern Australia in 1881 but not reported from New Zealand until 1920, suggesting possible introduction. Recent invasions by algae, as well as long-term climatic changes, suggest that the potential for permanent establishment by amphipod invaders will increase in the future.

*Monocorophium sextonae* was considered to be a successful New Zealand invader of European shores (Hurley 1954f), although this has recently been questioned (Costello 1993; Bousfield & Hoover 1997). First described from Plymouth and Wembury in 1937, this amphipod was present, albeit unrecognised, in Chilton’s (1921) material (Hurley 1954f). Crawford (1937) remarked that the ‘abundance of this species is the more surprising since it is not present in the rich collections of *Corophium* made from the same dredging grounds in 1895–1911. It seems possible, therefore, that it is not indigenous at Plymouth … I cannot guess its original locality’. In revising these species of the family Corophiidae, Bousfield and Hoover (1997) considered that *M. sextonae* ‘is almost certainly endemic to the eastern North Atlantic and Mediterranean regions, from whence it has been spread by commerce to world-wide temperate marine waters’.

### Amphipods in environmental investigations

Diverse approaches are used to assess and manage human impacts on the aesthetic and life-sustaining qualities of natural environments. Use of plants and animals as bioindicators is increasingly common because of the sensitivities and broad-spectrum responses of some species. Amphipods are ideal bioindicators for shallow marine environments (Conradi et al. 1997) because they are ecologically (trophically) important, tend to be numerically dominant within many habitats, have specific niche requirements, have generally low mobility and dispersive capabilities, and are known to be sensitive to several pollutants and toxicants. Indeed, Thomas (1993) reported that ‘[a]mphipods are so useful as bioindicators that U.S. Government agencies now require their identification to species in permitting operations such as oil leases and outfalls.’ In addition, individual species of amphipods may serve as very useful assays for pollutants (Lamberson et al. 1992). Several US agencies employ amphipods in bioassays to test toxicities and specific contaminant levels independent of chemical analyses and environmental surveys, particularly for marine environments.

Many of New Zealand’s estuarine and marine amphipods fulfil all of Thomas’s (1993) criteria for effective biomonitors (e.g. Fenwick 1976, 1985; Hickey & Martin 1995; Nipper & Roper 1995; Nipper et al. 1998). This is also true for some terrestrial (e.g. Rainbow et al. 1993) and freshwater species (Hunt 1974). Environmental survey research in New Zealand, however, continues to look at the total fauna and these investigations follow a trend of identifying and enumerating taxa to family level only (Somerfield & Clarke 1995) in attempts to reduce costs by minimising the taxonomic expertise and time required for identifications. Some workers (Thomas 1993; Conradi *et al.* 1997) advocated focusing on the amphipods alone in surveys of shallow marine environments and, certainly, their identification to species seems worthwhile in such surveys. There has been no specific examination of the merits of using amphipods alone for such surveys in New Zealand, and identification tools and knowledge of the group are inadequately developed for this to become a viable, standard approach in the short term.

New Zealand estuarine amphipods (*Paracorophium excavatum*, *P. lucasi*) have been used in bioassays of sediment contamination and toxicity (Nipper & Roper 1995). Additional studies (Nipper et al. 1998; De Witt et al. 1999) revealed the robustness of this assay approach, which is now used extensively. Only recently, however, has the taxonomy of these two species been resolved (Chapman *et al.* 2002), illustrating that taxonomic knowledge of New Zealand’s amphipod fauna is often inadequate for reliable ecological applications.
Gaps in knowledge and future research

New Zealand’s amphipod fauna is important ecologically on land, in fresh waters (especially groundwaters), and in marine habitats where species fill vital roles in food-webs and often provide appreciable direct or indirect economic benefits. Amphipods also offer considerable potential as bioindicators of environmental quality in many habitats. Obviously, the potential for ecological and environmental research using amphipods is huge, even when only the more urgent or applied issues are considered. Equally, the scope for academic investigation of amphipods is enormous.

Despite all this, their systematics is very incomplete, hindering attempts to work with the group. Certainly, the land-hoppers appear well known as a result of Duncan’s (1994) work, but the beach fleas require equivalent treatment. Freshwater amphipods require urgent attention in view of our scant knowledge of this group and the huge environmental pressures on fresh waters. Known species require extensive redescriptions and revision to facilitate work on the >50 new taxa in collections. Several other new species exist in other freshwater habitats that await collecting.

The marine gammaridean amphipods of shallow and continental-shelf waters comprise another substantial gap. Collecting has been sparse and the fauna at no one location is well known. Even the distribution of the algal-dwelling species along New Zealand is poorly known, despite Barnard’s (1972a) work. Amphipod faunas of shallow soft seafloors are very poorly known. A study in Pegasus Bay showed that 28% of species in the 4–10-metre depth zone are undescribed (Fenwick 1999). Similarly, less than 30% of the 98 species in a series of collections off Kaikoura are known and the unknown ones include several new genera. Also, just 24% (10 of 42 species identified by a leading taxonomist) of amphipods in another study of New Zealand shelf benthos were known to science (Probert & Grove 1998).

Amphipod research in New Zealand thus offers considerable scope for both economically important issues and questions of more academic interest. However, the present status of the group’s taxonomy hinders the successful development of this work, as well as discouraging many ecologists from using amphipods as ideal subjects for environmental and ecological investigations. The future, therefore, requires not just more taxonomy, but also the development of interactive guides and keys to overcome these barriers and make the local fauna accessible to non-specialists. This is particularly true for hypogean and other freshwater amphipods, given their role in maintaining the quality of groundwaters and the urgent need for effective management of this economically important resource in the face of increasing demands and human-induced threats.

Order Isopoda: Slaters, fish lice, and kin

The most diverse range of body plans of all the nine peracaridan orders, if not of all crustacean orders, is shown by the Isopoda, named, however, for the relative sameness of limbs (Greek *isos*, equal, like; *podos*, foot).

Only one of the isopod suborders, Oniscidea, is familiar to most people. The oniscideans are commonly called woodlice, slaters, pillbugs, or roly-polies. However, the order is predominantly marine, being less well-represented in estuarine and fresh waters. There are fewer common names for the marine groups but sea-lice, fish doctors, tongue-biters, and sea-centipedes are applied to some families. No common name, except isopod, applies to all members of the order.

Life-styles vary. Free-living predators, marine filter-feeders, scavengers in forest leaf-litter and on the sea floor, and various parasitic forms are represented in the order. The isopods have succeeded in two unusual habitats besides the shallow marine environments where most crustaceans are typically found. One is the land, where woodlice, slaters, and phreatoicideans are most often the sole...
crustacean representatives in some habitats, and the other is the deep sea, where the suborder Asellota has radiated into a variety of bizarre forms.

Although they are often said to be ‘dorsoventrally flattened’ while their close relatives the amphipods are ‘laterally flattened,’ there are many exceptions; some are cylindrical, others laterally compressed, and others extraordinarily ornamented. The smallest isopod adults are c. 1 millimetre long, many are in the range 4–12 millimetres, and the largest are deep-sea scavengers of the genus *Bathynomus*, growing to an astonishing 400 millimetres!

The only sure way to tell an isopod from an amphipod is that isopods lack strongly chelate first legs and have only one pair of uropods (tail appendages) and a free second thoracic segment. Character interpretation can be difficult, however, because uropods vary considerably. They may be flat limbs that lie in the same plane as the pleotelson, or enclose the pleopodal gills, or have any of several other forms. Technically, Isopoda are defined as follows: eyes sessile (not stalked); carapace absent; one pair of maxillipeds; seven pairs of pereopods (legs), without exopods (an outer branch); abdomen clearly differentiated from thorax and divided into a pleon of five segments (sometimes some fused) and pleotelson (fused pleonite six and telson); pleopods 1–5 similar or anterior pair operculiform, forked; one pair of uropods.

Isopods are of interest to marine biologists because of the important roles they play in ecosystems, especially on the sea floor. Here, species of many families are important scavengers of decaying material. Isopods of the family Cirolanidae are critical in cleaning up decaying dead fish (Bruce 1986a; Brusca et al., 1995; Keable 1995). Fish-lice of the family Cymothoidae are flesh- and blood-feeders that attach to the skin of living fishes. Aegids and juvenile gnathiids are blood-sucking micropredators of fishes, and in the tropics gnathiids can be so abundant that fishes attend cleaning stations where wrasses remove and eat them. Sea-centipedes (Idoteidae) feed on algae. The diverse Sphaeromatidae feed on living and dead material of all sorts. Many isopods are ideal food for many bottom-living fishes such as flounders and skates.

One family of economic significance is the Limnoriidae (gribble). These are wood-borers, formerly of ships but now only of wooden piles and wharves. Like timber borers on land, gribble make galleries throughout the timber and weaken it considerably (Menzies 1957; Cookson 1991). Species of *Sphaeroma* (Sphaeromatidae) behave similarly. Another important group, at least to gardeners, is the terrestrial slaters or woodlice. While most feed innocuously on decaying leaves and wood they can become so abundant as to attack vegetables and other garden plants.

Diversity of New Zealand Isopoda

The world’s isopod fauna exceeds 10,000 described species but the actual number of species is certainly several times this. There are big gaps in knowledge of the deep sea, the tropics, and some families with small individuals. The New Zealand fauna totals only 426 living species (and four fossil species) but it appears that few shallow-water isopod groups are well covered taxonomically. It would not be surprising if many species of Sphaeromatidae, Cirolanidae, Gnathiidae, anthuroids, Asellota, and Valvifera remain to be discovered, especially from shelf depths. Even so, the number of already described species (353) somewhat exceeds that of South Africa (cf. 275 species in Kensley 1978) but, not surprisingly, is far fewer than in Australia (1,118 species; Poore 2002, 2005). South African and Australian isopods have attracted greater taxonomic attention than those in New Zealand. As is the case for many marine and terrestrial animals, New Zealand isopods are largely endemic.

The only habitat that is relatively well known is intertidal and subtidal rocky shores, but even here the Asellota have been largely ignored. Museum collections from The Snares (partly described by Poore 1981) contain several undescribed species of small asellotes and more such species could be expected...
throughout New Zealand. While the benthos of the New Zealand continental shelf has been thoroughly sampled, the gear used has not deliberately targeted small invertebrates, and collections available for study seem not particularly diverse for isopods. NIWA collections appear from superficial examination to be far less rich than, for example, those from comparable habitats in Bass Strait at similar latitudes in Australia. Museum Victoria, Melbourne, houses a benthic collection that includes c. 250 species of isopods from sediments (Poore unpubl.). There are even fewer species described from the continental slope. Poore et al. (1994) recognised 359 species, mostly undescribed, from this habitat off the southeastern coast of Australia and a similar number could be expected for the New Zealand slope. Several species from bathyal depths north of New Zealand were described from collections of the Galathea Expedition but the rest of the EEZ is virtually unsampled. Another habitat as yet largely unexplored is fresh water in limestone caves; sphaeromatids are known from this environment near Nelson, South Island (Sket & Bruce 2004).

Three species of isopod fossils have been recorded from New Zealand (Grant-Mackie et al. 1996; Hiller 1999; Feldmann & Rust 2006).

Numerous families, 120 at last count in the world fauna, are arranged in a complex hierarchy within suborders (Martin & Davis 2001). Most of the widely used suborders are monophyletic groups, but the one that has traditionally included the most familiar marine species, Flabellifera, is not (Wägele 1989; Brusca & Wilson 1991; Brandt & Poore 2003). Here, Brandt and Poore’s (2003) classification is followed and the suborder Flabellifera is superseded by the three suborders Cymothoida, Limnoriidea, and Sphaeromatidea. Three other previously recognised suborders are subsumed within Cymothoida – Epicaridea as superfamilies Bopyroidea and Cryptoniscoidea, Anthuridea as superfamily Anthuroidea, and Gnathiidea as family Gnathiidae. Hurley and Jansen (1977) provided an effective key to identify some families but their classification is now out of date. Modern faunal treatments, also using the older classification, can be found in Kensley (1978) or Kensley and Schotte (1989). Only 49 families have so far been recorded from New Zealand.

Suborder Asellota
Some 93 New Zealand species are known, of which 36 remain unnamed or not fully determined. They have diverse shapes. Diagnostic characters include: coxal plates usually minute; one (rarely two or three) pleonites free, others fused; uropods attached posteriorly. Asellotes are common but small, difficult to find, and even harder to identify. A microscopic examination of tufts of algae from sheltered marine environments will often reveal several species of asellotes, rarely more than two millimetres long. Others live in freshwater streams. Globally, almost 30 diverse families exhibit an exceptional range of form on the floor of the deep sea. Some species are quite bizarre, with extraordinary ornamentation. Several species from the deep sea near New Zealand were described from collections of the Danish research ship Galathea (Wolff 1956a, 1962) but only one family from this environment in New Zealand has been treated in detail (Lincoln 1985). The identity of many of the species recorded from subantarctic New Zealand may be in doubt until specimens are compared with those from other islands or continents. Globally, Wilson and Wägele (1994) listed all known asellote species and provided a key to the genera of Janiridae, an important shallow-water family, and Cohen (1998) did the same for Dendrotiidae. The diverse Munnopsididae has been treated in part by G. D. F. Wilson (1989), the Stenetriidae by Serov and Wilson (1995), Pseudojaniridae by Serov and Wilson (1999), Joeropsididae by Just (2001), and Paramunnidae by Just and Wilson (2004, 2006).

Suborder Phreatoicidea
Nine New Zealand species are known, all endemic, and in endemic genera. They
are laterally flattened. Other diagnostic characters include: coxal plates extending ventrally; five pleonites free; uropods rod-like and attached posteriorly. Peculiar to southern continents and islands, phreatoicids comprise an unusual group of freshwater and terrestrial species. They superficially resemble amphipods but differ in having only one pair of uropods as well as other isopod features. Most of the New Zealand fauna was dealt with by Nicholls (1944), with one species described in detail by Wilson and Fenwick (1999). The suborder was reviewed by Wilson and Keable (2001).

Suborder Cymothoida

Comprising sea-lice, fish-lice and other mobile scavengers, predators, and microparasites, 116 described and 16 undetermined New Zealand species are known. Diagnostic characters: usually dorsoventrally flattened but otherwise diverse; mandibular molar blade-like or reduced; coxal plates expanded and free or reduced; five pleonites free or variously fused; uropods usually forming tail fan with pleotelson, rotating in horizontal plane and in broad contact with pleopods. All are marine, but habits and shapes vary. Numerous authors have contributed to knowledge of cymothoid families in New Zealand, notably the Cirolanidae (Jansen 1978; Bruce 1986a, 2003, 2004a; Svaravsson & Bruce 2000; Keable 2006), Cymothoidae (Bruce 1986b), Gnatidiidae (Cohen & Poore 1994; Svarvasson 2006), Tridentellidae (Bruce 1988, 2002), and Aegidae (Bruce 1983, 2004b, 2009a). The suborder contains four superfamilies – Anthuroidea, Bopyroidea, Cryptoniscoidea, and Cymothooidea.

Some 21 described New Zealand species of Anthuroidea are known (in the families Anthuridae, Expanathuridae, Hyssuridae, Leptanthuridae, and Paranthuridae). Diagnostic characters include: shape elongate and cylindrical; coxal plates indistinguishable from pereon wall; pleonites fused or free; uropodal exopod attached proximally on peduncle and dorsally arched over pleotelson. Anthuroids live in sediment and on macroalgae, although the New Zealand species Cruregens fontanus is unusual in living in artesian and river waters (Wägele 1982). Very few species had been described until the work of Wägele (1985). The family arrangement follows Poore (2001a), who synthesised many papers and whose earlier work, principally on the Australian fauna, is relevant.

The superfamily Bopyroidea comprises parasitic isopods of crustaceans, with 13 described New Zealand species in the family Bopyridae. Diagnostic characters include: individuals sexually dimorphic, females usually asymmetrical, males minute; mouthparts reduced; branchial parasites of crabs, shrimps etc., but also of other crustaceans and some hyperparasites of other bopyroideans. Page (1985) studied New Zealand species. Few modern taxonomists have tackled this confusing group, but Markham (1985) and other papers by this author are a good introduction.

The largest superfamily in New Zealand is Cymothooidea, with 93 species (15 unnamed or not fully determined) in the families Aegidae, Anuridae, Cirolanidae (with endemic genus Pseudago), Cymothoidae, Gnatidiidae, and Tridentellidae. The largest of these, with 37 species, is the recently monographed Aegidae (Bruce 2009a), a family of micropredators mostly associated with fishes. The Cryptoniscoidea has just five species in New Zealand, in the families Criniscoidea and Hemioniscoidea (Hosie 2008).

Suborder Limnoridea

These are wood-boring isopods, sometimes called gribble, with nine New Zealand species all in a single family, Limnoriidae, reviewed by Cookson (1991). Mandibles are specially modified, the body is cylindrical, and pleonites are free. Wood is not their only target in New Zealand. Limnoria limnoruan caused the 1916 failure of the Cook Strait submarine cable when some individuals bored through the gutta-percha that was around the inner cable core.
Suborder Sphaeromatidea
These comprise marine pillbugs in general, with 81 described New Zealand species known, including 61 species of Sphaeromatidae. Diagnostic characters: usually dorsoventrally vaulted, occasionally flattened, sometimes able to enroll; coxal plates well developed; pleonites variously fused; uropods usually forming tail fan with pleotelson, rotating in vertical plane and excluded from branchial cavity. All are marine, but habits and shapes vary. Notable taxonomic contributions include those on the Sphaeromatidae (Hurley & Jansen 1977) and the enigmatic, sometime sphaeromatid, genus Paravireia, herein placed as incertae sedis (Jansen 1973; Brökeland et al. 2001). A sphaeromatid species is host to a fecampiid flatworm, Kronborgia isopodica, described from Kaikoura, the adults of which live in the body cavity of Exosphaeroma obtusum (Blair & Williams 1987; Williams 1988).

Suborder Valvifera
These include the so-called sea-centipedes and other bizarre forms, comprising 25 described New Zealand species. The form of the uropods, as long plates attached to the side of the abdomen and tightly enclosing all the pleopods, defines the valviferans. Most are marine, but the three species of Austridotea are among the few freshwater members of the suborder (Chadderton et al. 2003). Some forms are ornately decorated. The only family-level reviews are by Poore and Lew Ton (1990, 1993) and Poore and Bardsley (1992). The family arrangement follows Poore (2001b).

Suborder Oniscidea
These are the land-dwelling woodlice, slaters, and pillbugs, with 72 described New Zealand species known. Four species are naturally occurring non-endemics and six others are introduced. Diagnostic characters: usually flattened but sometimes able to roll up; five pleonites usually free; pleopods highly modified for air-breathing. Oniscideans are exclusively terrestrial and are the only crustacean group to compete successfully with other arthropods on land. Seven pairs of legs immediately reveal that they are not insects or millipedes. There are examples high up on the seashore but none is truly marine. Although damp places, and under leaves and decaying logs, are favoured habitats, some overseas species are known from deserts. Like all isopods, oniscideans rely for respiration on their pleopods, which are kept damp with a variety of water-conservation measures. Most species are scavengers on dead plant litter but some can be pests in gardens. There are numerous families including five genera and many species endemic to New Zealand. But the most commonly seen species are introduced from Europe. The New Zealand fauna was reviewed by Hurley (1950) and one family revised by Green (1971). Some of the names listed by Hurley are now out of date and the present review follows the taxonomy of Green et al. (2002).

Historical overview of isopod studies
The first scientific collection of isopods in New Zealand was made by the French biologists J. R. C. Quoy and J. P. Gaimard when the l’Astrolabe, captained by Dumont d’Urville, visited in 1826. They discovered two shallow-water sphaeromatids from algae, described 13 years later as Isocladus armatus and Cassidina typa in a significant publication on isopods by H. Milne Edwards (1840). Earlier publication dates appear in the New Zealand checklist but these are of species either introduced to the country or of species described from elsewhere. Later, the United States Exploring Expedition visited New Zealand on its 1838–42 round-the-world voyage, and numerous species of marine animals were described by its chief scientist, James D. Dana. Among these are 19 species of isopods (Dana 1852b, 1853–55). The first review of the New Zealand crustacean fauna (Miers 1876) listed 28 isopod species in 16 genera. When a second review was completed 10 years later by Thomson and Chilton...
(1886), 60 species of isopods had by then been described, many by these two authors. A third checklist and key (Hurley 1961) listed 168 species; the increase in the intervening years was contributed largely by results from foreign deep-sea expeditions like the British HMS Challenger (1873–76) and Danish Galathea (1952). By 2009 the number had grown again, largely as a result of the work of New Zealand-based taxonomists Desmond Hurley and Peter Jansen in the 1970s and Niel Bruce in the 2000s, as well as overseas workers with an interest in specific families (J. Just, R. Lincoln, G. C. B. Poore, and J.-W. Wägele).

Special features of the New Zealand isopod fauna
Some 38 isopod families have marine representatives in the New Zealand fauna. Gaps can be explained by inadequate collecting. For example, it is safe to say that most deep-water asellote families will be recorded once appropriate sampling is done. It is possible that the Ancinidae and Corallanidae might one day be found in New Zealand. Four small families from the southwestern Pacific (Bathynataliidae, Hadromastaciidae, Keuphyliidae, and Phoratopodidae) are so far not recorded from New Zealand. The Serolidae, rich in species in shelf environments in Australia (Harrison & Poore 1984; Poore 1985, 1987), the southwestern Pacific (Bruce 2009b), and Antarctica (Brandt 1988; Wägele 1994), is represented in New Zealand by only a relatively small number of deep-water species, several of which have been described (Bruce 2008; Storey & Poore 2009).

The Gondwanan affinities of the fauna are evident in the largest families, Sphaeromatidae and Cirolanidae, where genera found in other Gondwanan continents dominate. This is clear too in Plakarthriidae, a family known only from three species, one each in South America, New Zealand, and southern Australia (Poore & Brandt 2001). The same is true for the terrestrial families, with many Palaearctic oniscidean families absent and strong radiation of southern ones. The Phreatoicidea is a typical high-level Gondwanan taxon, being confined to New Zealand, Australia, and India.

New Zealand isopods are largely endemic – 100% of freshwater species, 86% of terrestrial species, and almost 77% of marine species. The endemcity of some taxa reflects the long isolation of the fauna from Australia, the continent from which it last separated 85 million years ago. Close relatives (perhaps sister species) of New Zealand species are found in Australia within several families, e.g. Austrarcturellidae, Idoteidae, Leptanthuridae, Phreatoicideae, Plakarthriidae, and Sphaeromatidae. Much less is known about relationships among other apparent endemics. Many species from the shelf and deep sea are known only from type specimens from a single sample, so their true distribution is unknown. But even here evidence is emerging that endemism is truly high. For example, none of the anthurideans or haploniscid and dendrotiid asellotes described from New Zealand occurs in Australia (Cohen 1998; unpublished material and catalogues).

Non-endemic species fall into two groups – those apparently naturally widespread, and those thought to be introduced. The idoteids Batedotea elongata and Paridotea ungulata have been identified from algal communities in New Zealand and Tasmania and another, Idotea metallica, is cosmopolitan on oceanic algal wrack (Poore & Lew Ton 1993). Several other species may occur naturally in New Zealand and Australia and sometimes also elsewhere, e.g. Natatolana pellucida (Cirolanidae), Limnoria rugosissima, L. tripunctata (Limnoriidae), and Cymodoce convexa (Sphaeromatidae). Several species of aegid micropredators of fishes and at least three species of cymothoid fish ectoparasites seem widespread in the Tasman Sea (and sometimes beyond), as are their host species. A deep-sea gnathiid, Bathygnathia vollenhovia, which occurs on both sides of the Tasman Sea (Cohen & Poore 1994), is certainly naturally distributed. For other seemingly widespread species, identifications are suspect until type material has been compared. Specimens of the New Zealand sphaeromatid Pseudosphaeroma campbellense identified from Australia (Harrison 1984) may be specifically
different (Poore 1994; Bruce & Wetzer 2008). This suspicion is especially valid for some species recorded from the New Zealand subantarctic but whose type locality is elsewhere, e.g. the sphaeromatids *Exosphaeroma gigas* and *Cymodocella tubicuina* (Hurley & Jansen 1977; Brandt & Wägele 1989).

The most familiar isopods of gardens and farmland, the woodlice and pillbugs, are definite imports from Britain or continental Europe, namely *Armadillidium vulgare*, *Porcellionides pruinosus*, and *Porcellio scaber*. They arrived with garden plants or simply as stowaways with the first Europeans. An export of a Slater has occurred, too – the styloniscid *Styloniscus otakensis* to Australia’s Macquarie Island (van Klinken & Green 1992).

### Alien marine isopods

For marine isopods the presence in New Zealand of exotics is ambivalent, although the ability to be transported to and from New Zealand with fouling on ships is certain. Cranfield et al. (1998) recorded three isopods as potentially introduced to New Zealand. The first, Australian species *Cymodoce tuberculata* (Sphaeromatidae), recorded by Chilton (1911b) from a plank of the ship *Terra Nova* in Lyttelton, seems not to have become established in New Zealand. The second, a species of wood-boring gribble, *Limnoria tripunctata* (Limnoriidae), has potentially been distributed by shipping between widespread localities around the world but its origin is unknown (Cookson 1991). The third, *Limnoria rugosissima*, is a borer of algal holdfasts, not of timber, so is more likely to be distributed between southern Australia and New Zealand by drifting kelp. On the other hand, *Limnoria quadripunctata* (not listed by Cranfield et al. 1998) was first described from Europe and now globally recognised; its origin is more probably Southern than Northern Hemisphere (Cookson 1989; Poore & Storey 1999). Likewise, *Sphaeroma quoianum* (Sphaeromatidae), another wood-borer and its commensal, *lais californica* (Janiridae), could have been distributed similarly. *Eurylana arcuata* (Cirrolanidae) is possibly a New Zealand species introduced to Australia (or vice versa) and to North America (Bowman et al. 1981).

The affinities of the New Zealand fauna can only be understood if the taxonomy is accurate. Two species of *Phalloniscus* (Oniscidae) erroneously recorded from Australia, *P. kenepurensis* and *P. punctatus*, were excluded by Bowley (1935) and Green (1961). *Deto marina* (Scyphacidae), recorded from New Zealand by Schultz (1972), is endemic to Australia.

### Order Tanaidacea: Tanaids

Tanaids (there is no common name) are very small, shrimp-like creatures. They are mostly in the 2–5 millimetre range but adults of a few species can be as small as half a millimetre or as long as 75 millimetres (Gamo 1984). There are three living orders, the members of which exhibit characteristic morphologies and, to some extent, lifestyles. Species of Neotanaidomorpha are free-living surface dwellers, while those of Tanaidomorpha are largely tube dwellers and the Apseudomorpha are mostly burrowers or crawlers. The first two segments of the thorax are covered by a carapace forming, with the head, a cephalothorax. The first thoracic segment supports a small pair of maxillipeds, the second a distinctive pair of chelipeds, and each of the third to seventh segments bears a pair of pereopods. The first pereopod may be adapted for burrowing in the suborder Apseudomorpha, equipped with spinning glands for tube construction in the suborder Tanaidomorpha, or may be a simple ‘walking leg’ in the suborder Neotanaidomorpha. Sexual dimorphism is often evidenced in the chelipeds and the claw of the left cheliped can be greatly enlarged in the males of some species of Apseudomorpha. Each of the first five abdominal segments normally carries pleopods but these may be absent in many deep-sea species. The final pleonal segment is fused with the telson.
(forming a pleotelson) and carries a pair of uropods. Respiration takes place over the inner surface of the carapace.

As with other peracarid crustaceans such as isopods, amphipods, and cumaceans, tanaids carry their fertilised eggs and mancae (post-larval juveniles) within a ventral marsupium. In most groups this is formed out of four pairs of oostegites, attached to the first four pairs of pereopods. This is not the case in the Tanaidae, examples of which that are common in intertidal habitats; in this family the marsupium is seen as a ventral pair of elongate sacs (or sometimes just one sac). Similarly, species of Pseudotanaidae, common in the deep-sea, have only a single pair of oostegites arising from the fourth pair of pereopods. There is also some evidence to show that in some burrowing-tubicolous groups (such as the Typhlotanaidae) the female constructs a mucous brood pouch in which she and her young live (G. Bird unpubl.).

Tanaids are usually detritivores or grazers but some taxa are filter-feeders and opportunistic predation on smaller invertebrates (such as foraminiferans or juvenile echinoderms) may be common. Only a few species are considered to be parasitic but none are obligate parasites. Tanaids are preyed upon by a large number of other organisms including polychaetes, other crustaceans, migratory birds, and a large number of juvenile and adult fish such various rat-tails and grenadiers in the deep sea (Bird unpubl.)

Identification of tanaids is notoriously difficult, complicated by their small size and sexual and developmental variation (Larsen 2005) along with widespread and intense convergent evolution. So far, 25 families, more than 200 genera, and more than 1000 species have been described, but it is estimated that the order contains several thousand undescribed species, most of which are suspected to live in the deep sea. Tanaids live almost exclusively in marine or brackish habitats, with just a few species in fresh water. They occupy a wide range of depths. Marine species can be found intertidally among coralline algae, crevices, holdfasts, and in rock-pools. Shallow-water and shelf forms can be found in sand and mud, although tanaid sand-faunas are typically sparse. Tanaids are very common and species-rich in deep-sea oozes and some live in deep-ocean trenches to hadal depths exceeding 9000 metres (Kudinova-Pasternak 1972).

Apart from those species that are attached to floating objects, all tanaids are benthic, but some have short-lived males that can be found swimming above the seafloor in their search for females. Tanaids are free-living, tube-dwelling, burrowing, or live in association with other organisms in a variety of relationships. Some live as epifauna on solitary corals (Sieig & Zibrowius 1988), colonial corals and hydroids (Bacescu 1981), live scallops (Brown & Beckman 1992), oysters (Bamber 1990), barnacles (Reimer 1975), and even sea turtles (Caine 1986). Some species are true symbionts, living together with gastropods (Howard 1952), tube-dwelling sea cucumbers (Larsen 2005), in the canals of sponges (Hassack & Holdich 1987), and as cleaning commensals on mobile bryozoan colonies (Thurston et al. 1987). Tanaids may also have their own epifaunal associates such as stalked protozoans (Gardiner 1975) or bivalves (Warén & Carozza 1994) and deep-sea species can carry foraminiferans embedded in the cuticle. They may be parasitised internally by nematodes and externally by copepod-like tantulocarids (Larsen 2005).

The New Zealand fauna is so poorly known that even an approximate assessment is difficult but, if comparison is made with a similar area and range of habitats, based on the Rockall–Biscay region of the Northeast Atlantic (G. Bird unpubl.), then 250–300 species are possible. The cryptic habits of the group and the small number of active specialists globally and in New Zealand suggest that this state of affairs may continue for some time although progress is now being made. Knowledge of the New Zealand fauna is still largely based on the older published records of Chilton (1882c, 1883), Thomson (1880, 1913), Stephensen (1927), Wolff (1956b), and Lang (1968). As a consequence, there are only about 20 authoritative records among the species in the end-chapter checklist. The
remainder are unpublished records or undescribed species based on studies by Graham Bird, Elizabeth Hassack and the late Jürgen Sieg. Amongst these records are a number of undescribed species (indicated in the end-chapter checklist by bracketed numbers) and several new genera, the family affiliation of which is not currently available. This list is a snap-shot view and highly provisional. A few old records have been reappraised in the light of current tanaid taxonomy (Larsen & Wilson 1998, 2002; Knight & Heard 2006; Bird 2008). The New Zealand fauna also contains one of the few known freshwater tanaids – *Sinelobus stanfordi* from lakes in the Rotorua district.

**Order Cumacea: Comma shrimps**

The common name for cumaceans alludes to one of their distinctive features, i.e. resemblance to a comma when preserved. That is, they have an enlarged front section (head and part of the thorax) followed by a rather narrow posterior section (remainder of thorax and abdomen).

Comma shrimps live on the seafloor with their bodies generally slightly submerged in the sediment. They feed on diatoms, pieces of seaweed, foraminiferans, and detritus, which they collect from the sediment surface. For the most part, they will stay hidden in the sediment during the day, and some will make extended trips into the overlying water after sunset. The reasons for these excursions are not precisely known, but include molting and searching for mates. In fact, in some cumacean families, the body morphology of the mature male is completely modified for swimming, suggesting that at that stage the animal rarely visits the sediment. Swimming cumaceans are vulnerable to fish predation, and mature males are commonly found in fish stomachs.

The cumacean body is one of the more modified of the higher crustaceans. Anteriorly, the head and three segments of the thorax are covered with a carapace. As a result, the normal feeding appendages of the head are augmented by three thoracic appendages (known as maxillipeds) that are also used for feeding. The first of these is also highly modified for respiration. That is, the epipod, which is not present in amphipods and is reduced in isopods, is greatly enlarged in cumaceans as a branchial lobe. Respiration occurs as the branchial lobe is moved back and forth underneath the sides of the carapace.

The remaining thoracic segments bear appendages that function as walking legs. In some cases, especially in mature males, these legs will also have an outer branch, the exopod, that is used to aid in swimming. The abdomen is generally long and thin. Abdominal appendages are either pleopods, if they occur on one or more of the first five segments, and uropods when present on the last segment. Pleopods are not present in the females of species that occur in New Zealand, and may or may not be present on some or all segments in the males. A final, post-abdominal segment, the telson, may be present as a separate structure, or it may be fused to the last abdominal segment.

Cumaceans are rare in the fossil record. There are two species known from the Jurassic, but they are more or less similar to a modern cumacean family, suggesting that the group as a whole is quite old. On the other hand, cumaceans are among the last of their line to have evolved, so it possible that all peracarids were present by the end of the Paleozoic.

As with other members of the superorder Peracarida, cumaceans carry their young in a brood pouch, with the young hatchling looking like a miniature version of the adult minus the last pair of thoracic legs. Because of this direct development, cumacean species are generally not very widespread, and some genera are restricted to individual continents or ocean basins. Some families, such as the Bodotriidae and Nannastacidae, are primarily warm-temperate to tropical, while others such as the Lampropidae and Diastylidae are most diverse in colder oceans. All families are represented in the deep sea, but lampropods show the greatest diversity in that environment.
New Zealand Cumacea
The first cumaceans known from New Zealand were described by George Thomson (1892), who had spent a couple of days dredging in the Bay of Islands in 1883. Not being able to sort the material for some time, his two species went undiscovered for several years. It would be another decade before Zimmer (1902) would describe an additional two species, collected by Prof. Dr Thilenius from the Bay of Plenty and deposited in the Berlin Museum. The biggest contribution, to this day, of our knowledge of New Zealand cumaceans was made by W. T. Calman, who, over a 10-year period (Calman 1907, 1908, 1911, 1917), described 17 species from material sent to him by G. M. Thomson and Henry Suter. Norman Jones, a prolific cumacean worker, described a new species and added a new record from the Chatham Islands area (Jones 1960). He added five new species and two new records to the New Zealand fauna in his now classic monograph covering material in the collections of the former New Zealand Oceanographic Institute (now part of NIWA), the Zoology Departments of Auckland and Canterbury Universities, and the then Dominion Museum, Wellington (Jones 1963). A further eight deep-water species were described by Jones (1969) from material collected in the Tasman Sea by the Galathea Expedition.

Over the intervening 31 years, many samples containing cumaceans have been taken in the waters of New Zealand’s EEZ and stored in the NIWA Invertebrate Collection, Wellington. Until this present review, no one had taken the challenge of working up this material. Most of the new material examined was collected in the deep waters of the New Zealand microcontinent and contains much that is new, both at species and genus levels. From these collections, four new species of Gynodiastylidae were found and described in a recent monograph of the family by Gerken (2001). Several other new taxa have been sorted from the collections and will be described in future papers.

Of the eight currently recognised cumacean families, only six are represented in New Zealand waters. (The Ceratocumatidae is known only from abyssal depths in the Atlantic and Indian Oceans and the Pseudocumatidae are so far exclusively Eurasian–Atlantic in distribution.) The Gynodiastylidae is the smallest of the families represented in New Zealand, with only seven species, and the Diastylidae the largest, with 19 species formally known (and at least another six species remain to be characterised). Some remarks are now offered for each family, based on historical records as well as new findings from NIWA material.

**Family Bodotriidae: Subfamily Bodotriinae.** Members of this subfamily occur in all oceans, primarily in shallow water, but also in the deep sea. New Zealand is quite unusual in having only one (Cyclaspis) of the 13 genera represented in its fauna. This is most likely because the other genera are primarily warm-water and have invaded temperate waters only at the edges of their distributions. Because of the long isolation of the New Zealand microcontinent, temperate-water invasion would have been difficult. On the other hand, Cyclaspis is found in tropical to cool-temperate shelf waters as well as the cold waters of the deep sea, so its radiation in New Zealand waters might be expected. The level of endemicity is high in absolute numbers, but species in this genus are usually found in one, maybe two, zoogeographic provinces. Few new species are likely to be found in shelf waters, with most additions to the fauna coming from bathyal depths. If another genus is to be added, it will most likely be something completely new.

**Family Bodotriidae: Subfamily Vaunthompsoniinae.** This subfamily is largely austral in its distribution and is found from tropical-shelf habitats to cold bathyal waters. Only one New Zealand shelf species is known, and it is not endemic. One of the two bathyal species is endemic, as are both abyssal species. It is unlikely that more than one or two additional shelf species will be found, but the deep-water fauna could continue to contribute new genera and species.

**Family Diastylidae.** Of the seven genera represented, one (Colurostylis) is
Some New Zealand representatives of cumacean families.

Bodotriidae: A (female), B (male), Cyclaspis elegans; C (female), D (male), Cyclaspis thompsoni.

Diastylidae: E (female), Diastyris acuminata (Diastylidae); F (female), G (male), Coluroystylis pseudocuma.

Gynodiastylidae: H (female), Gynodiastylis milleri. Lampropidae: I (female), Hemilamprops pellucida.

Leuconidae: J (female), K (male), Paraleucon suteri. Nannastacidae: L (female), Campylaspis rex; M (male), Nannastacus pilgrimi.

A–K, M, from Jones 1960; L, from Gerken & Ryder 2002
endemic. The others are broadly distributed in the colder waters of the world ocean. The genera *Makrokylindrus* and *Vernakylindrus* are exclusively bathyal or deeper. Specific endemicity is very high (18 of 19 known species) for this family considering the widespread nature of the genera. In addition, diastylids are very abundant and at least one or two individuals can be found at any benthic sampling station.

*Family Gynodiastylidae.* This is a predominantly southern hemisphere family (but ranges as far west as the Persian Gulf and east to Japan) and exhibits its greatest radiation in southern Australia. There are seven endemic species in New Zealand shallow waters, of which three are in the widespread genus *Gynodiastylis.* One of the new species, in the genus *Allodiastylis*, was found at bathyal depths.

*Family Lampropidae.* The lampropids are a worldwide, cold-water, primarily deep-sea group. The taxonomy of the family is in need of serious revision, so some of the species found in the current study may be assigned to new endemic genera when revision is completed. Prior to this study only one lampropid, *Hemilamprops pellucidus*, was known from New Zealand. It is a widely distributed southern hemisphere species. Bathyal waters, however, have so far produced eight new species and one new genus (Gerken 2010), suggesting that the Chatham Rise and Campbell Plateau have much higher-than-average lampropid diversity.

*Family Leuconidae.* This family has very high generic endemicity (three of six genera) in New Zealand, especially in shelf waters. Further, the endemic genera are morphologically advanced within the family, anchoring a group (clade) where the male second antenna becomes reduced in length and modified so it can be used to grasp the female during mating. This trend continues in other eastern Pacific genera, with the second antenna possessing a more complete grasping structure in one Japanese genus and finally culminating in a western North American slope-dwelling genus where the grasping structure is all that is left of the appendage. All species of leuconids are endemic, with the single exception of *Eudorella truncatula*, which is surely an introduced species, broadly distributed in the North Atlantic and North Pacific. This family does not seem to be well represented in New Zealand bathyal samples, in contrast to what is seen in northern hemisphere waters.

*Family Nannastacidae.* There are two groups of genera in this family in New Zealand – deposit-feeding *Cumella* and its relatives and carnivorous *Campylaspis* and its relatives. Of the deposit-feeders, only one genus, *Scherocumella*, has been found in shallow waters, and two genera were found in the bathyal samples. This group seems to be under-represented in New Zealand. In contrast, there are at least six species of the carnivorous genus *Campylaspis* and two of *Procampylaspis*. The radiation within these genera is typical of that seen in other shelf and slope cold-water environments in both northern and southern hemispheres. All species in this family are endemic. The finding of a species of *Styloptocuma* extends the range of this genus into the Pacific.

In summary, there are two groups of cumaceans in the New Zealand fauna – the highly endemic species and genera of shallow water and the continental shelf, and the bathyal and abyssal species that belong to genera and families that are widespread throughout the cold deep waters of the world. Notably, within one family, the Leuconidae, there has developed a specialised morphology among the males that seems to have spread northwards in the eastern Pacific, culminating in advanced forms in Japan. Finally, New Zealand lacks representatives of many warm-temperate genera, even though it has a warm-temperate zoogeographic province and the Kermadec Islands within its EEZ. This may be a consequence of the geological history of the microcontinent, which, after it became isolated, went through a cooling period, thus eliminating resident warm-water species.

**Gaps in knowledge of New Zealand Cumacea**
The cumacean fauna of New Zealand’s EEZ currently comprises 31 genera (two not yet named) and 74 species, not all formally named. Of these, about half, i.e.
15 genera and 37 species, are from shelf waters. In 1999, a brief collection by Les Watling in a few areas of the North and South Islands produced one new species of *Colurostylis*. Additional collecting is probably not likely to result in the addition of more than 10 new species from shelf depths, with the possible exception of Stewart Island and the subantarctic islands, which so far remain unexplored with respect to cumaceans. The relatively few samples (ca. 15) obtained by Watling have so far yielded 31 new species and two new genera, with the Diastylidae still to be studied in detail. None of the species in the new NIWA and Watling samples can be matched to the eight species Jones (1969) described from the Tasman Sea, suggesting either that there is a high level of endemicity between the east and west deep waters of New Zealand or that the deep-water fauna is very diverse. Neither of these hypotheses is unlikely. Because they brood their young, cumacean species are highly restricted to zoogeographic provinces in shallow water, and may well be restricted to individual tectonic plates in deep water. Since cumacean diversity is generally highest in the Southwestern Pacific, one might expect the overall diversity of bathyal waters to be much higher, at least by a factor of two, than that which has been observed to date. In addition, the lack of correspondence between the shallow New Zealand and southern Australian faunas lends credence to the fact that there is little natural water-borne transport of cumaceans. Most likely the shelf-dwelling cumaceans of New Zealand evolved in situ from whatever stock was present after Zealandia (the New Zealand continental mass) separated from Antarctica about 56 million years ago.

**Order Euphausiacea: Krill**

We’ve all heard of ‘krill’, shrimp-like crustaceans congregating in vast swarms in cooler latitudes of both hemispheres, and famous as whale food. The term krill was originally used by Norwegian whalers for the northern hemisphere cold-water euphausiids *Meganyctiphanes norvegica* and *Thysanoessa inermis* (Mauchline & Fisher 1969) but is now applied to all species of the order Euphausiacea. ‘Euphausiids’ is itself an unusual word because the ending ‘-ids’ is commonly reserved for family names, not orders. But all except one species of Euphausiacea belong in just one family, the Euphausiidae and, based on long-term use, ‘euphausiids’ is here to stay. The Euphausiidae contains 85 species and the Bentheuphausiidae one species.

The Euphausiacea is notable among the crustacean orders because all the species have conceivably been described. One or two new species may yet be discovered, but only eight have been added in the last 50 years, two in the last 30, with the very deep-water *Thysanopoda minyops* Brinton, 1987, the most recent. However, in some species, particularly in the genus *Stylocheiron*, up to six distinct ‘forms’ are recognised (Brinton et al. 1999). A few species such as *Euphausia similis* and *E. similis* var. *armata* are also extremely similar. In some cases these forms and species are geographically separate and in others overlapping. It is unclear what the taxonomic significance of these forms is, but new taxonomic techniques such as gene-sequence analysis may resolve this problem. If so, it seems likely that any future changes in the number of euphausiid species are more likely to result from redefinition of current taxa than from new discoveries. There is a further, informal subdivision of the family Euphausiidae, with Brinton et al. (1999) listing several ‘species groups’ within five of the larger genera based on morphological similarity. The 19 species found in New Zealand waters are named in one or another of these groups.

Krill are of great importance in the marine economy because of their vast numbers. They constitute a major proportion of oceanic biomass, are major grazers of phytoplankton and consumers of small zooplankton, and are themselves essential in the diets of whales, fish, seals, seabirds, and even people.
Morphology and distinguishing characters of krill

Krill are rather uniform in appearance and easily distinguished from other crustaceans. Their morphology is well illustrated and described in several publications, including Baker et al. (1990), who gave a particularly clear overview of their structure, and Brinton et al. (1999). Only the more distinctive characters are described here. Typical of shrimp-like crustaceans, krill are adapted to a natant (swimming) life-style, having an elongate body with the cephalothorax covered by a carapace, a six-segmented abdomen, and a telson with uropods that form a tail fan. They also have moveable eyes, biramous first and uniramous second antennae, and, behind the mandibles, two pairs of maxillae. There are eight pairs of thoracic limbs. Each has a two-segmented outer exopod and a five-segmented inner ‘leg’ but the posteriormost pair of limbs (eighth pair) is reduced to lobes in all but Bentheuphausia amblyops. The form of the seventh pair of limbs also varies between genera. While the first pair of limbs is used in the manner of maxillipeds they are similar in form to those behind. Abdominal segments 1–5 bear a pair of pleopods, the first pair in males being modified to form a handlike copulatory organ (petasma). This is used to transfer sperm packages to a midventral female structure (thelycum). The petasma and thelycum are diagnostic of species although they can be difficult to examine and other, more accessible, structures are generally used for this purpose if they are present and undamaged. Of particular use in this respect are the proximal three segments of the antennule (the antennular peduncle), which may bear a lappet having a characteristic shape or number of spines. The peduncle is usually present in collected specimens and used in combination with other characters.

Thysanopoda acutifrons.
From Holt & Tattersall 1906
**Classification**

Martin and Davis (2001) placed the order Euphausiacea, with the Decapoda and Amphionidae, in the superorder Eucarida, well separated from the Mysidacea and other orders of the Peracarida. Brinton et al. (1999) recorded earlier recognition of the similarities between krill and the pelagic decapod shrimps of the Sergestidae (suborder Dendrobranchiata). Krill and sergestid shrimps have free-swimming nauplius larvae, metamorphose to the post-naupliar larval stage, have reduced posterior thoracic limbs, and have a petasma in the male and thelycum in the female. However, Brinton (1966) had suggested these similarities might reflect parallel evolution rather than a close relationship. A recent analysis of ribosomal DNA sequences in krill (Jarman et al. 2000) indicates that they may be more closely related to the Mysida than to the Sergestidae, which accords with Brinton’s suggestion.

**Discovery and diversity of New Zealand krill**

Most krill are oceanic in distribution, with consequent low endemicity, and no species is confined to the New Zealand region, so the history of studies of species recorded in the region is mostly international. The first species recorded from the New Zealand region were those collected by the 1873–76 Challenger Expedition (Sars 1883, 1885). Sars’s reports included 12 of the 21 species now known from New Zealand waters (see end-chapter checklist). H. J. Hansen (1905a,b–1911) described many species in several papers published in the early 20th century, including five species that occur in the New Zealand EEZ.

Tattersall (1924) provided the first list of seven New Zealand krill species gleaned from the reports of Sars (1883), Thomson (1900), and Hansen (1911) and added six more collected by the Terra Nova Expedition of 1910. Soon after, Chilton (1926) listed them again but included two species that Tattersall had reported, although rather unclearly, as occurring only in Australian waters (*Pseudo euphausia latifrons* and *Euphausia tenera*). Neither has been recorded from New Zealand since, meaning Chilton’s (1926) list more accurately gives 13 New Zealand species. The remaining 12 recorded species have resulted from surveys of pelagic faunas and plankton off New Zealand’s coasts (Roberts 1972; Bradford 1972; Bartle 1976; Robertson et al. 1978). The work of Bartle (1976) focused on krill in Cook Strait and is the most extensive study of the New Zealand fauna to date. Four new records are included in the current checklist from collections held at the Museum of New Zealand.

The only identification guide to krill that includes the New Zealand region was produced by Kirkwood (1982), but, apart from the early works listing New Zealand species and referred to above, no taxonomic works on krill in New Zealand waters have appeared. Sheard (1953) reported in detail on the taxonomy, distribution, and development of the Euphausiacea with particular emphasis on the Australasian species *Nyctiphanes australis*. A number of recent papers have reported on aspects of the biology of *N. australis* in southern New Zealand waters and/or included useful distributional and biological observations (e.g. Bary 1956, 1959; Jillett 1971; Bradford 1972; Dalley & McClatchie 1989; McClatchie et al. 1989, 1990, 1991a,b; Murdoch 1989; O’Driscoll 1998a,b; O’Driscoll & McClatchie 1998). Research on krill biology continues around the world, especially on species of economic importance such as *Euphausia superba*, but the review of Mauchline and Fisher (1969) remains the major source of information. These authors brought

![Thysanoessa gregaria.](image-2)

*After Sars 1885*
together a large and disparate literature on all aspects of euphausiid biology, and Mauchline (1980) updated this. Baker et al.'s (1990) guide to the world’s krill species is indispensable. It includes a good brief description of euphausiid anatomy and well-illustrated keys to the species. A paper on krill fisheries of the world (Nicol & Endo 1997) was recently published by FAO, and an easy-to-use CD by Brinton et al. (1999), giving illustrated identification of species, synonymies, references and distribution maps, was published by UNESCO.

The genus best represented in the New Zealand region is Stylocheiron. Half of the 12 species known globally occur in New Zealand waters, whereas only two (20%) of 10 Thysanoessa species have been recorded here. Nyctiphanes australis is one of four and Nematobrachion flexipes one of three species in their genera. Two of seven species of Nematoscelis (29%) and five of 14 Thysanopoda species (36%) are present. Euphausia, the largest euphausiid genus with 31 species, is represented in New Zealand waters by just six species and one subspecies (22%). Records from New Zealand include three ‘round-eyed’ genera (Euphausia, Nyctiphanes, Thysanopoda) and three genera with bilobed eyes and elongated legs (Nematobrachion, Nematoscelis, Stylocheiron). Both Thysanoessa species found in New Zealand waters also have bilobed eyes.

Species recorded in the literature as present, and species believed to be correctly identified, are listed in the end-chapter checklist, but this probably does not give the full picture. Other species are very likely to occur in New Zealand waters. Brinton (1962a) and Brinton et al. (1999) have given Pacific-wide and worldwide distributions of krill. Because they are typically offshore and pelagic in habit, mostly with wide geographic distributions, these distributional data and maps are, of necessity, generalised. Records from outside New Zealand’s EEZ suggest that some species may range within the EEZ boundary, and shading on some maps in both works (Brinton 1962a; Brinton et al. 1999) indicates that they do. It is possible, though unlikely, that one or two species have been recorded from New Zealand in food studies of their many predators (fish, birds and whales), not reviewed here. Unrecorded krill species likely to be present include some medium-to-large sized species that may escape capture; not all krill swarm, and swarming species are easier to catch. Some species also live at depths where fine mesh nets are seldom deployed. The deep-living species Nematoscelis tenella and oceanic N. atlantica fit these criteria and have yet to be found in New Zealand waters.

More species of Thysanopoda are also likely to be present in New Zealand waters. Mesopelagic T. astylata, T. cristata, T. orientalis, and T. pectinata occur widely in the Pacific to about 35° S and a few Thysanopoda species are meso- or bathypelagic and seldom sampled, e.g. T. spinicaudata, found at 2000–3000 metres. Species such as T. cristata are sparsely distributed and not caught regularly. Distributional records in Brinton et al. (1999) suggest at least some of these species may occur in the deep offshore waters of New Zealand but have yet to be collected, which is also the case for Benth euphausia amblyops (Benth euphausiidae) found throughout the Pacific to 54° S.

The species considered above live either in tropical or subtropical waters or are bathypelagic. Several species present in colder, Antarctic circumpolar water lying south of the Subantarctic Convergence (Euphausia superba, E. frigida, E. triacantha, Thysanoessa macrura, and T. vicina) must also come close to encroaching on the southern areas of New Zealand’s EEZ. However, Morris et al. (2001) have shown that the Subantarctic Front (Convergence) forms a boundary between the colder, fresher Antarctic water to the south and warmer saltier subantarctic water to the north of the front. This abrupt, hydrographic and biological barrier extends deeply into the water column and is apparently a permanent phenomenon. The front also skirts the southern edge of the Campbell Plateau, 200 kilometres south of Campbell Island. This suggests that these circumpolar species are unlikely to be found within the EEZ, except perhaps as stragglers.
Nyctiphanes australis, a small species with adults 10–17 mm long and first recorded in New Zealand more than a century ago (Thomson 1900), is probably the best-known euphausiid of New Zealand waters, being abundant around the main islands and south to The Snares. It has also been studied more than any other species occurring here or in Australian waters, where it is also plentiful from New South Wales to South Australia including Tasmania.

The New Zealand species of Euphausia are all small to medium-sized; as adults, E. recurva is smallest at 10–14 millimetres long; E. longirostris, the largest, can reach 34 millimetres. Euphausia similis and E. similis armata, both 22–26 millimetres long as adults, are difficult to distinguish but the latter is more often caught and is one of the commonest krill species encountered in New Zealand.

Three of the five species of Thysanopoda found in New Zealand waters are new records (T. cornuta, T. egregia, T. monacantha). The largest of these is T. cornuta at 50–120 millimetres adult length; purple-red T. egregia reaches 50–62 millimetres, and T. obtusifrons is the smallest at 18–23 millimetres (Brinton et al. 1999).

The identity of Stylocheiron longicorn is complicated by the existence of three ‘forms’ – a North Indian Ocean form, a short form, and a long form. The latter is present in New Zealand waters and throughout all three main oceans, while the short form is almost as widespread and may occur in northern New Zealand. Stylocheiron longicorn is also one of three species of the ‘S. longicorn species group’ (Brinton et al. 1999) in New Zealand waters, the other two being S. elongatum and S. suhmi.

Ecology and distribution of New Zealand krill species
Most krill live in the upper layers of the oceans or in coastal areas. Because they are pelagic at all stages in their life cycles and strongly influenced by currents and environmental factors (light intensity, oxygen saturation, temperature, salinity, and food availability), they tend to be confined to certain water-masses. The majority of species undertake daily migrations, swimming upwards into shallower strata of the water column by night and back down before daylight. Most species are omnivores and feed day and night. Upward migration at night into shallower waters may enable consumption of phytoplankton, while retreat to deeper layers during daylight probably helps to avoid pelagic predators.

Kril are well known for swarming, which they do at regular seasonal intervals or irregularly (Mauchline 1984). Aggregations form at or below the surface for feeding or reproduction and swarming by Nyctiphanes australis during the breeding season is well developed. Swarms of N. australis have been found in harbour and coastal waters of Otago in summer and autumn and a very dense swarm of about four cubic metres was photographed off The Snares by Fenwick (1978). Such swarms tend to be patchy and ephemeral (O’Driscoll & McClatchie 1998) but can be huge and occasionally wash ashore. The largest of a series of strandings of N. australis on Otago Harbour beaches in January 1990 was estimated to be ca. 100 tonnes (McClatchie et al. 1991b). Euphausia similis armata also intermittently strand in large numbers. In March 1985 and February 2002, millions of live individuals were washed ashore at Waikanae Beach north of Wellington. Drifts were hundreds of metres long and ‘ankle deep’, as reported by locals, who also observed gulls gorging themselves on the windfall. The krill had apparently been brought ashore by unusual wind and current patterns in the Cook Strait area.

Although krill actively swim, they are classified as plankton because they are moved about by currents, but the larger-sized species may behave more as nekton. Nyctiphanes australis lives mainly over the continental shelf and further inshore than other species recorded in the New Zealand region (Bary 1956; Blackburn 1980; Brinton et al. 1999). Offshore transport of N. australis is limited by coastal currents running parallel to the coast and by behaviour generated by environmental factors, possibly including vertical movements that place the krill in currents that retain them near the coast (Bradford 1979). Murdoch (1989)
and O’Driscoll and McClatchie (1998) found that *N. australis* off Otago became entrained in an anticlockwise gyre off Blueskin Bay and are most numerous in low-salinity coastal waters resulting from river runoff. Bary (1956) observed that the species tolerates a wide salinity range and also penetrates semi-enclosed waters such as Otago and Wellington Harbours and the Marlborough Sounds. *Nyciphanes australis* undertakes diel vertical migrations from below 150 metres into the top 40 metres of the water column (Bartle 1976) and Bradford (1979) observed that *N. australis* off Kaikoura was able to exist in water temperatures from 8–10° to 23°C.

All species of *Euphausia* recorded in New Zealand waters are oceanic with a circumboreal distribution in the Southern Hemisphere. Only one subspecies, *Euphausia similis similis*, occurs in both hemispheres; the remaining New Zealand representatives of the genus are confined to the Southern Hemisphere, with each distributed in a circumboreal band. South of the Equator *E. similis similis* ranges from 25°S to 55°S (Brinton et al. 1999), which coincides with the northern and southern extremities of the EEZ and encompasses the distribution of its co-subspecies *E. similis armata*. Both subspecies inhabit depths of 0–300 metres but it is not clear if either migrates vertically. Baker (1965) observed what seems to be an inverse relationship between the numbers of the two subspecies and Bartle (1976) suggested this may reflect a difference in depth as he found *E. similis similis* mostly in the upper 100 metres of cook Strait while *E. similis armata* was mainly deeper.

*Euphausia longirostris*, *E. lucens*, and *E. spinifera* also occur north and south of the Subtropical Convergence in New Zealand waters (Bary 1956; Bartle 1967; Robertson et al. 1978; James 1989). *Euphausia recurva* is a more tropical species found as far south as Cook Strait (Bartle 1976) and is bi-antitropical in the major oceans, meaning it is distributed both north and south of the Equator but not across it, although it can be found at lower latitudes than 20°S and 20°N. On the other hand, *E. vallentini* is a colder-water species, recorded by Brinton et al. (1999) from 50°–60° south of mainland New Zealand, but also found within or just to the north of the Subtropical Convergence Zone off Kaikoura (Bradford 1972).

Recognition of *Nematobrachion boopis* in New Zealand waters was only a matter of time since it is very widespread in the three main oceans from 42°N to 50°S. It is the deepest-living species in its genus, the adults being mesopelagic at 300 metres or more, but it also performs daily migrations. *Nematobrachion flexipes* is a deeper mesopelagic species (100–600 metres). It is very widespread though more patchily distributed than *N. boopis* (Brinton et al. 1999).

Two species of *Nematoscelis* are found in New Zealand – *N. megalops* and *N. microps*. The former is a warm-temperate species found in all main ocean basins in the Southern Hemisphere and in the North Atlantic. *Nematoscelis microps* is widespread in warm-temperate seas in all three main oceans between 40°N and 35°S (Brinton et al. 1999) but has been recorded only once off northern New Zealand (Tattersall 1924).

*Stylocheiron elongatum* is widespread in all oceans from 40°N to 35°S (Brinton et al. 1999) although Bartle (1976) collected two juvenile specimens from Cook Strait. He did not consider this unusual since waters of subtropical origin are known to penetrate southwards along the Hikurangi Trench into Cook Strait at 300–500 m, the appropriate depth for *S. elongatum*. *Stylocheiron carinatum*, *S. suhni*, and *S. abbreviatum* have been recorded only in northern New Zealand waters (Tattersall 1924) but *S. maximum* is very widespread in the three main oceans. Its distribution encompasses New Zealand to 63°S in the Pacific Ocean (Brinton et al. 1999) although Robertson et al. (1978) found it only north of the Subtropical Convergence east of central New Zealand. *Stylocheiron maximum* is mesopelagic, being mostly caught at depths exceeding 400 metres, while *S. carinatum* occupies near-surface waters above 140 metres both day and night (Brinton et al. 1999).
Thysanoessa gregaria is biantitropical in all three oceans, is found throughout New Zealand waters, and has been caught regularly in eastern and southern areas (Bartle 1976; Bary 1959; Bradford 1972; Murdoch 1989). While it is usually found above 150 metres depth, Bartle (1976) noted that it is deeper in subtropical than subantarctic waters and suggested it also undergoes extensive vertical migrations. Brinton et al. (1999) indicated that it occupies thermocline waters, rising and falling with them day and night, and that it has been found as deep as 1200 metres. Roberts (1972) identified Thysanoessa macrura at the Auckland Islands but Brinton et al. (1999) placed this species in circumpolar Antarctic waters south of 55° S. It seems likely that Roberts was dealing with T. vicina rather than T. macrura since the two species are difficult to distinguish and, according to Brinton et al. (1999), T. vicina overlaps and occurs north of T. macrura to 50° S.

Thysanopoda cornuta has been found at scattered locations in the three main oceans at 1200–2500 metres depth, while larvae and juveniles are present at 700 metres or deeper. Thysanopoda egregia occurs at 800–2000 metres, while T. monacantha is mesopelagic at 300–400 metres, rising into the upper layers at night. Like several other widespread krill found at these depths, T. monacantha requires water fully saturated with oxygen and is absent from oxygen-deficient areas of the northern Indian and eastern central Pacific Oceans (Brinton 1962b). Thysanopoda obtusifrons inhabits the low-nutrient central water masses of the main oceans and is found up to 140 metres deep at night, migrating below 300 metres during the day.

Breeding and development of krill
Krill sexes are separate. During mating, a sperm package is transferred to the female and sperm are stored in a reservoir until eggs are laid and fertilised externally. In the species of Nematobrachion, Nematosceles, Nyctyphanes, Pseudeuphausia, Stylocheiron, and Tessarabrachion, eggs are attached to the posterior three pairs of thoracic limbs until they hatch at the second nauplius (metanauplius) larval stage. As in other Nyctyphanes species, N. australis females not only retain their eggs until this stage, but also secrete a paired, membranous ‘egg sac’ to hold the eggs (Brinton et al. 1999). Nematosceles megalops lays 220–250 small eggs per brood and Stylocheiron species 2–50 larger eggs (Mauchline & Fisher 1969), both taxa being represented in New Zealand. In the remaining genera (58 species), the first nauplius hatches from eggs that are shed directly into the water. Thus krill have two nauplius stages, but in those with attached eggs the first stage is passed through in the egg.

Nauplius larvae swim using their antennae, and all subsequent developmental stages through to the adult are pelagic. The nauplius metamorphoses to the first of three calyptopus stages in which the abdomen develops its full complement of six segments, a telson and uropods. Throughout the calyptopus phase the eyes remain beneath the carapace, and locomotion continues to be provided by the antennae. The final calyptopus moult to the first of several furcilia stages in which the eyes become stalked and free of the carapace, the antennae are no longer natatory, the thoracic legs and gills appear, and, throughout a series of mouls, the pleopods and photophores become fully developed. The furcilia passes through various numbers of mouls both between and within species and the rate of addition of functional parts varies, depending on environmental conditions. Euphausia superba has the least number of furcilia stages of any euphausiid (six) while species of Thysanoessa may have as many as 11 stages (Mauchline & Fisher 1969).

Sheard (1953) described these complex larval phases of the life-cycle in several species that happen to occur in New Zealand waters, including a detailed description of those in Nyctyphanes australis. Typical of coastal species, the number of larval instars and the sequence of addition of morphological characters (the developmental pathways taken) in N. australis is variable, and
more so than in oceanic species. The final furcilia moults to the first adolescent stage with little morphological change.

**Food, predation, and parasitism**

Krill are omnivorous, feeding on phytoplankton, zooplankton, and organic detritus from bottom sediments. Species with highly fringed feeding limbs use them to filter minute protozoans and algal plankton from the water. The bristles effectively form a fine net to strain food from currents created by the thoracic limbs and pleopods. Species with less setose appendages feed more on zooplankton.

The anterior thoracic limbs can be held in such a way as to form a ‘food basket’ between them and the mouthparts (Mauchline 1984). Bottom-feeding krill employ two methods of collecting food. In one, the animal approaches the bottom in a near-vertical position and, by beating the thoracic exopods, raises into suspension sediment that is filtered by the mouthparts. In the second method, the animal approaches the bottom at a flatter angle and ploughs up the soft sediments with its antennae to form a lump, which it ‘sucks’ into the food basket by a sudden lateral movement of the thoracic limbs. This method is also used repeatedly as the animals swim, to trap planktonic prey such as copepods or chaetognaths in the food basket.

Among New Zealand krill, ‘round-eye’ *Euphausia, Nyctiphanes,* and *Thysanopoda* species have more highly fringed feeding limbs than ‘bilobed-eye’ *Nematobrachion, Nematoscelis, Stylocheiron,* and *Thysanoessa* species. In general, the former group is omnivorous, consuming bottom detritus as well as small plankton and non-living particles from the water column. The two large deep-sea species *Thysanopoda cornuta* and *T. egregia* are also known to eat live prey, having been found with copepods, arrow worms, and juvenile fish in their stomachs (Brinton et al. 1999). Carnivory had been suspected in the latter group of krill because bilobed eyes and elongated legs are thought to be adaptations for the capture of live prey (Mauchline & Fisher 1969). The two large deep-sea species *Thysanopoda cornuta* and *T. egregia* are also known to eat live prey, having been found with copepods, arrow worms, and juvenile fish in their stomachs (Brinton et al. 1999).

*Nyctiphanes australis* is the only one among the above species whose feeding has been studied in New Zealand waters. Bradford (1972) found maximum numbers of this species in Kaikoura waters underneath concentrations of copepods, eating their faecal pellets. Blackburn (1980) listed diatoms, copepods, and copepod faecal pellets in its diet and McClatchie et al. (1991a) also confirmed omnivory in the species in Otago waters.

Dalley and McClatchie (1989) carried out a detailed study of the feeding morphology of *Nyctiphanes australis* in Otago, and McClatchie et al. (1991a) measured the spaces between setae of the food basket at 2–8 micrometres, the finest of any euphausiid measured to that time. This suggested *N. australis* is equipped to filter nanoplankton-sized particles. However, Dalley and McClatchie (1989) also concluded that the species is an ‘opportunistic omnivore’ since it has both a mandibular molar process typical of predators and a mandibular palp and stomach armature characteristic of herbivores. Gut contents, measured using a pigment fluorescence technique (McClatchie et al. 1991a), also revealed substantial amounts of chlorophyll pigments from phytoplankton much larger than nanoplankton, consumed directly, or secondarily in the gut contents of prey. The swarming of *N. australis* in Otago Harbour also coincides with the spring diatom bloom (McClatchie et al. 1991a).

Krill are eaten by a wide variety of cetaceans, fish, and birds. Mauchline (1980) listed the euphausiid species, their major predators, and whether they swarm or not, swarming being an important aspect of their consumption in large numbers. Little appears to be known about predators of *Euphausia longirostris* but five of the other six New Zealand *Euphausia* species that swarm are an important
constituent in the diets of baleen whales. *Euphausia vallentini* was reported by Nemoto (1962b in Mauchline and Fisher 1969) to be eaten by fin and sei whales in waters south of New Zealand. Among the six species of *Stylocheiron*, only *S. abbreviatum* is reported as swarming, but all are known to be important food for planktivorous and micronektonic fish. Being mesopelagic, *S. maximum* is also found in the stomach contents of some demersal fish. Whales, planktivorous fish, and seabirds all eat *Thysanoessa gregaria* when it swarms at the sea surface but, while *T. macrura* has been found in whale stomachs, much less is known about it as a food item. *Nematoscelis megalops* swarms but both it and *N. microps* apparently do not approach the surface and are preyed on by demersal and planktivorous fish. Pelagic and midwater fish feed on *Thysanopoda monacantha* and whales and demersal fish on *T. acutifrons*.

Studies of feeding in New Zealand fish and seabirds have revealed that *Nyctiphanes australis* plays an important role in their diets. Kahawai (*Arripis trutta*) around Kaikoura depend on *N. australis* for much of their diet (Bradford 1972) and barracouta (*Thrysites atun*) also eat this species (Bartle 1976). O’Driscoll and McClatchie (1998) used side-scan radar to study schooling behaviour in barracouta off Otago and came to the conclusion that ‘schooling of barracouta seems to be a feeding strategy to exploit surface swarms of krill’. They also found that jack mackerel (*Trachurus murphyi*) and slender tuna (*Allothunnus fallai*) prey on *N. australis*. Blackburn (1980) reported that southern bluefin (*Thunnus thynnus maccocyii*) and skipjack tuna (*Katsuwonus pelamis*), common in New Zealand waters, eat *N. australis* off Australia. No doubt other pelagic fish prey on this species, and Fenwick (1978) saw six different species of bottom–dwelling fish attacking a swarm near The Snares.

With the exception of penguins, seabirds can exploit krill only at or near the sea surface. Rockhopper penguin (*Eudyptes chrysocome*) stomachs have been found with *N. australis* remains – mainly eyes, which seem to resist digestion longer than other body parts (Te Papa unpubl. data). Many flying birds also exploit this species, e.g. grey-faced petrels (*Pterodroma macroptera*), fairy prions (*Pachyptila turtur*) (Bartle 1976), and, importantly, black-billed gulls (*Larus bulleri*) (McClatchie et al. 1989). They are eaten at sea by red-billed gulls (*Larus novaehollandiae*) but not by black-backed gulls (*Larus dominicanus*), which prefer stranded krill (McClatchie et al. 1991b).

Krill are hosts to various parasites. Mauchline (1980) listed three types of ectoparasites – ellobiopsid and apostome protozoans and dajid isopods. The effects of ectoparasites on the host are not always obvious but it is thought that they impair swimming, increase the risk of predation, and damage the cuticle, allowing bacterial infections (McClatchie et al. 1990). Among krill species found in New Zealand, *Euphausia lucens*, *E. recurva*, *E. similis*, *E. vallentini*, *Nyctiphanes australis*, and *Thysanoessa gregaria* have been recorded as being infested with the ellobiopsid protozoan *Thalassomyces fagei* (phylum *Myzozoa*) (Mauchline 1980). Its precise life-history is not known, but *T. fagei* first appears under the upper carapace of the host, sends a root-like structure down among the organs to gain nourishment, then grows a ‘neck’, up through the carapace, that branches and produces spores. Dajid isopods attach themselves to the cephalothorax of the host. Among the krill recorded in New Zealand, dajids have been observed in *Nematoscelis megalops*, *T. gregaria*, and *Stylocheiron longicorne*. McClatchie et al. (1990) discovered that a stalked pennate diatom also grows externally on *N. australis* caught in Otago Harbour, the first record of such an infestation; 50–70% of *N. australis* sampled in the Harbour were infested. The effects of the diatom on the host were unclear but diatom chlorophyll introduced error into their chlorophyll pigment fluorescence experiments on the krill’s diet.

**Commercial exploitation and resource potential of krill**

The publication by Nicol and Endo (1997) on the world’s krill fisheries is an accessible and essential reference for anyone interested in the subject. These
authors listed six species of krill commercially harvested in various parts of the world – *Euphausia superba* in the Antarctic Ocean, *E. pacifica* off Japan and British Columbia, *E. nana* off southern Japan, *Thysanoessa inermis* off northern Japan and in the Gulf of St Lawrence (eastern Canada), and *T. raschi* and *Meganyctiphanes norvegica* also in the Gulf of St Lawrence. In 1997, the annual catch of krill for human use was estimated at 160,000 tonnes, with *E. superba* the most important species.

Japan is the major fishing nation of both Antarctic krill and northern species, but Ukraine and Poland also have an important stake in the Antarctic fishery. Russia, Korea, and Chile have also been involved at various times. Probably of more interest to New Zealand is research carried out in Tasmania on the potential for a fishery there for *Nyctiphanes australis*, since the species is abundant in New Zealand coastal waters as well.

Human uses of krill include food, bait for sport fishing, aquarium food, and aquaculture food, which is the major use. Krill are of high nutritional value and in Japan are also used to add colour to fish flesh for human consumption. Like the exploited species, *N. australis* has also been shown to have high nutritional value. Krill contain a wide variety of biochemicals, some of possible pharmaceutical value, and Nicol and Endo (1997) listed and discussed their properties and potential uses. They also outlined conservation needs for krill. Current catch rates are thought to be far below the potential for sustainable fishing but the importance of krill in marine food-webs is enormous. The probable effects of overfishing on the many bird, cetacean, and fish predators of krill was important in setting the regulatory Convention on the Conservation of Antarctic Marine Resources in 1980.

Scope for future work

New records of krill species found elsewhere can be expected in the New Zealand region and there is a need to clarify the status of species ‘forms’ and species groups. Compared to the northern Pacific and Atlantic Oceans there is a lack of data on krill in the SW Pacific. Should a fishery for *Nyctiphanes australis* prove commercially viable off Tasmania, investment in further research on this and other species in New Zealand waters will probably follow.

Order Decapoda: Shrimps, lobsters, crabs, and kin

Decapods (‘10-footed’) are the most familiar crustaceans, numbering more than 10,000 living species worldwide – almost half the named species of Crustacea. They occur in a great diversity of forms and habitats and some are highly specialised. Most decapods are marine, living from above high tide to depths of more than 5000 metres and at all levels of the ocean. Some live in fresh water and on land but all land dwellers, including the forest crabs of tropical latitudes, must have access to water to hatch their eggs and to drink. Decapods range in size from tiny shrimps about a millimetre long to the largest of all arthropods, the giant Japanese spider crab *Macrocheira kaempferi* with claws that can span up to four metres. There are tiny crabs that live out their lives within coral galls and the huge xanthid crab *Pseudocarcinus gigas* of southern Australia that reaches 15 kilograms in weight. While North American clawed lobsters are the heaviest of all crustaceans, the largest rock (spiny) lobster is the packhorse rock lobster *Sagmariasus verreauxi* of New Zealand and eastern Australia that can weigh 16 kilograms.

Behaviourally, some shrimps and prawns spend their whole lives swimming, while others associate with various bottom habitats. Lobsters and crabs inhabit all kinds of rocky or soft substrata, some bury themselves temporarily, and others live in permanent burrows in mud and sand. Certain genera of squat lobsters are found only on deep-sea branching corals, while small shrimps are often closely associated with algae, adjusting their colours to blend in. A small number
of shrimp species have become specialised fish cleaners and a few decapods are confined to very circumscribed habitats such as coastal anchialine caves, underwater geothermal vents and cold-water or hydrocarbon seeps, or are specialised to live on decaying wood or whale bone.

The relationships of decapods with other orders of Malacostraca continue to be argued as do relationships among decapod groups (e.g. Martin et al. 2009). The classification followed here is that of De Grave et al. (2009). The traditional separation of decapods into natants and reptants has no formal status but is useful when discussing the ‘swimming’ and ‘crawling’ members of the order and is used here informally.

The Decapoda is divided into two suborders, the Dendrobranchiata, which includes the penaeoid and Sergestoid prawns with gill lamellae divided into many dendritic branches, and the Pleocyemata, including all remaining Decapoda, whose gill lamellae are not dendritic (gills are lamellar in the caridean shrimps and prawns, Brachyura and most Anomura; filamentous in crayfish, lobsters and some dromiid crabs – see McLaughlin 1980 for description of gill types). The Pleocyemata thus includes the majority of shrimp and prawn species as well as freshwater crayfish, clawed, slipper and rock lobsters, true crabs and king crabs, hermit crabs, and squat lobsters.

Along with all other members of the class Malacostraca, the decapod body consists of five cephalic (head) somites (six if the eyes are taken as representing a separate somite), eight thoracic, and six abdominal somites. Appendages of the anterior three thoracic somites are modified as food-handling maxillipeds, a principal diagnostic character of the Decapoda since other Crustacea have no more than two pairs of maxillipeds, while the legs articulate with the five posterior thoracic segments. In all decapods the cephalic and thoracic segments are fused, and protected by a carapace that extends down each side of the cephalothorax to enclose the gills and form branchial chambers. The carapace varies from more or less cylindrical in shrimps, prawns, and lobsters to rounded and flattened in crabs but it is the abdomen that has undergone the greatest modifications. In the natants, the decapod abdomen is at its largest, most muscular, and least flexible. It is substantial but proportionately smaller in the reptant lobsters and their relatives, and able to be curved under the cephalothorax, but is reduced to a flap normally held firmly beneath the cephalothorax, in crabs and crab-like Anomura. Despite this variation, all but males of a few hermit-crab species retain at least some abdominal pleopods. Pleopods provide propulsion in natant forms and penis-like organs in male decapods, and in female Pleocyemata remain large enough to carry eggs, even in the shell-inhabiting hermit crabs, whose abdomens are soft and pleopod numbers reduced.

The chitinous integument (exoskeleton) of crustaceans is variously hardened by the addition of calcium salts to increase its strength and rigidity. In crabs and lobsters the skeleton is generally hard and well calcified, except of course at the joints of appendages and abdominal segments, and most extreme in the huge claws of lobsters and mature male crabs. But calcium also adds weight and is therefore minimal in open-water shrimps and prawns. There is also little calcification in burrowing forms, particularly the callianassid ‘ghost shrimps’, which seldom if ever venture from their protective tunnels, and in hermit crabs the claws and front end of the body are well calcified while the abdomen remains membranous and flexible.

In decapods the sexes are usually separate, although protandry (in which males change to females as they grow) occurs in a number of species and protandric hermaphroditism (where male and female reproductive systems remain functional after the female system develops) has been observed in a shrimp genus. Mating involves the deposition of non-motile sperm, packaged in spermatophores, either externally on the cuticular surface of the female, or internally. Eggs are laid into the surrounding water by dendrobranchs but in the Pleocyemata are retained by the female’s pleopods until hatching.

Alvinocaris niwa, a hot-vent shrimp. From Webber 2004
Historical overview of studies on New Zealand Decapoda
Sydney Parkinson, artist on Cook's first voyage to the South Pacific in 1769, illustrated the spider crab now known as *Notomithrax peronii* from material collected in New Zealand. Early settlers and explorers observed and collected intertidal and shallow-water Crustacea (Yaldwyn 1957a) and Cook and his crews traded 'crayfish' with Maori in the Bay of Plenty (Begg & Begg 1969), a hundred years before the species *Jasus edwardsii* (Hutton, 1875) was formally described.

In the last half-century, major reviews of some New Zealand decapod groups have appeared, summarising historical research on these taxa. Forest et al. (2000) monographed the hermit crabs (Diogenidae, Paguridae, Parapaguridae, and Pylochelidae). Their historical account documents an increasingly confused taxonomy of these families in New Zealand, a problem not confined to the hermits. Thirteen years earlier, McLay (1988) published his indispensable book on New Zealand crabs and listed previous contributors to the group. These included Melrose (1975) who reviewed the hitherto poorly known Hymenosomatidae, Griffin (1966) who reviewed the majid spider crabs and their research history, and Bennett (1964) who had himself monographed the Brachyura and provided a critical history of contributions to the group. In two unpublished theses, Yaldwyn (1954, 1959) detailed the history of contributions to New Zealand shrimp and prawn systematics. Wear and Fielder (1985) outlined the very brief history of local larval taxonomy in a monograph on New Zealand brachyuran larvae, a publication that probably advanced knowledge of New Zealand's crab larvae beyond that of any other region.

The first decapod described from New Zealand is probably the shallow-water spider crab *Notomithrax ursus* (Herbst, 1788) collected on one of Cook's voyages. *Halicarcinus planatus* (Fabricius, 1775) may have been the first but McLay (1988) considered this unlikely. No further descriptions of New Zealand material appeared for 46 years (although 14 species now recorded in New Zealand were described from other localities prior to 1834). The mid-1830s saw an increase in taxonomic activity resulting from collections made during exploratory voyages by ships from Europe and North America visiting the New Zealand region.

Several explorations of the region provided early knowledge of decapod diversity. These included d'Urville's first voyage to New Zealand (1826–29) (decapods reported by H. Milne Edwards, e.g. 1834–1840); the U. S. Exploring Expedition (1838–42) (decapods reported by Dana, e.g. 1853–55); HMS *Erebus* and *Terror* (1839–43) (decapods reported by White, e.g. 1847); and the Austrian frigate *Novara* (1857–59) (some decapods reported by Heller, e.g. 1868). Decapoda from early exploratory work were first listed with the 'Annulose Animals' by White and Doubleday (1843) in Dieffenbach's *Travels in New Zealand*. The 1880s were the most significant decade of the 19th century in terms of additions to the fauna. The 1874 French Mission de l'Île Campbell made collections from Cook Strait, Stewart Island, and the subantarctic islands (decapods reported by Filhol, e.g. 1886). HMS *Challenger* visited New Zealand on its round-the-world journey (1873–76) and was the first to sample deep-water stations east and west of the country and off the Kermadec Islands (Yaldwyn 1957). Bate (1881, 1888) reported on the mostly meso- and bathypelagic natants, Henderson (1888) the Anomura, and Miers (1886) the Brachyura. Miers (1876) also compiled a *Catalog of the Stalk- and Sessile-eyed Crustacea of New Zealand* from the literature, museum collections, and a collection borrowed from the New Zealand Government.

New Zealanders began to contribute to local decapod taxonomy with the first publication of G. M. Thomson (1879b) describing two natant species. Thomson went on to make an important contribution to New Zealand crustacean studies, including revisions of the New Zealand hermit crabs (1898) and natants. With Charles Chilton he provided a list of New Zealand decapods for Hutton's (1904) *Index Faunae Novae Zealandiae*. Chilton made a valuable contribution to crustacean systematics in New Zealand in a career lasting more than 40 years. Beginning in 1882 he dealt with a variety of reptants and natants,
from the Subantarctic to the Kermadec Islands and greatly increased knowledge of their distributions. Chilton (1911c) reported on the New Zealand Government *Nora Niven* Trawling Expeditions that covered most of New Zealand’s coastlines. His 1910 paper on crustaceans from the Kermadec Islands, collected by Oliver in 1908, remained the major reference to the Decapoda of these islands until the 21st century. The British *Terra Nova* expedition of 1911 sampled a single but very valuable bottom station off Northland from which Borrodaile (1916) described brachyurans, hermit crabs, chirostylids, and natants. Decapods collected from the Auckland and Campbell Islands by Mortensen’s Pacific Expedition of 1914–16 were described by Stephensen (1927), and Balss (1929) reported on those collected by the 1924 German Expedition to the Subantarctic Islands led by Kohl-Larsen.

Foreign expeditions continue to visit New Zealand but the contribution of local surveys has greatly increased since World War II, such as those organised by university and museum researchers (e.g. Yaldwyn 1957) and the former New Zealand Oceanographic Institute of the DSIR (incorporated into NIWA since 1992). The Ministry of Fisheries’ Observer Programme, in which onboard observers monitor commercial fish catches within the EEZ, has yielded a steady flow of interesting decapods from deep water. In addition, NIWA vessels are currently adding new and rare decapods taken in deep water, on and around seamounts and other locations not previously sampled.

In the postwar period, crab systematics was advanced by the work of Richardson (1949a,b) and Dell (e.g. 1960, 1963a,b, 1968a,b, 1971, 1972, 1974), sometimes in collaboration (e.g. Richardson & Dell 1964; Dell et al. 1970). The first recognition of lithodid king crabs in New Zealand waters came from the identification of *Paralomis zealandica* (as *Lithodes* sp.) from Cook Strait by King (1958), and, as deep-water investigations increased, five further species were added (Yaldwyn & Dawson 1970; Dawson & Yaldwyn 1970, 1971, 1985; Dawson 1989; O’Shea et al. 1999), with the total New Zealand fauna now numbering at least 13 species (Ahyong 2010). Schembri and McLay (1983) published an annotated key to hermit crabs of the Otago region that, in the absence of any similar publication, proved a particularly useful guide to identification until the comprehensive review by Forest et al. (2000).

John Yaldwyn of the Dominion (later National) Museum published on several decapod groups but his most extensive contribution concerned the New Zealand shrimp and prawn fauna. In 1957, he described the Sergestidae of Cook Strait, a significant contribution to this difficult group (Yaldwyn 1957b). He and L. R. Richardson published keys to New Zealand’s natant decapods (Richardson & Yaldwyn 1958), now outdated but still the only comprehensive guide available. He added numerous new species to the fauna, notably those collected by the Chatham Islands 1954 Expedition (Yaldwyn 1960) and from the National Museum’s collection (Yaldwyn 1971), and published or contributed to numerous other works (e.g. Yaldwyn 1954a,b, 1959, 1961, 1974; Yaldwyn & Dawson 1985).

Since 2000, the rate of publication on New Zealand decapod taxonomy has increased. Papers on brachyuran crabs have predominated, with the emphasis on collections from the Kermadec Islands (e.g. Takeda & Webber 2006; McLay 2007; Ahyong 2008) and sea mounts and chemosynthetic habitats (Ahyong 2008). Reviews of the chirostylid squat lobsters (Schnabel 2009) and king crabs (Ahyong 2010) added many new species.

It appears the first systematically collected and recorded New Zealand collection of decapods (and other Crustacea) was that of Charles Chilton, who deposited his material in the Canterbury Museum. Another collection of note is that of A. W. B. Powell at the Auckland Institute and Museum, collected in the 1930s and ’40s. After World War II, the collection of Decapoda at the then Dominion Museum increased steadily with the efforts of Moreland and Dell and was continued at greater pace by Yaldwyn between 1959 and 1969 and by Webber into the 1990s. This museum collection is particularly strong in offshore natants.
and decapod larvae but has a wide coverage of New Zealand decapods as well as some valuable material from Pacific Islands. A small collection made by Betty Batham in the 1940s and ’50s is housed at the Portobello Marine Laboratory of Otago University. NIWA, Wellington, has a major collection of decapods, which has become the fastest growing in New Zealand.

The New Zealand decapod fauna
Some 591 decapod species (492 living, ~99 fossil) are known from New Zealand, not all of them formally named, and there are still more to be discovered. New Zealand’s decapod fauna is generally considered depauperate compared to other regions (Dell 1968a), given the extent of the EEZ over 30 degrees of latitude, the exceptionally large area of continental shelf and slope, and the wide variety of seafloor relief and ecological niches available. It is difficult to find comparable areas but the numbers of New Zealand crabs have been compared with South Australia by Dell (1968a) and with the Galápagos, Chile, eastern USA, China, and Japan by Feldmann and McLay (1993). These comparisons certainly indicate the limited nature of New Zealand’s crab fauna. This is more simply observed in the lack of variety and number of crabs found on seashores or the small number of locally caught crabs, shrimps, or lobsters in fish shops compared with neighbouring Australia and many places further afield. It is generally felt that this limited diversity of species has resulted from New Zealand’s isolation from centres of diversity that might have acted as sources of recruitment. Dell (1968a) suggested that New Zealand’s separation from Australia in the Early Tertiary occurred before evolutionary radiation gave Australia its diverse fauna but it is unclear why a similar process has not occurred in New Zealand. It is reasonable to view most of New Zealand’s decapod taxa as depauperate but there are exceptions – New Zealand is well represented by southern hemisphere oceanic natants that live independently of shallow water and are less limited by constraints on dispersal, but there is also a high diversity of hermit crabs and some squat lobster genera and the two crab families Majidae and Hymenocomatidae are also well represented.

Taxonomic knowledge of New Zealand’s present-day Decapoda is comprehensive for the hermit crabs and squat lobsters, and reasonably good for coastal and shelf natants and the Brachyura, but not so for the thalassinids and penaeoid and sergestoid shrimps and prawns. Present exploration of deep-sea rocky habitats, notably the many seamounts in the New Zealand region, is rapidly increasing our knowledge of decapods in these places. Geographically, the least well-known areas are the Kermadec Islands (although knowledge of the shallow-water crab fauna is rapidly increasing), and much of the west coast of New Zealand.

Decapods are an important component of the luxury food market worldwide. Despite New Zealand’s limited variety of edible species, some nevertheless support very valuable fisheries, most notably the red rock lobster Jasus edwardsii. Interest in developing new crustacean fisheries is growing, and considerable research effort is now expended on ways of improving rock-lobster productivity and quality through habitat enhancement, ongrowing of juveniles, and the possibility of culturing.

The main collections of New Zealand decapods are held at the Museum of New Zealand and NIWA, but considerable historic collections and the majority of types are kept at the Natural History Museum (London) and the Muséum National d’Histoire Naturelle in Paris. Other significant collections are located in the Senckenburg Museum (Frankfurt) and the Australian Museum (Sydney), while further important material resides in a number of other institutions, notably Museum Victoria, the U. S. National Museum of Natural History, and the National Science Museum in Tokyo. The largest type collection in the country is housed at the Museum of New Zealand, where there are 202 lots, including just 42 primary types. A smaller collection of types is held by NIWA and type material is also kept at Auckland, Canterbury, and Otago Museums.
A total of 492 living decapod species have been recorded within New Zealand’s EEZ (see end-chapter checklist). When the first Decapoda checklist was compiled for Species 2000 New Zealand in 2002 the classification used was that of Martin and Davis (2001). The greatest effect their revised classification had on the hierarchy of New Zealand decapods was to increase the number of families recognised locally, mainly by raising subfamilies to family status, especially in the Brachyura. Since then, there has been less change in the classification of shrimps and prawns and other non-brachyuran groups but changes continue to be made in brachyuran families (e.g. Ng et al. 2008). New Zealand has 84 of the 151 families of Martin and Davis (2001) although a large proportion of them (43%) contain only one or two species (20 with only one species, 15 with two).

In contrast, the three most species-rich families contain 112 species, or almost a quarter of the decapod fauna. Of these three, the Galatheidae has the greatest number with 46 species, the Paguridae with 34 species and the Chirostylidae with 33. The Chirostylidae also includes the most speciose New Zealand genus, Uroptychus, with 27 named species. The largest natant family is the Oplophoridae with 18 species, all named. Among the subfamilies raised to family in Martin and Davis (2001) are those of the superfamily Majoidea (previously family Majidae), which contains 33 species. Despite this division, however, the previous subfamily Majinae (now the Majidae in the strict sense) contains 17 species, almost as many as the largest New Zealand brachyuran family, Xanthidae (18 species).

**Endemism**

Of the 492 living New Zealand decapods known, 12 are unnamed or not yet fully determined. The level of endemism is only ~30% (144 species). As might be expected, endemism is lowest in pelagic offshore species and highest among benthic and shallow-water forms. Thus all seven dendrobranch families (23 named species, two undetermined) contain no endemics at all and the four pelagic carid families Nematocarcinidae, Oplophoridae, Pandalidae, and Pasiphaeidae (44 species in total) include only one endemic species. New Zealand’s dearth of nearshore pelagic natants in any of these groups is reflected in this low endemism and, although an estimated 35 additional penaeoid and serrastroid species may be anticipated for the fauna, few if any are likely to be restricted to New Zealand waters. Subtract offshore natant groups from the named decapods and the proportion of endemics rises. But lower endemism is not characteristic of all natants – of the 471 named living New Zealand Decapoda, 97 are carid shrimps of which 30 (~31%) are endemic, the same proportion as for the reptants alone, of which 106 (~31%) are confined to the New Zealand region. Ten of the 253 New Zealand decapod genera are endemic, viz the brachyurans Euryalomabrus, Halibena, Heterozius, Jacquinotia, Neohymenius, Neommatocarcinus, Nepinnotheres, Pteropeltarion, and Trichoplatus and the slipper lobster genus Antipodarctus – all of which contain a single species. One family, Belliidae, is endemic.

Most New Zealand species of Crangonidae and Palaemonidae are endemic, as are both species of Spongicolidae, probably reflecting their close association with hexactinellid sponges. There is also higher-than-average endemism of Axideida and Gebiidea (former Thalassinidea), Diogenidae, and Paguridae. This is in contrast to the deeper-water hermit crabs of the Pylochelidae and Parapaguridae, which each have only a single endemic species.

While the two freshwater parastacid crayfish Paraneoprops planifrons and P. zealandicus and the only freshwater shrimp Paratya curvirostris are endemic, the freshwater hymenosomatid crab Amarinus lacustris is not, occurring also at Norfolk and Lord Howe Islands and in southeastern Australia and Tasmania.

A number of rarely caught deep-sea species previously thought to be endemic to New Zealand have been found in greater numbers and further afield, particularly in southeast Australian waters (e.g. Lipkius holthuisi, Teratomaia...
The apparent endemism and rarity of some deep-sea species are probably the result of insufficient sampling. Endemism in New Zealand’s second-largest crab family, Majidae, is rather low at 35% (six of 17 species) but includes intertidal (e.g. Notomithrax peronii) and shelf/slope (e.g. Thacanophrys filholi) taxa. Hymenosomatid crabs are well represented in New Zealand and 10 of the 14 species (71%) are also endemic. One of the non-endemics, Halicarcinus innominatus, is thought to be of New Zealand origin but accidentally introduced to Tasmania.

New Zealand’s two species of Pinnotheridae (pea crabs) are both endemic, as might be expected of shallow-water associates of bivalve molluscs, but endemism in the crab families Portunidae (paddle crabs) and Xanthidae is quite low at less than 30%. Just three of 11 native portunids and three of 15 native xanthids (all found only at the Kermadec Islands) are endemic. Portunids and species of Varunidae tend to have long larval lives and some are able to travel great distances as adults so that most species are distributed widely. Even New Zealand’s only terrestrial decapod, Geograpsus grayi of the Kermadec Islands, is widespread in the Indo-West Pacific.

Of New Zealand’s 132 endemic decapods, 14 are recorded from the Kermadec Islands and nine are restricted there. Five are hermit crabs, all from moderately deep water except Pagurixus kermadecensis, which is found in rock pools. Like a number of other apparent endemics, the shrimp Stylodactylus discissipes is known from only a single station at 1100 m depth and is likely to be more widespread.

Ecological studies

Paddle crabs (Ovalipes catharus) are numerous enough to comprise a small fishery, encouraging investigation of marketing (Cameron 1984) and reproductive biology (Haddon 1994, 1995; Haddon & Wear 1993). University research has made a considerable contribution to decapod biology, particularly that carried out over the years by Malcolm Jones and Colin McIay (Canterbury) and Bob Wear (Wellington), with their students. The physiology of musculature, haemolymph, locomotion, and eye function in shore crabs have been addressed (e.g. Jones & Greenwood 1982; Bedford et al. 1991; Forster 1991; Meyer-Rochow & Reid 1994; Palmer & Williams 1993; Meyer-Rochow & Meha 1994; Depledge & Lundbye 1996) as have the effects of low oxygen and varying pH on freshwater shrimp (West et al. 1997; Dean & Richardson 1999). Feeding studies of shore crabs were carried out (e.g. Wear & Haddon 1987; Creswell & McIay 1990; Woods 1999; Woods & McIay 1994). Jones (1976, 1977, 1978, 1980, 1981), Jones and Winterbourn (1978), and Jones and Simons (1981, 1982, 1983) undertook significant work on intertidal crabs of the Avon-Heathcote Estuary and Kaikoura, and other ecological studies were made by McIay and McQueen (1995), Palmer (1995), and Morrisey et al. (1999). Several papers on the behaviour and associations of shore crabs have also appeared (e.g. Field 1990; Taylor 1991; Chatterton & Williams 1994; Woods & McIay 1994; Woods 1995; Woods & Page 1999) and Berkenbush and Rowden (1998, 1999) studied population dynamics and sediment turnover in the burrowing ghost shrimp Callianassa filholi.

Alien species

Interest in adventive species is growing rapidly in New Zealand (see Cranfield et al. 1998 for a list of adventive decapods and the Ministry of Fisheries for details of potential invaders (Marine Pest Identification Guide series)). Some decapods have been introduced intentionally but mostly without success; this is probably a good thing as some crab and lobster species are among the most destructive of invaders. The first such introduction appears to have been of the Australian penaeid prawn Melicertus canaliculatus (as Penaeus canaliculatus), released at Nelson in 1892 and at the entrance to Otago Harbour in 1894 (Thomson 1922). They were never seen again. Between 1906 and 1918, a more serious attempt
was made to introduce the European lobster *Homarus gammarus* into New Zealand. A similar project was undertaken with the European edible crab *Cancer pagurus* between 1907 and 1914 (Thomson & Anderton 1921). Live crabs and lobsters were imported from the United Kingdom and kept at the Portobello Marine Fish-Hatchery in Otago Harbour. Several million crab larvae and more than 750,000 lobster larvae were hatched and liberated in the harbour during those years. Some young lobsters were reared for several years before release, and mature adults of both species were also liberated but no trace of free-living specimens of either species has been found in Otago or New Zealand waters since.

There was a short-term attempt in the early 1990s to farm a ‘saltwater king prawn’ from Hong Kong, probably the penaeid *Fenneropenaeus chinensis*, at South Kaipara Heads. Like the *H. gammarus* and *C. pagurus* experiments this also failed but in this case the stock was destroyed. So too was the entire stock at a pond farm of the Western Australian crayfish or marron, *Cherax tenuimanus*, at Warkworth, north of Auckland in the late 1980s and early 1990s (Hughes 1988; Lilly 1992). Fear of their escape into waterways led to this action but the same problem does not occur with large palaemonid prawns farmed at Wairakei, near Taupo. Here, *Macrobanchium rosenbergii* from South-east Asia and northern Australia is successfully farmed in artificially heated water. This is drawn from the Waikato River and warmed by a heat exchanger using hot-water runoff from a geothermal power station nearby. *Macrobanchium rosenbergii* cannot breed or survive in ambient New Zealand fresh waters.

Foreign decapods periodically appear accidentally in New Zealand, apparently introduced in ships’ ballast water or on hulls. Some species disappear but others threaten to become established and compete with the local biota. The hymenosomatid crab *Halicarcinus ovatus*, normally found around western, southern, and eastern Australia, was recorded just once at Port Chalmers, Otago, by Filhol (1886) but has not been recorded in New Zealand since (Melrose 1975; McLay 1988). In 1978, the small inachoidid spidercrab *Pyromaia tuberculata*, originally from the central American west coast but subsequently found in other localities in the Pacific and Atlantic Oceans, was discovered in the Firth of Thames (Webber & Wear 1981). It has become established but is not often found and does not seem to be a major threat to endemic species.

In the early 1990s live specimens of three species of crab were found in a ship’s sea chest at a Nelson slipway – *Pilumnus minutus*, *Carupa tenuipes*, and *Charybdis hellerii* (Dodgshun & Coutts 1993). The significance of sea chests (recesses in ship hulls housing the intakes of ballast water) as a mode of introduction quickly became apparent. *Pilumnus minutus* is small and uncommon and *C. tenuipes* tropical, and neither is likely to become established, but the Asian and northern Indian Ocean portunid *C. hellerii* is a successful invader of the eastern Mediterranean and western Atlantic from Florida to Brazil. It is unlikely that *C. hellerii* could establish itself in New Zealand, except perhaps in the far north, but a close relative has. First reported from Waitemata Harbour in 2001, hundreds of *Charybdis japonica*, including egg-bearing females, have since been caught, and it is also present in the Firth of Thames (Webber 2001; Smith et al. 2003). Almost as large, and far more aggressive than the paddlecrab *Ovalipes catharus*, *C. japonica* is likely to exclude the local species from harbour and estuary mouths but is unlikely to spread to open sand beaches or much further south, as it is a warm-water species. Its behaviour in nets causes problems for flounder fishers but if it remains in large-enough numbers, it may at least become a new fishery.

Introductions have also occurred in the opposite direction. The small hymenosomatid crab *Halicarcinus innominatus* and the larger pie-crust crab *Metacarcinus novaezelandiae* were probably accidentally introduced to Tasmania when *Ostrea angasi* was imported from New Zealand to enhance the oyster fishery (Lucas 1980).
New Zealand fossil Decapoda

The fossil decapod fauna comprises approximately 99 species, although only 56 of these are named unequivocally owing to the high proportion of small or unique specimens or their often incomplete or fragmentary state. There are 48 named genera in 27 families, and six of the seven Recent reptant infraorders (only Polychelida lacking), and only the Glyphidea (superorder Pleocyemata) among the natants. Nineteen of the 58 Recent reptant families include fossil species, with five families represented in New Zealand only by fossils. Some 22 fossil genera also occur in the present-day New Zealand fauna and four Recent species are represented in the New Zealand fossil record, possibly six, should fossil *Ctenocheles* cf. *maorianus* and *Ommatocarcinus* cf. *Neommatocarcinus huttoni* prove indistinguishable from their living namesakes.

Although the fossil decapod fauna of 99 species is small relative to the present-day fauna, recent research has revealed its significance to the origins of decapods in New Zealand and in the South Pacific (Feldmann 2003). The xanthid crab *Tumidocarcinus tumidus* was the first fossil decapod described from New Zealand, but 94 years were to elapse before additional records were published. Glaessner (1960) published his signal work on the New Zealand fossil Decapoda, recognising 29 species in eight genera, including a new genus and 16 new species. Most of these were brachyurans (22 crabs in seven families) but Glaessner also identified five callianassid ghost shrimps and three astacoidean lobsters of the families Glyphidea and Mecochiridae. In addition, he described the palinurid rock lobster *Sagmariasus flemingi* (as *Jasus flemingi*), the only fossil yet discovered among the nine Recent species of non-stridulating Palinuridae (*Jasus*, *Projasus*, and *Sagmariasus* species, all austral).

Glaessner’s (1960) work remains the most important contribution in terms of numbers of taxa added to the fossil fauna, although subsequent work has trebled the known fauna. Only three more new species were added to the fauna during the 1960s and 1970s, but momentum and diversity then increased, with nine new species described in the 1980s and 16 in the 1990s. Crabs predominate among the new records, but several other new taxa have also been identified, leading to fresh interpretations of their origins and relationships to Recent forms. For example, New Zealand’s first fossil nephropid lobster, *Metanephrops motunauensis*, was described from north Canterbury.

The first decapod added to the fauna by a New Zealand worker (*Trichopeltarion greggi*) was also the first fossil species of the extant family Atelecyclidae (Dell 1969). The tymoloid family Tornormmidae was erected by Glaessner (1980) to contain several extinct Australasian crabs including two new New Zealand species, and in the same paper Glaessner named three new species of raninids for New Zealand. Hyden and Forest (1980) described the first, and so far the only named, fossil hermit crab from New Zealand (*Diacanthurus spinulimanus*), and the late Sir Charles Fleming (1981) described *Miograpsus papaka*, so far the only fossil grapsid recorded from New Zealand.

The description of the squat-lobster-like anomuran *Haumuriaegla glaessneri* was significant, both for the implications it had for the interpretation of New Zealand’s fossil record and as the beginning of a major and continuing contribution to New Zealand decapod palaeontology by its author (Feldmann 1984). *Linuparus korura* was the second palinurid added to the New Zealand fossil fauna (Feldmann & Bearlin 1998) and Feldmann and Maxwell (1999) described five more decapods – two raninids, two majids, and a single goneplacid, the first New Zealand fossil of the genus *Carcinoplax*. At this point, a review of the fossil decapods of New Zealand by Feldmann and Keyes (1992) appeared, listing all previously published records, giving a detailed index of locality records and an updated checklist of taxa, and tabulating their stratigraphic ranges in the Mesozoic and Cenozoic. Some 81 decapods were recorded, although just 38 species were named. Forty genera were recorded in 21 or 22 families, a considerable increase from the eight genera in 11 families recognised by Glaessner (1960). Five more
new species were soon added to the fauna by Feldmann (1993), including the first published record for New Zealand of the Calappidae (*Calappilia maxwelli*), the first record of the genus *Glyphia* (*G. stilwelli*), and one further species in each of the Holodromiidae, Torynommidae, and Majidae.

Feldmann and Keyes’ (1992) review and McClay’s (1988) survey of New Zealand’s Recent crab fauna were closely followed by a substantial paper on the paleogeographic history of the New Zealand Brachyura (Feldmann & McClay 1993). In their analysis, these authors compared New Zealand’s extant Brachyura with that of other, mostly Pacific, regions and went on to identify significant relationships not recognised previously between New Zealand’s Recent and fossil faunas. A number of new taxa have come to light since these works, supporting their observations.

The first recognition of the family Parastacidae in the fossil record (*Paranephrops fordycei*) was published from a single specimen found in Miocene deposits of Central Otago (Feldmann & Pole 1994). Two further majids were added to the fauna by McClay et al. (1995) and a new cancrid by Feldmann and Fordyce (1996). The world’s first fossil lithodid (king) crab (*Paralomis debodeorum*) was described only in the 1990s (Feldmann 1998), along with a glypheid lobster, *Glyphea christeyi* (Feldmann & Maxwell 1999), both from Canterbury.

The origins of New Zealand’s decapod fauna are far from clear and continue to be debated, particularly because of fossil discoveries over the past 20 years in both New Zealand and Antarctica. Until the early 1980s it was believed that New Zealand’s decapod fauna was primarily of Australian and Indo-Pacific origin. Gaessner’s (1960) Tertiary material occurred no earlier than the middle Eocene (45–50 million years ago). He considered the presence of *Tumidocarcinus* in the middle Tertiary of Australia and in the Eocene and Miocene of New Zealand as indicative of a ‘distinctive zoogeographical province’ and that Australasian genera could be considered as originating in the ancient Tethys Sea. Fleming (1962, 1979) also concluded that New Zealand decapods were primarily of Tethyan origin and that typical New Zealand marine decapod faunas had appeared since the Oligocene. In his analysis of the distribution and composition of New Zealand’s extant Brachyura, Dell (1968a) found that the strongest external elements in the present-day crab fauna are Australian and Malayo-Pacific in practically equal strength, which also implies a Tethyan origin.

The late Mesozoic *H. glaesneri* from North Canterbury was a shallow-water marine species and the earliest known representative of the extant freshwater anomuran family Aeglidae, which is confined to temperate latitudes of southern South America. This discovery, and analysis of fossil and recent species of *Lyreidus* (Raninidae), led Feldmann (1984, 1986, 1990) to believe that these and other decapod genera had evolved in high-latitude southern waters rather than originating in the Tethys. This occurred during the late Mesozoic prior to New Zealand’s split from Australia and Australia’s split from Antarctica, which also had a cool-temperate climate. Feldmann considered that species evolving along this coast would be dispersed eastwards by the southern Pacific gyre but that this would have discontinued with a cooling climate and the break of Australia from the Antarctic, allowing the circumpolar current to develop.

Newman (1991), however, questioned this view and suggested that taxa like the entirely austral *Jasus* species may have resulted by reliction (reduction in range) following an amphitropical (northern as well as southern hemisphere) distribution. He offered three hypotheses on how such southern hemisphere endemism could have come about – centres of origin, dispersal to the southern hemisphere, or vicariance (see Newman 1991).

This debate continues, with research on fossil decapods worldwide increasing in recent years. Schweitzer (2001) has summarized decapod paleobiogeography and the diverse literature on decapod fossils and their interpretation was reviewed by Feldmann (2003).
Decapod development
No discussion of decapod diversity would be complete without reference to their larvae. The morphology of decapod developmental stages is an important aspect of decapod systematics, and knowledge of larval biology and recruitment to adult populations is essential to managing decapod fisheries.

Development in the great majority of Decapoda, both natants and reptants, includes free-swimming planktonic larvae. In the penaeoid and sergestoid (dendrobranch) shrimps and prawns, eggs are laid into the surrounding water and tiny, motile nauplius larvae subsequently hatch into the plankton. All other decapod groups (the Pleocyemata) retain their eggs attached to the pleopods until larvae hatch. In the plankton, larvae grow through a series of instars until, at the final moult, they metamorphose into a post-larva, an intermediate form looking more or less like the adult but retaining the ability to swim. The role of the post-larva is to relocate itself to the milieu of the adult phase where it again molts to become a juvenile crab, lobster, shrimp, or prawn. Like their larvae, shrimps and prawns are pelagic. The transition from larva through post-larva to juvenile is less abrupt although the final larval moult is still marked in pelagic species by a fundamental change in locomotion from using appendages of the cephalothorax to propulsion by the abdominal appendages (pleopods).

Most decapod families have different though predictable numbers of larval growth stages and a single post-larva during development, but a few groups and species have either extended or abbreviated development. Some have even eliminated free-swimming larval or post-larval phases altogether, with juveniles hatching directly from the eggs. The number of larval stages relates to the duration of the larval phase, and those species with abbreviated or direct development usually occur in habitats where free-swimming larvae would be lost. Some of these different strategies are exemplified by New Zealand Decapoda.

Larval decapods are of taxonomic interest because they differ morphologically from adults. This is particularly so in benthic forms, which make up the majority of decapod species and occupy very different habitats from their offspring. Pelagic larvae have evolved their own adaptations to planktonic life, yet the medium they frequent is in many ways more uniform than the variety of substrata or depths occupied by the adult phase, which serves to emphasise the importance to taxonomy of differences in larval features.

Limits to the use of larval features are more practical than theoretical, however; while larvae caught in plankton can usually be attributed confidently to higher taxa, incorrect identifications of genera and species based on morphology are often made (e.g. McWilliam et al. 1995). The only foolproof method of putting names to larvae caught in plankton is to hatch them from eggs of known parentage or rear planktonic larvae through to identifiable adults. Since Vaughan Thompson (1828) first put the provenance of decapod larvae beyond doubt by observing larvae hatching (see Gurney 1942), rearing techniques have improved, but maintaining ovigerous females and their delicate offspring in captivity, even when robust berried females can be caught, is always difficult and sometimes impossible. However, this impasse has begun to be resolved in the last few years as molecular analysis has enabled more precise matching of adult and larval forms. DNA analysis has even enabled the type species of some old larval genera and species to be matched to the adults they correctly belong with (Palero et al. 2008).

New Zealand’s larval decapods, particularly the Brachyura, are comparatively well known, thanks largely to the work of Robert Wear and his students (1965–1985) at Victoria University in Wellington. Their efforts are summarised in two particularly useful publications. One (Wear & Fielder 1985) consists of a comprehensive illustrated atlas of all previously described New Zealand brachyuran larvae, with keys and some new descriptions; the other (Wear 1985), is an annotated list of all non-brachyuran New Zealand species whose larvae had been described to that time. Prior to 1985, numerous authors published
descriptions of New Zealand decapod larvae but only the more significant are referred to here. Thomson and Anderson were the first New Zealanders to describe the larvae of brachyurans of the region, hatched at Portobello marine station. Prior to the 1960s, the most substantial contribution to New Zealand larval taxonomy was made by Gurney (1924, 1936, 1942), who described eight decapod species (in seven families) collected by the Terra Nova and Discovery Expeditions. Webber (1979) described the developmental stages of eight majid spider crabs, published later by Webber and Wear (1981). Larvae of 12 species of carid shrimps, in the families Crangonidae, Hippolytidae, and Palaemonidae, were described in detail by Packer (1983) who published a guide to these and six other shallow-water shrimp species in 1985. Since then, the output of larval taxonomy has slowed. Horn and Harms (1988) completed the larval description of Halicarcinus varius; Lemaitre and McLaughlin (1992) described the megalopa of the deep-water parapagurid Symphysarbus dimorphus; the complete development of the packhorse rock lobster Sagmariasus verreauxi was described by Kittaka et al. (1997); and those of the red rock lobster Jasus edwardsii by Kittaka et al. (2005) from lobsters cultured in Japan; Cuesta et al. (2001) re-examined the zoeas of Cyclograpsus lavauxi, Hemigrapsus sexdentatus, and H. crenulatus; and detailed descriptions of the phyllosomas and nisto of a slipper lobster Scyllarus sp. Z (probably S. aoteanus) were published by Webber and Booth (2001).

Developmental stages of 94 species (21%) of New Zealand Decapoda have been described, but a much greater proportion of higher taxa is represented by this number. Descriptions of larvae, post-larvae, or both have been published from 45 (54%) of the 84 families recorded from New Zealand. These percentages reflect the high proportion of families containing only one species (larval descriptions of single species account for 27 families) but it also indicates the broad spectrum of decapods whose various larval forms are known to some degree. Best documented are the Brachyura, with 22 of New Zealand’s 39 families represented by larval descriptions. The remaining 17 families contain 54 of the 167 brachyuran species, while, in the larger families, 11 of 14 hymenosomatid and five of 12 portunid species include larval descriptions.

Descriptions of all stages in the development of New Zealand’s crayfish and lobsters were completed relatively recently, but commercial interest has now generated considerable investment in research into all aspects of their biology. The freshwater crayfish Paranephrops planifrons provides an example of direct development in which there are no larval stages and crayfish hatch from the eggs (Hopkins 1967). Young crayfish, with the cephalothorax packed with yolk, attach themselves to the female’s pleopods and pass through three stages with the third having exhausted its supply of yolk. Development in scampi (Metanephrops challengeri) is not direct but apparently abbreviated. Wear (1976) found that while larvae hatch as prezoeas the prezoeal cuticle is quickly shed and the single-stage large zoea appears to last only two to three days or less before moulting to the post-larva. Scampi zoeas are not found in surface plankton and have a restricted ability to swim, which led Wear (1976) to suggest they are very short-lived and settle as a post-larva soon after hatching.

At the other end of the scale are the palinurid and scyllarid lobsters. New Zealand’s rock lobsters Jasus edwardsii and Sagmariasus verreauxi, and slipper lobsters whose larval development is known (Ibacus alticrenatus and Scyllarus sp. Z), are typical of the Palinuroidea in having a long-lived larval phase. Longest of all is that of J. edwardsii, with 11 phyllosoma stages that can last more than a year, perhaps as long as 24 months, in the plankton (Booth & Phillips 1994). Sagmariasus verreauxi has a similar number of stages but of shorter duration (up to a year) (Booth & Phillips 1994), I. alticrenatus still shorter (4–6 months) with seven stages (Atkinson & Boustead 1982), and Scyllarus sp. Z with 10 phyllosoma stages that probably have a duration as short as or shorter than I. alticrenatus. Planktonic larval sampling has concentrated on J. edwardsii because of its high economic value, but the incidental capture of phyllosomas
of other species has enabled useful comparisons to be made. After hatching and
shedding the naupliosoma cuticle, early-stage phyllosomas drift out to sea. Most
sampled mid- to late-stage larvae of *J. edwardsii* appeared to become entrained
in the Wairarapa Eddy southeast of the North Island, while those of *Scyllarus*
sp. Z are found much closer to the North Island east and northeast coasts but
also in oceanic waters to the north and northwest of New Zealand (Webber
& Booth 2001). While mid- and late-stage *J. edwardsii* are rarely found inside
the continental-shelf break, all stages of *Scyllarus* sp. Z are found there in good
numbers, indicating that they go through larval development closer to shore.
This accords with the much shorter larval duration in the scyllarid species and
it is assumed that the widely scattered phyllosomas to the north and northwest
are lost. The distribution of adult *Scyllarus* sp. Z is confined to the northeast
coast of the North Island between Cape Maria van Diemen and Gisborne and
is completely overlapped by *J. edwardsii*, yet the larvae they produce become
distributed in different geographical areas. Phyllosomas have very limited ability to
swim horizontally but they can move vertically through the water column. Coupled
with changing phototactic responses during development, vertical mobility
enables larvae to exploit currents flowing in different directions at different depths,
a strategy that enables them to position themselves in water masses from which
they can return to the coast as post-larvae (Webber & Booth 2001).

Commercial exploitation and resource potential of decapods
Studies of decapod biology and ecology have increased in the last half-century,
especially of commercially important species. Early surveys of fishing potential
included the southern spider crab *Jacquinotia edwardsii* (Ritchie 1970, 1971; Ryff
& Voller 1976), prawns in the Bay of Plenty in the 1970s, and experiments aimed
at culturing freshwater crayfish. As one of New Zealand’s most valuable fisheries,*Jasus* rock lobsters are the subject of numerous and continuing studies. Their
movements and migratory behaviour have been investigated for more than 30
years (e.g. Street 1969, 1971, 1973, 1994; Annala 1981; McCoy 1983; Booth 1984,
1997; MacDiarmid 1991, 1994; MacDiarmid et al. 1991; Andrew & MacDiarmid
1991; Annala & Bycroft 1993; Kelly 1995; Babcock et al. 1999; Butler et al. 1999;
Kelly et al. 1999). Because rock lobsters have pelagic larvae and post-larvae,
research has been carried out on the ecology and recruitment of developmental
1990; Booth & Grimes 1991; Booth et al. 1991; Booth & Stewart 1992; Booth &
Chiswell & Booth 1999; Chiswell & Roemmich 1999). Rearing of New Zealand
lobster larvae has advanced greatly (Kittaka 1994a,b; Kittaka et al. 1997; Tong et
al. 1997, 2000a,b; Moss et al. 1999), while additional research on their biology
and fisheries has also appeared (e.g. Booth & Breen 1994; James & Tong 1998;
MacDiarmid & Butler 1999a,b). Genetic techniques have been employed to
improve *Jasus* species stock identities (Ovenden et al. 1992; Ovenden & Brasher
1994; Booth & Ovenden 2000). Allozyme variation has also been identified in
scampi populations around New Zealand.

Acknowledgements
Drs Paul Sagar (NIWA) and Wolfgang Zeidler (South Australian Museum)
provided information on amphipods (literature on amphipods as prey for birds,
and Hyperiidea, respectively). Dr Merlijn Jocqué (University of Leuven, Belgium)
checked the section on Mysidacea and added a new endemic species. Thanks
are due to Dr Bob McDowall (NIWA, Christchurch) for his constructive review
of the Amphipoda section. Drs Michael Ayress (Ichron, UK) and Kerry Swanson
(University of Canterbury, Christchurch) clarified aspects of ostracod taxonomy
for the checklist; John Simes provided information on pre-Tertiary fossils.
Authors

Dr Shane T. Ahyong  National Institute of Water & Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington, New Zealand [s.ahyong@niwa.co.nz] Hoplocarida

Dr Graham J. Bird  8 Shotover Grove, Waikanae, Kapiti Coast 5036, New Zealand [zeuxo@clear.net.nz] Tanaidacea

Dr Janet M. Bradford-Grieve  National Institute of Water & Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington, New Zealand [j.grieve@niwa.co.nz] marine Copepoda, Branchiura, Tantulocarida

Dr Niel L. Bruce  Museum of Tropical Queensland, 70–102 Flinders Street, Townsville, Queensland 4810, Australia [niel.brace@qm.qld.gov.au] Isopoda

Professor John S. Buckeridge  School of Civil, Environmental and Chemical Engineering, RMIT University, GPO Box 2476V, Melbourne, Victoria 3001, Australia [john.buckeridge@rmit.edu.au] Cirripedia

Dr M. Anne Chapman  Deceased. Formerly Department of Biological Sciences, Waikato University, Private Bag 3105, Hamilton, New Zealand Freshwater crustacean ecology

Dr W. A. (Tony) Charleston  488 College Street, Palmerston North, New Zealand [charleston@inspire.net.nz] Pentastomida

Mr Elliot W. Dawson  Museum of New Zealand Te Papa Tongarewa, P. O. Box 467, Wellington, New Zealand [edawson@xtra.co.nz] Leptostraca, Syncarida

Mr Stephen H. Eagar  School of Earth Sciences, Victoria University of Wellington, P.O. Box 600, Wellington, New Zealand [stephen.eagar@paradise.net.nz] Ostracoda

Dr Graham D. Fenwick  National Institute of Water & Atmospheric Research (NIWA), P. O. Box 8602, Christchurch, New Zealand [g.fenwick@niwa.co.nz] Amphipoda

Dr John D. Green  36 Paturoa Road, Titirangi, Waitakere, Auckland 0604, New Zealand [john.green@worldnet.co.nz] Freshwater copepod ecology

Dr Ju-Shey Ho  Department of Biological Sciences, California State University, Long Beach, 1250 Bellflower Boulevard, Long Beach, California 90840–3702, USA [jsho@csulb.edu] Parasitic copepoda

Dr J. Brian Jones  Fisheries WA, C/o Animal Health Lab., Agriculture WA, Locked Bag 4, Bentley Delivery Centre, WA 6983, Australia [bjones@agric.wa.gov.au] Branchiura, parasitic Copepoda

Dr Kim Larsen  CIIMAR, University of Porto, Rua dos Bragas n. 289, 4050-123 Porto, Portugal [tanaids@hotmail.com] Tanaidacea

Dr Anne-Nina Lörz  National Institute of Water & Atmospheric Research, Private Bag 14901, Kilbirnie, Wellington, New Zealand [a.lorez@niwa.co.nz] Rhizocephala

Dr Jørgen Olesen  Zoological Museum, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark [j10lesen@zmuc.ku.dk] Branchiopoda

Dr Gary C. B. Poore  Museum Victoria, GPO Box 666E, Melbourne, Victoria 3001, Australia [gpoore@museum.vic.gov.au] Isopoda

Dr Carlos E. F. Rocha  Universidade de São Paulo, Departamento de Zoologia, Caixa Postal 11461, CEP 05422 970, São Paulo, Brazil [cefrocha@usp.br] Copepoda: Oithonidae

Dr Russell J. Shiel  Department of Environmental Biology, University of Adelaide, Adelaide, South Australia 5005, Australia [russell.shiel@adelaide.edu.au] Freshwater Copepoda

Dr Les Watling  Department of Zoology, University of Hawaii at Manoa, Honolulu, HI 96822, USA [watling@hawaii.edu] Cumacea

Dr John B. J. Wells  Department of Biological Sciences, Victoria University of Wellington, P. O. Box 600, Wellington, New Zealand [wellsjm@xtra.co.nz] Harpacticoida

Mr W. R. (Richard) Webber  Museum of New Zealand Te Papa Tongarewa, P. O. Box 467, Wellington New Zealand [rickw@tepapa.govt.nz] Decapoda, Euphausiacea, Mysidacea


BUCKE RIDGE, J. S. 1999b: A new deep-sea barnacle, Tetrachela tursonianum sp. nov. (Cir-
NEW ZEALAND INVENTORY OF BIODIVERSITY


CAMACHO, A. I.; VALDECASAS, A. G. 2008: Global diversity of syncarids (Syncarida; crustacea) in freshwater. Hydrobiologia 595: 257–266.


CHAPMAN, M. A. 1973: Calanemocia lucasi (Cope‐ poda: Calanoida) and other zooplankton in two Rotorua, New Zealand, lakes. Internationale Verhandlungen der gesamten Hydrobiologie 58: 79–104.


MCCLAY, C. L. 2007: New crabs from hydrothermal
vents of the Kermadec Ridge submarine volcanoes, New Zealand: Caldofina gen. nov. (Bythograeidae) and Xenosquonus (Varuniidae) (Decapoda: Brachyura). Zootaxa 1524: 1–22.


McLay, C. L.; McQueen, D. J. 1995: Inter-tidal zonation of Cylogypsis lassaei H. Milne Edwards, 1853 (Brachyura: Grapsidae) along the coast of the South Island of New Zealand. Crustacean Research 24: 49–64.


of Kansas and Geolocial Society of America, Lawrence.


## Checklist of New Zealand living Crustacea

The following classification is based mostly on Martin and Davis (2001). All species are to be regarded as marine unless indicated otherwise by habitat codes.

- **All species:** A, adventive; B, brackish/estuarine; C, commensal; E, endemic; F, freshwater; S, supralittoral; T, terrestrial; *, unpublished (new) record; ? after a genus name or before a species name indicates uncertainty or a possible misidentification. Endemic genera are underlined (first mention).

### Notostroca: Hs, hypersaline environments.

### Cirripedia: Letters in parentheses following new records indicate where material is held, i.e. AUT (Earth and Oceanic Sciences Research Centre, Auckland University of Technology); GNS (GNS Science, Lower Hutt); NIWA (National Institute of Water & Atmospheric, Wellington); UA (Geology Department, University of Auckland).

### Other groups, especially Copepoda: Habitat codes – Be, benthic; L, littoral; Sl, sublittoral (to ca. 10 metres depth); Sh, shelf (ca. 10–200 metres depth); Ba, bathyhal (>200 metres depth); Bp, benthopelagic; Co, coastal; F, freshwater (including wells, as well as species found in terrestrial mosses as they comprise an essentially aquatic habitat); O, oceanic; P, parasitic; Pe, pelagic (planktonic); Ep, epipelagic; Me, mesopelagic; By, bathypelagic; Ph, phytal (if marine, usually in algal and seagrass communities in the littoral or sublittoral, but W indicates decaying or mollusc-bored wood, which may have been dredged from depths up to 2000 metres. If freshwater, usually in algal or flowering-plant communities but m indicates moss or liverwort and includes water courses and damp terrestrial situations. Zoogeography codes: Ant, Antarctic; Ca, Campbell Island; Ch, Chatham Islands; Sa, subantarctic; Sn, Snares Islands; Tr/St, tropical/subtropical; Tz, transition zone; W, widespread.


![SUBPHYLUM CRUSTACEA](image)

<table>
<thead>
<tr>
<th>Class</th>
<th>Branchiopoda</th>
</tr>
</thead>
<tbody>
<tr>
<td>Subclass</td>
<td>Phyllopondida</td>
</tr>
<tr>
<td>Order</td>
<td>Anostraca</td>
</tr>
<tr>
<td>Suborder</td>
<td>Spinicaudata</td>
</tr>
<tr>
<td>Family</td>
<td>Limnadiidae</td>
</tr>
<tr>
<td>Suborder</td>
<td>Cladocera</td>
</tr>
<tr>
<td>Subclass</td>
<td>Anomopoda</td>
</tr>
<tr>
<td>Superorder</td>
<td>Spinicaudata</td>
</tr>
<tr>
<td>Family</td>
<td>Podonidae</td>
</tr>
<tr>
<td>Suborder</td>
<td>Onychopoda</td>
</tr>
<tr>
<td>Subclass</td>
<td>Podonidae</td>
</tr>
<tr>
<td>Family</td>
<td>Eulimnadia marplesi Timms &amp; McLay, 2005</td>
</tr>
<tr>
<td>Order</td>
<td>Anostroca</td>
</tr>
<tr>
<td>Superorder</td>
<td>Cladocera</td>
</tr>
<tr>
<td>Subclass</td>
<td>Phyllodida</td>
</tr>
<tr>
<td>Class</td>
<td>Branchiopoda</td>
</tr>
<tr>
<td>Subclass</td>
<td>Phyllopondida</td>
</tr>
<tr>
<td>Order</td>
<td>Anostraca</td>
</tr>
<tr>
<td>Suborder</td>
<td>Spinicaudata</td>
</tr>
<tr>
<td>Family</td>
<td>Limnadiidae</td>
</tr>
<tr>
<td>Suborder</td>
<td>Cladocera</td>
</tr>
<tr>
<td>Subclass</td>
<td>Anomopoda</td>
</tr>
<tr>
<td>Superorder</td>
<td>Spinicaudata</td>
</tr>
<tr>
<td>Family</td>
<td>Podonidae</td>
</tr>
<tr>
<td>Suborder</td>
<td>Onychopoda</td>
</tr>
<tr>
<td>Subclass</td>
<td>Podonidae</td>
</tr>
<tr>
<td>Family</td>
<td>Eulimnadia marplesi Timms &amp; McLay, 2005</td>
</tr>
<tr>
<td>Order</td>
<td>Anostroca</td>
</tr>
<tr>
<td>Superorder</td>
<td>Cladocera</td>
</tr>
<tr>
<td>Subclass</td>
<td>Phyllodida</td>
</tr>
</tbody>
</table>

**Chiltoniella elongata** Knox & Fenwick, 1977 E

- **Class** Maxillopoda
- **Subclass** Thecostracea
- **Infraclasse** Ascothoracica
- **Order** Larida
- **Superorder** Synagogidae
- **Gen. et sp. indet.** Te Papa Palmer 1997

**Order Dendrogastriida**

**Dendrogastriidae**

- **Dendrogaster argentennis** Gygger & Salvat, 1987
- **Dendrogaster olegonensis** Palmer, 1997 E

**Infraclasse** Cirripedia

- **Superorder** Acrothoracica
- **Order** Pygofhora
- **Cryptopalidae**
- **Australophilus melampygus** (Brandt, 1907) E

- **Superorder** RHizocephala
- **Order** KENTROGONIDA
- **Lernaeodisciidae**
- **Triangularia muniidae** Smith, 1906
- **PELTOGASTRIDAe**
- **Boschmaia munida** Reinhard, 1958
- **Briarosaccus callosus** Boschma, 1930
- **Galatheacuscabai** Lützen, 1985
- **Pelagostera** Lützen et al. 2008 E
- **Tortugaster duxalidus** Lützen, 1985 E
- **Sacculinidae**
- **Sacculina** sp. Brockerhoff, McLay & Kluzo 2006

- **Order** AKENTROGONIDA
- **THOMPSONIIDAE**
- **Thompsonia affinis** Krüger, 1912
- **Thylacoleotidus** neozelandiae Lützen, Glenner & Lörz, 2009 E
- **INcertae Sedis**
- **Parthenopea vulcanophila** Lützen, Glenner & Lörz,
NeW zealand Inventory of biodiversity

2009 E
Gen. et sp. indet. Lützen, Glenner & Lorré 2009

Superorder THORACICA
Order IBLIFORMES
IDIOBLIDAE
Cheratolepas segmentata Studer, 1889 E
Cheratolepus spiniferus Buckridge & Newman, 2006 E
Idiobia idiotica (Batham, 1945) E

Order LEPADIFORMES
Suborder LEPADOMORPHA LEPADIDAE
Aleyx pacifica Pilsbry, 1907
Conchoeroma auritum (Linne, 1767)
Conchoeroma virgatum (Spengler, 1790)
Dosima fascicularis (Ellis & Solander, 1786)
Lepus anatuerus Linne, 1758 A
Lepus australis Darwin, 1851
Lepus pectinatus Spengler, 1793
Lepus testudinata Aurivillus, 1892

OXYNASPIDIDAE
Oxynaspis indicus (Annandale, 1910)
Oxynaspis terraeotum (Linne, 1753) E
POECILASMATIDAE
Megalasma carinatum (Hoek, 1883)
Megalasma striatum (Hoek, 1883)
Poecilasma kaempferi (Darwin, 1851)
Trilasinis bernaenus Hinds, 1883

Suborder HETEERALADOMORPHA ANELASMATIDAE
Anelasma squalicola Lovén, 1845* HETEERALADIDAE
Heretolepas japonica (Aurivillus, 1892)
Paralepas minuta (Phippeli, 1836)
Paralepas quadrata (Aurivillus, 1894)

Order SCALPELLIFORMES
CALANTICIDAE
Calantica spinosa (Quoy & Gaimard, 1834) E
Calantica spulaireta Foster, 1979 E
Calantica villosa (Leach, 1824) E
Scalpellus fosteri Neuman, 1980 E
Scalpellus sp. 1* NIWA E
Scalpellus n. sp. 2* NIWA E
Smilium acutum (Hoek, 1883)
Smilium zancleanum (Fabricus, 1798)

Suborder HETEERALADOMORPHA ANELASMATIDAE
Anelasma squalicola Lovén, 1845* HETEERALADIDAE
Heretolepas japonica (Aurivillus, 1892)
Paralepas minuta (Phippeli, 1836)
Paralepas quadrata (Aurivillus, 1894)

Order SCALPELLIFORMES
CALANTICIDAE
Calantica spinosa (Quoy & Gaimard, 1834) E
Calantica spulaireta Foster, 1979 E
Calantica villosa (Leach, 1824) E
Scalpellus fosteri Neuman, 1980 E
Scalpellus sp. 1* NIWA E
Scalpellus n. sp. 2* NIWA E
Smilium acutum (Hoek, 1883)
Smilium zancleanum (Fabricus, 1798)

Suborder HETEERALADOMORPHA ANELASMATIDAE
Anelasma squalicola Lovén, 1845* HETEERALADIDAE
Heretolepas japonica (Aurivillus, 1892)
Paralepas minuta (Phippeli, 1836)
Paralepas quadrata (Aurivillus, 1894)

Order SCALPELLIFORMES
CALANTICIDAE
Calantica spinosa (Quoy & Gaimard, 1834) E
Calantica spulaireta Foster, 1979 E
Calantica villosa (Leach, 1824) E
Scalpellus fosteri Neuman, 1980 E
Scalpellus sp. 1* NIWA E
Scalpellus n. sp. 2* NIWA E
Smilium acutum (Hoek, 1883)
Smilium zancleanum (Fabricus, 1798)
Clausocalanus paululus
Farran, 1926 pe Ep tr/St
Giesbrecht, 1888 pe Ep St

Clausocalanus parapergens
Frost & Fleminger, 1968

Clausocalanus lividus
Frost & Fleminger, 1968 pe Ep

Clausocalanus laticeps
Clausocalanus ingens

Gladioferens pectinatus
Centropages violaceus
Centropages elegans

Candacia ethiopica
(Giesbrecht, 1863) pe Ep/me tr/St
Candacia longimana
Candacia tenuimana
(Giesbrecht, 1888) pe me tr/St

Centropages aucklandicus
Krämer, 1895 pe co Ep

Boeckella symmetrica
Boeckella propinqua
Boeckella minuta
Grice, 1981 pe Ep tr
Paracandacia worthingtoni
Boeckella tanea
Brehm, 1928 F pe E
Boeckella hamata
Sars, 1904 F pe E
Boeckella delicata
Perca ll, 1937 F pe E

Pachyptilus eurygnathus
(Giesbrecht, 1892) pe Ep/me tr/St
Temora elongata
(Giesbrecht, 1888) pe Ep tr
Canthocalanus pauper
Giesbrecht, 1902 pe Ep Sa

Calanoides macrocarinatus
Cosmocalanus darwinii
(dana, 1849) pe Ep t/St/ Sa
dana, 1849 pe Ep tr/St

Neocalanus tonsus
(Brady, 1883) pe Ep/me St/Sa
dana, 1849 pe Ep tr/St

Neocalanus gracilis
Nannocalanus minor
(Giesbrecht, 1888) pe Ep/me
cAndaciidaE

Haloptilus ornatus
Euaugaptilus laticeps
Euaugaptilus longimanus
Euaugaptilus nodifrons
(Sars, 1905) pe By tr/St/Sa
Euaugaptilus palumbii
(Giesbrecht, 1889) pe me tr
Euaugaptilus oblongus
Haloptilus fons
(Farran, 1908) pe me/By tr/St/Sa
Euaugaptilus humilis

Metridia curticauda
Giesbrecht, 1889 pe me/By tr/
(Sars, 1905) pe By W
Metridia venusta
Pleuromamma abdominalis
(Wolfenden, 1905) pe By St
Lucicutia curta
(Sars, 1888) pe Ep tr/St
Lucicutia cf. flavicornis
Bradford, 1971 pe me St

Heterorhabdus spinifer
(davis, 1949) pe me St
Heterorhabdus papilliger
(Brodsky, 1950) pe By tr/ St
Heterorhabdus abyssalis
Heterorhabdus caribbeanensis
Heterorhabdus austrinus
Giesbrecht, 1902 pe Ep/me tr/St/Sa

Pareuchaeta biloba
Rhincalanus rostrifrons
(dana, 1852) pe Ep tr
Rhincalanus gigas
Pareucalanus sewelli
(Subeucalanus mucronatus
(Flower, 1911) pe By tr/St
Subeucalanus longiceps
(Disseta palumbii
Brodsky, 1950 pe By tr/ St
Subeucalanus papilferus
Heterorhabdus caribbeanensis
Heterorhabdus austrinus
Giesbrecht, 1902 pe Ep/me tr/St/Sa

Subeucalanus longiceps
Pareucalanus sewelli

Scaphocalanus echinatus
(Vervoort, 1951) pe me Sa/ant
Scaphocalanus subbrevicornis
Scaphocalanus magnus
Scaphocalanus longifurca

Lophothrix frontalis
(Park, 1980) pe By St
Amallothrix parafalcifer
(Sars, 1888) pe Ep tr/St
Amallothrix gracilis

Phaenna spinifera
Neoscolecithrix ornata
(Bradford-Grieve, 2001 Bp
Neoscolecithrix magna
Grice, 1972) Bp
Neoscolecithrix exigua
Tanaka, 1960 pe By tr/St/Sa
Neoscolecithrix sp.

ScolecithricidaE
Amallothis arcuata
(Sars, 1920) pe By/tr/St
Amallothis dentipes (Vervoort, 1951) pe Me Sa/Ant
Amallothis emarginata
(Farran, 1905) pe By/tr/St
Amallothis gracilis
(Sars, 1895) pe By/tr/St
Amallothis parafalcifer
(Park, 1980) pe By St

Phyllum Arthropoda
Crustacea
Hormitis brigisi Swanson, 1979
Jacobella papathuris Swanson, 1979
Maulus cf. pmulis (Brady, 1866)
Poseidonius major Benson, 1972
Poseidonius minor Benson, 1972
Poseidonius oculatus Whatley, Downing, Kesler & Harlow, 1986
Poseidonius munis Jellinek & Swanson 2003
Poseidonius spp. Ayress, Neil, Passlow & Swanson 1997
Procyclothere (Serratocyclothere) lytelettonesis Hartmann, 1982
Quadacythere birugia Hornibrook, 1952
Quadacythere medilaga Hornibrook, 1952
Quadacythere radicata Hornibrook, 1952
Waisyacyclothere joanne Swanson, 1969
IILYCYPRIDIDAE
Krithe antinovasvanni Ishizaki, 1966
Krithe comma Ayress, Barrows, Passlow & Whatley, 1999
Krithe compressa (Seguenza, 1980)
Krithe dolichoderia Bold, 1946
Krithe marialauee Abate, Barra, Aiello & Bonaduce, 1997
Krithe minima Coles, Whatley & Mogulvsky, 1994
Krithe morkheveni morkheveni Bold, 1960
Krithe nittida Whatley & Downing, 1993 'Rec
Krithe products Bold, 1880
Krithe pseudoconus Ayress, Barrows, Passlow & Whatley, 1999
Krithe reversa Bold, 1958
Krithe swansvanni Milau, 1993
Krithe trinidadensis Bold, 1958
Krithe Ayress, Neil, Passlow & Swanson 1997
Krithe 2 Ayress, Barrows, Passlow & Whatley 1999
Parakrithe swans 1979
LEGUMINOCYPRIDIDAE
Tringiglymus? sp. Hornibrook 1952
LEPTOCYPRIDIDAE
Callisocyclothere dorosotuberculata Hartmann, 1979
Callisocyclothere iminusvanni (Brady, 1898)
Callisocyclothere muduegi (Brady, 1880)
Callisocyclothere murrachua (Brady, 1880)
Callisocyclothere neopiana Swanson, 1979
Callisocyclothere obtusa Swanson, 1979
Callisocyclothere puri McKenzie, 1967
Callisocyclothere no. sp. cf. crispata Hornibrook, 1952
Callisocyclothere sp. Hornibrook 1952
Clathia australis Ayress & Drapela, 1996
Kangurina unispinos Swanson, 1980
Leptocythere hartmanni (McKenzie, 1967)
Leptocythere lacustris De Deckker, 1981
Leptocythere swansvanni Hartmann, 1982
Spongiomma novazaluzaldica (Hartmann, 1982) E
Swanswollen newbrighttonensis Guise, 2002 E
LIMNOCYPRIDIDAE
Gomphocythere duffi (Hornibrook, 1955 F)
Gomphocythere problematica (Brehm, 1932) F
Krassieweine amare Martens, 1992 B E
Krithe vulgaris (McKenzie & Swanson, 1981) F
Parahemicythere vulgaris McKenzie & Swanson, 1981
PHELUM ARTHROPODA CRUSTACEA
Cytherella intonsa Swanson, Jellinek & Malz, 2003
Cytherella latia Brady, 1880
Cytherella parishii Whatley & Downing, 1983
Cytherella permutata Swanson, Jellinek & Malz, 2003
Cytherella plummosa Swanson, Jellinek & Malz, 2003
Cytherella polita Brady, 1880
Cytherella pulchra Brady, 1880
Cytherella punctata Brady, 1880
Cytherella sp. Morley & Hayward 2007
Cytherelloidea iulii Swanson, 1969* E
Cytherelloidea n. sp. van den Bold 1963
Glynnymyella dymmetrica Swanson, Jellinek & Malz, 2003
Inversicytherella tanantia Swanson, Jellinek & Malz, 2003
Order MYODOCOPIDA
Suborder MYODOCOPINIA
CYPRIDINIDAE
Bathygurugula walfordi Poulsem, 1963
Cypridinoides cruenta Brady, 1902
Cypridinoides irini Poulsem, 1906
Cypridinoides reticulata Poulsem, 1962 E
Cypridinoides concentrica Kornicker, 1979 E
Gigantocypris austriaca Poulsem, 1962 Poulsem
Gigantocypris danae Poulsem, 1962 Pe
Macrocyprina castanea Brady, 1897 Pe
Metavargula iuta Kornicker, 1975 Pe
Metavargula bradfordi Kornicker, 1979 E
Metavargula mazzieri Kornicker, 1979 E
Paracypridina abertana Poulsem, 1962 Pe
Vargula asensus Kornicker, 1979 Pe
Vargula stathmik Kornicker, 1975 E
PHILOMEDIDA
Euphilomedes aglae (Thomson, 1879)
Euphilomedes ferox Poulsem, 1962
Harthamus n. sp. Eager 1995
Scolecorina arcuata Poulsem, 1962 E
Scolecorina sculpta (Brady, 1898) Pe
Scolecorina flexilla (Brady, 1898) E
Scolecorina wefii Kornicker, 1975 E
CYLINDROLEBERIDIDAE
Batyleberis oculata Kornicker, 1975 E
Cyctoleberis bradyi Poulsem, 1965
Diaspero grisea (Brady, 1880) E
Dolasterope johansoni Poulsem, 1965 E
Leuroleris zealandica (Baird, 1850) E
Parasterope pectinata Poulsem, 1965 E
Parasterope quadrata (Brady, 1898) Pe
Pasterope cristata Kornicker, 1975 E
Synasterope empousl Kornicker, 1975 E
SARSELIIDAE
Anchoenia n sp. Eager 1995
Chelocopa tasmanensis Kornicker, 1981
Cymbiohopa brevicostata Kornicker, 1975 E
Cymbiohopa hansini (Brady, 1880) E
Cymbiohopa hispida (Brady, 1898) E
Cymbiohopa zealandica (Poulsem, 1965) E
HALOCYPRIDIDAE
Archiconchoecia cuculata (Brady, 1802)
Archiconchoecia versicola (Deevey, 1978)
Archiconchoecia acuticauda Poulsem, 1906
Archiconchoecia aequipectora Poulsem, 1906
Archiconchoecia brachiopoda Poulsem, 1906
Archiconchoecia chuii Poulsem, 1906 E
Archiconchoecia ophiochaeta Poulsem, 1906
Archiconchoecia ophiochaeta Deevey, 1982
Archiconchoecia hyalophyllus Poulsem, 1906 E
Archiconchoecia loricata (Claus, 1894)
Order BATHYHELLEIDAE

Bathyhelleidae sp. 1 Schminke 1971 E

Bathyhelleidae sp. 2 Schminke 1971 E

PARABATHYHELLEIDAE

Atopobathysella compagana Schminke, 1973 E

Hexabathysella aurora Schminke, 1973 E

Notobathyhellea chilensis Schminke, 1973 E

Notobathyhelle hinnosea Schminke, 1973 E

Notobathyhelle longipes Schminke, 1978 E

Notobathyhelle sp. Schminke 1973 E

Superorder PERACARIDA

Order LIVING McGRASTIDAE

GNAUTHUSIDAE

Gnathophaius elegans G.O. Sars, 1883

Gnathophaius zeus Willems-Soehn, 1875

Neognathophaius ingenis (Dohrn, 1870)

Neognathophaius gigas (Willems-Soehn, 1875)

LOPHOGASTRIDA

Lophogaster sp. MNZ

Paralophauster glaber Hansen, 1910

Order MYSIDAE

Myidae

Boreomysis rostrata Illig, 1906

Euchaeotoma ozalata Hansen, 1910

Euchaeotoma typica G.O. Sars, 1884

Euchaeotoma zurstrasseni (Illig, 1866)

Gastrosaccus australis W. Tattersall, 1918

Tenagnostus similis W. Tattersall, 1923 E

Tenagnostus longisquama W. Tattersall, 1923 E

Tenagnostus minimus W. Tattersall, 1923 E

Tenagnostus tenures W. Tattersall, 1918 E

Tenagnostus thomsoni W. Tattersall, 1923 E

PETALOPHthalmIDAE

Petalophthalmus sp. MNZ

Order AMPHIPODA

Suborder INGOLFIELLEDAE

INGOLFIELLIDAE

"Pseudoingolfella" sp. a Schminke & Noodt 1968

"Pseudoingolfella" sp. b Schminke & Noodt 1968

Suborder GAMMARIDAE

AMARYLLIDAE

Amaryllis macrophthalmus Haswell, 1880

AMPELISCIDAE

Amphipus alfredi Barnard, 1961 E

Amphipus cisternonii Stebbing, 1888 E

Bathynella edeni Barnard, 1961 E

Haplochirina barbimana (Thomson, 1879)

Haplochirina lenfeldti Chilton, 1884 E

Lembo? sp. No. 1 Barnard 1972

Lembo? sp. No. 3 Barnard 1972

Meridoleomys alectronis (Myers, 1981) E

Meridoleomys pertinax (Myers, 1981) E

Microdonotopsis apoyo Barnard, 1972 E

CAPRELLIDAE

Caprella asparagis Say, 1818

Caprella nigrofusca Barnard, 1979 E

Caprella mutica Schurin, 1935 A

Caprella longicollis (Niclot, 1849)

Caprellaparvena substantarctica Guerra-Garcia, 2003 E

Caprellineoides myeri (Pfeffer, 1888)

Psuedoengelina campbellensis Guerra-Garcia, 2003 E

Psuedopontoma hurleyi McCain, 1969 E

CEINIDAE

Ctena egregia (Chilton, 1883) E

Tintinnale karevi Barnard, 1972 E

Wartomo manene Barnard, 1972 E

CHELURIDAE

Chelura trisexualis Philippi, 1839 A

Chevalia sp. Ahyong

CHITONIIDAE

Chitonidae

Chitoninae

Chiton unio Bousfield, 1964 E

Chitoninae

Chitoninae

COLOMASTIGIDAE

Colomastix myriangula Hurley, 1954 E

Apocorophium acutum Chevreux, 1908 A

Mesocorophium archeriowum (Costa, 1857) A

Mesocorophium insidiosum (Crawford, 1937) A

Mesocorophium sectonea (Crawford, 1937) A

Paracorophium brackenhamensis Chapman, 2002 B A

Paracorophium excavatum (Thomson, 1884) F B E

Paracorophium lucasi Hurley, 1954 F B E

CYMIDAE

Cyamus balanopterane Barnard, 1931

Cyamus boops Lutken, 1873

Cyamus erraticus Roussel de Vauzeme, 1834

Cyamus gracilis Roussel de Vauzeme, 1834

Cyamus ovalis Roussel de Vauzeme, 1834

Iphimedia thomsonii Guerin-Meneville, 1849

Iphimedia plumbeus (Pfeffer, 1888)

Scutocyamus antipodensis Hurley, 1960 E

CYPHOCARIDIDAE

Cyphocaris archaicus Smyth, 1874

Cyphocaris richardi Boeck, 1871

CYPHOCARIDIDAE

Cyphocaris archaicus Smyth, 1874

Dubnovathysella levicaudata (Chilton, 1884) E

Echinocyamus dianae (Thomson, 1879) E

Echinocyamus dianae (Thomson, 1879) E

Gondogeneia subantarctica (Stephensen, 1898) E

Gondogeneia subantarctica (Stephensen, 1898) E

Gondogeneia sp. Chilton 1909 E

Oradarea novazelandiae (Thomson, 1879) E

Paramoera aucklandica (Walker, 1908) E

Paramoera chevreuxi (Stephensen, 1927) E

Paramoera fasciata (Dana, 1852) E

Paramoera rangatira Barnard, 1972 E

Paramoera sp. Barnard 1972 E

Paramoera sp. Barnard 1972 E

Priapobranchia? levis (Thomson, 1879) E

Regalia fasciulata Barnard, 1930 E

Rhachotropis chathamensis Lorz, 2010 E

Rhachotropis delicata Lorz, 2010 E

Schneideria serraticauda (Stebbing, 1888) E

Whangaroa translucens (Chilton, 1884) E

EUSKIRIDAE

Ashbyella makel Barnard, 1972 E

Bathycaridaria magnifica Dahl, 1959 E

Eusiriidae monoculoides (Haswell, 1880)

Eusiriidae antarcticus Thomson, 1880

Gondogeneia dianae (Thomson, 1879) E

Gondogeneia dianae (Thomson, 1879) E

Gondogeneia subantarctica (Stephensen, 1898) E

Gondogeneia sp. Chilton 1909 E

Oradarea novazelandiae (Thomson, 1879) E

Paramoera aucklandica (Walker, 1908) E

Paramoera chevreuxi (Stephensen, 1927) E

Paramoera fasciata (Dana, 1852) E

Paramoera rangatira Barnard, 1972 E

Paramoera sp. Barnard 1972 E

Paramoera sp. Barnard 1972 E

Priapobranchia? levis (Thomson, 1879) E

Regalia fasciulata Barnard, 1930 E

Rhachotropis chathamensis Lorz, 2010 E

Rhachotropis delicata Lorz, 2010 E

Rhachotropis levicata Barnard, 1961 E

Schneideria serraticauda (Stebbing, 1888) E

Whangaroa translucens (Chilton, 1884) E

EXOERECIDOTOIDAE

Pakali brevirostrus Cooper & Fincham, 1974 E

Pakali rogeri Fenwick, 1983 E

HADZIIDAE

Zhadi substantarctica Lowry & Fenwick, 1983 E

HYALIDAE

Apohyale hirtpalma (Dana, 1852)

Apohyale media (Dana, 1852)

Apohyale novazelandiae (Thomson, 1879) E

Protohyale (Protohyale) campbelli (Filhol, 1885) E

Protohyale (Boreohyale) glavelli Chilton, 1916 E

Protohyale (B.) marco bruce Stebbing, 1899

Protohyale (B.) rubra (Thomson, 1879)

Hyale sp. Thompson 1899

IPEHYMIDAE

Amathilopis grevei Barnard, 1961

Anisophasiidae haurakensis (Hurley, 1954) E

Curidia knoxi Lowry & Myers, 2003 E

Epimeria bruni Barnard, 1961 E

Epimeria gauchoes Barnard, 1961 E

Epimeria australis Barnard, 1961 E

Iphimedia spinosa (Thomson, 1880) E

Labriphelina hinemou (Hurley, 1954) E

ISAIEDAE

Gammaropus chiltoni (Thomson, 1897) E

Gammaropus crusipes (Haswell, 1881)

Gammaropus haswelli (Thomson, 1897)

Gammaropus kermaidezii (Stebbing, 1888) E

Gammaropus longimanus (Chilton, 1884) E

Gammaropus novaezealandiae (Thomson, 1879) E

Gammaropus typica (Chilton, 1884) E

Phylum ARTHROPODA

Crustaceae

219
EPULAXIDAE

Epulaea fraca (Hale, 1940)
Rocinella bonisa Bruce, 2009 E
Rocinella garricki Hurley, 1957 E
Rocinella leptopus Bruce, 2009 E
Rocinella pakari Bruce, 2009 E
Rocinella resima Bruce, 2009 E
Rocinella runga Bruce, 2009 E
Rocinella satygio Bruce, 2009 E
Rocinella sp. Bruce 2009

SYNECUS

Syneucus latus Richardson, 1909 Pe
Syneucus springthorpeae Bruce, 1997 Pe
Syneucus sp. Bruce 2009

ANTHRIDIACE

Aegiochus tara
Aegiochus piihuka
Aegiochus nohinohi
Aegiochus laevis
Aegiochus kanohi
Aegiochus kakai
Aegiochus insomnis
Aegiochus gordoni

VANHOEFFENIA

Vanhoeffenia novaezelandiae (Beddard, 1885) E
Sursumura affinis Malyutina, 2004

PARAMUROIDEA

Aegapheles hamiota
Aegapheles copidis
Aegapheles birubi

PHREATOICUS

Phreatoicus typicus chilton, 1883 F
Phreatoicus flavius Nicholls, 1944 F
Phreatoicus kirkii (Chilton, 1906) F
Phreatoicus littoralis Nicholls, 1944 F
Phreatoicus percariali Nicholls, 1944 F
Phreatoicus orari Nicholls, 1944 F
Phreatoicus typicus Chilton, 1883 F

SUBORDER PHREATOTICIDA

PHREATOTICIDAE

Aegiochus
Aegapheles

PHREATOTICUS

Phreatoicus javanicus

SUBORDER CYMOTHOIDA

AEGIIDAE

Aegi sphenoides
Aegi strevelorei Bruce, 2009
Aegi urutoma Barkard, 1914

AEPIPHILIDAE

AEPIPHIUS

AEPIPHILUS

AEPIPHILUS

SUBORDER LIMNORIDEA

LIMNORIDAE

Limnoria

SUBORDER SPHAEROMATIDA

PLAkarthridae

PLAKARTHRIDAE

PLAKARTHRIDAE

SUBORDER SEROLIDAE

SEROLIDAE

SUBORDER ACUTISORLIDAE

ACUTISORLIDAE

ACUTISORLIDAE

SUBORDER GNATHIIDAE

GNATHIIDAE
**NEW ZEALAND INVENTORY OF BIODIVERSITY**

**ANARTHURIIDAE**
Siphonodrilus spp. NIWA G. Bird
Gen. et spp. indet. (2) NIWA G. Bird

**COLLETTIDAE**
Colletta cylindrotoides Larsen, 1999*
Leptognathidae spp. (2) NIWA G. Bird

**LIBNIANIDAE**
Libunia spp. NIWA G. Bird

**MACROSTOMIIDAE**
Macrostomella spp. (2) NIWA G. Bird

**LEPTOCHELIDIDAE**
Konarus sp. G. Bird
Leptochelia mirabilis Stebbing, 1905

**LEPTONAGHIDAE**
Leptognathia spp. (5)*
NOTOTAENIIDAE
Nototanais sp. G. Bird Ca

**PARATANIDAE**
Bathytanais spp. (2) NIWA G. Bird
Paratanais ocellatus (Vanhoeffen, 1914) B
Paratanais tenalis (G.M.Thomson, 1880) E
Paratanais sp.* Auckland Is.
Paratanais spp. (3)*

**PSEUDOTANIDAE**
Akanthotanais spp. NIWA G. Bird
Cryptocopeidae arcuatae (Hansen, 1886)
Cryptocopeidae sp. NIWA G. Bird
Myxiostranxus sp. NIWA G. Bird
Pseudotanaidae nordenkildi (Sieg, 1977)
Pseudotanaidae sp. (3)*

**TANAELLIDAE**
Arapinha spp. (2) NIWA G. Bird
Anaphruoides sp. NIWA G. Bird
Arthura monoscanthus (Vanhoeffen, 1914) n. comb.*
Tanella forcifera (Lang, 1968)* B
Tanella spp. (4) NIWA G. Bird

**TANAIIDAE**
Pancolleidae litoralis (Vanhoffen, 1914)*
Pancolleidae sp.* NIWA G. Bird
Sinelobus stanfordi (Richardson, 1901) F B C (sponge)
Synaptotanais sp. NIWA G. Bird
Tanais sp.*
Zexu novaeanzaculariae (Thomson, 1879) E
Zexu phyladesis Sieg, 1980*
Zexoides aka Bird, 2008 E
Zexoides helleri Sieg, 1980*
Zexoides oh Otto (Stebbings, 1914)*
Zexoides pseudolitoralis Sieg, 1980*
Zexoides rinnaehardtii Bird, 2008 E
Zexoides sp.*

**TYPHLOTANIDAE**
Hamnitudeidae spp. (2) NIWA G. Bird
Larenstonatias NIWA G. Bird
Meronomastias Calman, 1905 E
Pariaptanais sp. NIWA G. Bird
Typhlotanfeis greeniachensis Shinuo, 1970*
Typhlotanfeis sp. (10)*

**INCERTAE SEDIS**
Akanthophorellae sp. (2) NIWA G. Bird
Chauldromela sp. (2) NIWA G. Bird
Espino typica Lang, 1968 C (holothurian)
Mirandolutias vorax Kusakin & Tzareva, 1974*
Stenotonais sp. NIWA G. Bird
Tanais sp. (2) NIWA G. Bird

**ORDER CUMACEA**
BODOTRIDAE
Apoxa n. sp. 1 E B
Bathyxoma longirostrum Calman, 1905 B
Cyclaspis argus Zimmer, 1902 E
Cyclaspis celobis Calman, 1907 E
Cyclaspis elegans Calman, 1907 E
Cyclaspis laurens Thompson, 1892
Cyclaspis similis Calman, 1907
Cyclaspis tasmanica Jones, 1969 B E
Cyclaspis thomsoni Calman, 1907
Cyclaspis triplicata Calman, 1907 E

**EUPHAUSIIDAE**
Euphausia recurva Hansen, 1905
Euphausia similis G.O. Sars, 1883
Euphausia s. armata Hansen, 1911
Euphausia spinifera G.O. Sars, 1883
Euphausia taliuntini Stebbing, 1900.
Nematothenia flexipes (Ortmann, 1893)
Nematoteles megalops G.O. Sars, 1883
Nematoteles micros G.O. Sars, 1883
Nyctiphanes australis G.O. Sars, 1883
Stylocheiron abbreviatum G.O. Sars, 1883
Stylocheiron elongatum G.O. Sars, 1883
Stylocheiron longicorne G.O. Sars, 1883
Stylocheiron maximinus Hansen, 1908
Stylocheiron subinae G.O. Sars, 1883
Thysanoessa gregaria G.O. Sars, 1883
Thysanoessa macrura G.O. Sars, 1883
Thysanoessa australis Holt & Taftersall, 1905
Thysanoessa ohlsoni G.O. Sars, 1883

**ORDER DECAPODA**
Suborder DENDROMORPHIPA
ARISTEIDAE
Aristaeomorpha floeaceae (Risso, 1826)
Aristieomorpha edwardsiana (Johnson, 1867)
Aristeis semidentatus Bate, 1881
Aestropeneus c. nitidus (Barnard, 1947)
BENTHECTIDAE
Benthectus cerus Burkenroad, 1936
Benthectus investigatoris Alcock & Anderson, 1899
Genadas capensis Calman, 1925 P e
Genadas gilchristi Calman, 1925 P e
Genadas incertas (Bals, 1927)
Genadas kempi Stebbing, 1914 P e
Genadas tiaooyei Bouvier, 1906 P e
LUCIFERIDAE
Lucifer typhus H. Milne Edwards, 1857 P e
PENAEIDAE
Funchalia villosa (Bouvier, 1905) P e
Funchalia woodwardi Johnson, 1867 P e
SARGIDAE
IS Regeris arcuatae Kröyer, 1855 P e
Sergestes darwinensis Burkenroad, 1940 P e
Sergestes index Burkenroad, 1940 P e
Sergestes cf. seminudus Hansen, 1919 P e
Sergia japonica (Bate, 1881) P e
Sergia kröyeri (Bate, 1881) P e
Sergia potens (Burkenroad, 1940) P e
SICYONIIIDAE
Sicyonia inflata (Kubo, 1940)*
Sicyonia truncata (Kubo, 1949)
Sicyoninae
Sicyoidea sibogae (de Man, 1907)
Hymenopanaeus obliquirostris (Bate, 1881)
Solenocera comata Stebbing 1915

**INFAOJDER CARIDEA**
ALPHHEIDAE
Alphheis garricki Yaldwyn, 1971 E
Alphheis euporosyre richardsoni Yaldwyn, 1971 E
Alphheis haittoni Coutière, 1905
Alphheis novaeanzaculariae Miers, 1876
Alphheis socialis Hacker, 1865
Athenes indicus Coutière, 1903
Betaeopsis aquinana (Dana, 1852) E
ALVINOCARIDIDAE
Alvinocaris alexandrier Ahyong, 2009 E
Alvinocaris longirostris Kikuchi & Ohta, 1995
Alvinocaris mira Webber, 2004 E
Alvinocaris saintlaurentae Komai & Segonzac, 2004
ATYIDAE
Paratau curvirostri (Heller, 1862) F E
CAMYPLONIDAE
Camyplonotus rathbournii Schmidt, 1926
CRANGONIDAE

224
Lophopagurus (A.) triserratus (Ortmann, 1892)
Lophopagurus (Lophopagurus) foresti McLaughlin & Gunn, 1992 E
Lophopagurus (L.) lacertosus (Henderson, 1888) E
Lophopagurus (L.) ?nanus (Henderson, 1888)
Lophopagurus (L.) nodulosus McLaughlin & Gunn, 1992 E
Lophopagurus (L.) pumilis de Saint Laurent & McLaughlin, 2000 E
Lophopagurus (L.) thompsoni (Filhol, 1885) E
Michelopagurus? sp. E
Pagurinus hectori (Filhol, 1883) E
Pagurixus kermaudensis de Saint Laurent & McLaughlin, 2000
Pagyrops esnarris McLaughlin & Gunn, 1888
P. jakacynsca pacatophora (de Saint Laurent & McLaughlin, 1999)
Pagurus albidusinaxis de Saint Laurent & McLaughlin, 2000 E
Pagurus iridocarpus de Saint Laurent & McLaughlin, 2000 E
Pagurus novozelandiae (Dana, 1852) E
Pagurus sinausus (Stimpson, 1858)
Pagurus traversi (Filhol, 1885) E
Porcellanopagurus chilini de Saint Laurent & McLaughlin, 2000
Porcellanopagurus edwardsi Filhol, 1885 E
Porcellanopagurus filholi de Saint Laurent & McLaughlin, 2000
Porcellanopagurus tridentatus Whitelegge, 1900
Propaguris deprefundus (Stebbing, 1924)
PARAPAGURIDAE
Ctenopagurus sp. E
Paragammarus diogenes (Whitelegge, 1900)
Paragammarus hirsutus (de Saint Laurent, 1972)
Paragammarus abyssorum (Filhol, 1885)
Paragammarus bouvieri Stebbing, 1910
Paragammarus latimanus Henderson, 1888
Paragammarus richeri Lemaire, 1999
Sympagurus dimorphus (Studer, 1883)
Sympagurus papposus Lemaire, 1996
P. perchele pisideus (Heller, 1865)
Petrocheles spinosus (Miers, 1876) E
Petrolisthes elongatus (H. Milne Edwards, 1837)
Petrolisthes lamarkii (Leach, 1820)
Petrolisthes novozelandiae Filhol, 1885 E
PYLOCHELIDAE
Chiroptopula puncticola Forest, 1987
Ptychopetes mortenseni Boas, 1926
Trichoeus brachyopus Forest & de Saint Laurent, 1987
Trichoeus perple克斯 Forest, 1987 E
Trichoeus spinosus (Henderson, 1888)
Trichoeus pilumnus Forest & McLaughlin, 2000
Infracarida BRACHYURA
AETHIDIAE
Acteomorpha erosa Miers, 1877
ATELECYCLIDAE
Parapagurion newzealandiae Dell, 1972 E
Trichopetralion fantasticum Richardson & Dell, 1964 E
Trichopetralion janetiae Ahyong, 2008
BELIIDAE E
Heterozius rotundifrons A. Milne Edwards, 1867 E
BYTHOGRACIDAE
Gandalfia puna McLaughlin, 2000 E
CALAPPIDAE
Marsia australiensis Campbell, 1971
Marsia microspinosa Davie & Short, 1989
CANCIRIDAE
Glebocarcinus amphioetus (Rathbun, 1898) A
Metacarcinus novozeelandiae (Hornbom & Jacobson, 1846)
Romaleon gibbolous (Rathbun, 1898) A
CRYPTOCRIBIDAE
Cryptocerus coralliodytes Heller, 1861
CYMOMIDAE
Cymonocerus achaeus Mellor, 1881
Cymonomus australiensis Whitelegge, 1900
Cymonomus kermadecensis (Stebbing, 1924)
CRYPTODROMIDAE
Cryptodromus undulatata (Ruppell, 1833)
Metadromia wilsoni (Fulton & Grant, 1902)
Timidia dromia (Linnaeus, 1763)
DYNOIDAE
Dynamene plumonoides Alcock, 1900
Dynamene lanecius (Koyama, 1933)
EPIALIDAE
Huenia herkendia (de Haan, 1839)
Leptomaia tuberculata Griffin & Tranter, 1986
Orepleurodon waipounamu Webber & Richer de Forges, 1995
Rechia ahyongi McLean, 2009 E
Rechia riversandersoni (Alcock, 1895)
ERIPHIDAE
Bouetiana norcensis (Grant & McLuccoh, 1907)
ETHUSIDAE
Ethusa setosa Ahyong, 2008 E
Ethusa rossiana Ahyong, 2008 E
GERONYIDAE
Chaceon bicolour Manning & Holthuis, 1989
Chaceon yaldwyni Manning, McLean & Webber, 1990 E
GONEPLACIDAE
Goneplax maritae Komatsu & Takeda, 2004
Neomonachocaris huttoni Filhol, 1886 E
Pycnoexus meridionalis (Rathbun, 1923)
Pycnoexus victorienis (Rathbun, 1923)
GRAPSIDAE
Geopapagurus graji (H. Milne Edwards, 1853) T
Leptogammarus variegatus (Fabricius, 1793)
Porcellanopagurus minenus A. Milne Edwards, 1873
Planus major (MacLeay, 1838)
Planus marinus Rathbun, 1914
HOMOLIDAE
Dugasus petteri (Grant, 1905)
Homola orientalis Henderson, 1888
Homola tauranutzui Guinot & Richer de Forges, 1995
Homolochunia pallida Griffin & Brown, 1976
Yaldwynopagus spinimanus (Griffin, 1915)
HOMOLIDOROMIDAE
Dicranodromia delli Ahyong, 2008 E
Dicranodromia spinulata Guinot, 1995
Homolodromia kai Guinot, 1993
HYMENOSOMATIDAE
Amarinus lacustris (Chilton, 1882) F
Elamena longirosis Filhol, 1885
Elamena monona Melrose, 1975 E
Elamena producta Kirk, 1879 E
Halicarcinus cookii (Filhol, 1885) E
Halicarcinus insinuatus Richardson, 1949
Halicarcinus ovatus Stimpson, 1858
Halicarcinus planatus (Fabricius, 1775)
Halicarcinus tongi Melrose, 1975 E
Halicarcinus varius (Dana, 1853) E
Halicarcinus whitei (Miers, 1876) E
Halimena aotearoa Melrose, 1975 E
Hymenosoma depressum Hornbom & Jacquinot, 1846 E
Neothalamites pulex (Dana, 1851) E
NOTOMIDAE
Achaeus achatinus Sakai, 1938
Achaeus curirostris (A. Milne Edwards, 1873)
Achaeus kermaudensis Webber & Takeda, 2005 E
Cytromia cornuta Richer de Forges & Guinot, 1988
Cytromia lamelulata Rathbun, 1906
Checklist of New Zealand fossil Crustacea

Letters in parentheses following new records indicate where material is held, i.e. AUT (Earth and Oceanic Sciences Research Centre, Auckland University of Technology); GNS (Institute of Geological and Nuclear Sciences, Lower Hutt); NIWA (National Institute of Water and Atmospheric Sciences, Wellington); UA (Geology Department, University of Auckland). Stratigraphic ranges, using abbreviations for New Zealand stages (Cooper 2004), follow each fossil species listing.

SUBPHYLUM CRUSTACEA

Class MAXILLOPODA

Infraclasse CIRRIPEDIA

Superorder ACROTHORACICA

Order PYGOPHORA

CRYPTOPHALIDAE

Australophalidinae: sp. nov. * Po–Pi (AUT)  E
Gen. et sp. indet. * Po–Pi (UoA)

INCERTAE SEDIS

Zapfella sp. * Bm (GNS)
Zapfella? sp. * Ko (UoA)

PHYLUM ARTHROPODA CRUSTacea

Ocyvide pallidula Jacquinot in Hombron & Jacquinot, 1846

OZIIAE

Ozius truncatus H. Milne Edwards, 1834

PALIDAE

Pseudopalaicus declivis Castro, 2000

Pseudopalaicus oahuensis (Rathbun, 1906)

Pseudopalaicus undulatus Castro, 2000

PARTHENOPIAE

Actaeomorpha eroa Miers, 1877

Garthambrus allisoni (Garth, 1992)

Garthambrus tani Ayhong, 2008

Platyambrus constictus (Takeda & Webber, 2007)

PILUMIDAE

Actuneus griffini Takeda & Webber, 2006 E

Pilumnopus serratifrons (Kinahan, 1856)

Pilumnus fimbriatrics H. Milne Edwards, 1834

Pilumnus lumpsinus Bennett, 1964 E

Pilumnus novaezeelandiae Filhol, 1886 E

PINNOTHERIDAE

Neopinnotheres atrioculata (Page, 1983 E

Pinnotheres novaezeelandiae (Filhol, 1885) E

PLAGUSIIDAE

Miersيضاذغus novaezeelandiensis Turkey, 1978

Percnon planissimum (Herbst, 1804)

Plagusha calabar (Linnaeus, 1758)

Plagusha dawsonii de Haan, 1835

Plagusha squamosa (Herbst, 1790)

PORTUNIDAE

Capthura ankerovae Takeda & Webber, 2006 E

Charybdis japonica (A. Milne Edwards, 1861 A

Liochristus corrigatus (Pennant, 1777)

Nectocarcinus antennarius (Jacquinot, 1853) E

Nectocarcinus bennetti Takeda & Miyake, 1969 E

Ovalipes catharus (White, 1843)

Ovalipes elongatus Stephenson & Rees, 1968

Ovalipes molleri (War, 1933)

Portunus pelagicus (Ward, 1933)

Ovalipes elongatus Stephenson & Rees, 1968

Ovalipes molleri (War, 1933)

Portunus pelagicus (Ward, 1933)

Ovalipes elongatus Stephenson & Rees, 1968

Ovalipes molleri (War, 1933)

Portunus pelagicus (Ward, 1933)

Ovalipes elongatus Stephenson & Rees, 1968

Ovalipes molleri (War, 1933)

Portunus pelagicus (Ward, 1933)

TRAPEZIDAE

Trapezia nana (Buckler, 1893)

Trapezia pustulosus (Wood-Mason, 1876)

Garthambrus dawsonii de Haan, 1835

Platymaia maoria (H. Milne Edwards, 1873)

Komatsu & Takeda, 2007 E

Ebalia webberi (Buckler, 1893)

Ebalia tuberculosa (Buckler, 1893)

Ebalia jordani Rathbun, 1906

Ebalia humilis Rathbun, 1906

EUROPEOIDEA

Latreillia metanesa (Buckler, 1893)

Eplumula australiensis (Buckler, 1893)

LATREILLIDAE

Sacculinidae

Superorder RHIZOCEPHALA

Order KENTROGONIDA

SACCULINIDAE?


Superorder THORACICA

Order LEPADIFORMES

LEPADIDAE

Lepas ?austalis Darwin, 1851 Qu

Lepas claudiaina Buckleridge, 1983 SI-Ti E

Lepas motoaurenensis Maxwell, 1968 Pb E

Tristoleonopels harringtoni (Laws, 1948) Lw–Pi E

Pristoleonopels haunakeiensis (Buckleridge, 1983) Lw–Pb E

Pristoleonopels pukaanangensis (Buckleridge, 1983) Po–Pi E

Pristoleonopels waikakapangensis (Buckleridge, 1983) Lw–Pi E

Pristoleonopels n. sp. Ar E

Order SCALPELLIFORMES

ARCOSCALPELLIDAE

Anguloscalpellum complanatum (Withers, 1924)

Lw–Ld E

Anguloscalpellum cf. complanatum (Withers, 1924) E

Po E

Anguloscalpellum crossiforme Buckleridge, 1983 Lw

227
NEW ZEALAND INVENTORY OF BIODIVERSITY

E Anguloscalpellum euglypha (Withers, 1924) Lwh-Ld E
Anguloscalpellum granitumackei Buckeridge, 1983 Po-Sw E
Anguloscalpellum? striatulum (Withers, 1924) Lwh-Ld E
Anguloscalpellum unguatum (Withers, 1913) Lsw E
CALANTHIDAE
Calancta spinulatera Foster, 1979 Ww-Rec E
Cretisalpinum cf. glabrum (Roemer, 1841) Uk
Cretisalpinum? sp. nov.? Cn (GNS) E
Cretisalpinum? sp. Buckeridge 1983 Mp-Dt
Escoallinum euglypha Buckeridge, 1983 Ww Sw
Pachyscalpellum cramptoni Buckeridge, 1991 Mp
Pachyscalpellum deboae Buckeridge, 1999 Mb E
Scialpes argatus (Withers, 1924) Lwh-Ld E
Scialpes? pittiness Buckeridge, 1948 Ab-Ar E
Scialpes cf. studeri (Wither, 1922) Ab-Ar
Scialpes varitata Buckeridge, 1983 Lw Ww E
Smillium calanticodenum Buckeridge, 1983 Dw-Dm
Smillium chathieum Buckeridge, 1984 Pt E
Smillium subplanum (Withers, 1913) Lw-Po E
Zeacalpella crassum Buckeridge, 1983 Dm-Ab E
Gen. nov. et sp. nov.? Mfh-Dt (GNS) E
Gen. et sp. indet. Buckeridge 1983 Mp-Mb
EOLEPAPIDAE
Eolpes? novozelandiae Buckeridge 1983 Ce E
ZEUMLOPRADAE
Zeuzeplatypus? sp. Buckeridge 1983 Kh
Order SESSILIA
Suborder VERRUCOMORPHA
VERRUCIDAE
Metaverrucula recta (Aurivillius, 1898) Po-Rec E
Verrucula nystromi Buckeridge, 1983 Dm-Po E
Verrucula sauria Buckeridge, 2010 Mb E
Verrucula tasmannica chathecum Buckeridge, 1983 Dw-Dm
Verrucula t. tasmannica Buckeridge, 1983 Lwh
Suborder BALANOMORPHA
ARCHAEOBALANIDAE
Armatobalanus motulektekensis Buckeridge, 1983 Po E
Armatobalanus? sp. Buckeridge 1983 Po E
Striatobalanus zelandicus (Withers, 1924) Sl-Ti E
Notobalanus vesitius (Darwin, 1854) Lw-Rec E
Pilarobalanus lornensis Buckeridge, 1983 Ab-Ak E
Pilarobalanus? xuitaiaensis Buckeridge, 1983 Ab E
Tasmanobalanus acutus acutus (Withers, 1924) Pt-Sw E
Tasmanobalanus a. clifdensensis Buckeridge, 1983 Po-Po E
Tasmanobalanus a. clifdensensis Buckeridge, 1983 Sc E
Tasmanobalanus a. convexus Buckeridge, 1983 Pa E
Tasmanobalanus grantmackiei Buckeridge, 1983 Sw-Sw E
Zoolobalanus everetti (Buckeridge, 1983) Lhw E
Zoolobalanus novozelandicus (Buckeridge, 1983) Ld-Lw E
AUSTROBALANIDAE
Australobalanus imperator aotea Buckeridge, 1983 Ld-Po E
Australobalanus macdonaldensis Buckeridge, 1983 Lw E
Epopeella espicata Buckeridge, 1983 Po E
Epopeella cf. picta Gray, 1843* Wp (AUT) E
Protobalanus pohahuhuensis (Buckeridge, 1984) Ld E
BATHYSALMATIDAE
Bathybalanus aucklandicum (Hector, 1888) Lw-Ww E
Bathybalanus rangatina Buckeridge, 1983 Dt-Dm E
BALANIDAE
Amphibalanus variegatus (Darwin, 1854) Ww-Rec E
 Fistulobalanus konakouli (Tarasov & Zevina, 1957)
Macrocospha? sp. Ayress 1995 Ak
NEOCYTHERIDIDAE
Caryocythereis pseudolongata Ayress, 1995 Ak
Caryocythereis sp. Ayress 1993 Ld-Lw
Neocoelocythere mediana Swanson, 1969 Ld-Lw
Neocoelocythere reticulata Ayress, 1995 Ak-Lw
Pentodyocythere hayleri (Chapman, 1906) Ak-Rec
NOTOCYTHEIDAE
Nexunhania fenestralis King, 1855 Wc-Rec
PARACYTIDAE
Agui?ia praeora Chapman, 1926 Ld.
Paracythere coccina (Hornibrook, 1953) Ab-Lhw
Paracythere sp. 5040 Dingle 2009 Mh
Paracythere? sp. 5080 Dingle 2009 Mh
Pluteunophora zeulandica Brady 1880 Ld-Lw
PARADOXOSTOMATIDAE
Certhyris parallela Milau, 1993 Po
Paracythereis cf. gracilis (Chapman, 1915) Ak
Paracythereis sp. Ayress 1995 Ld
PECTOCYTHEIDAE
Amebocythere ogari Dingle, 2009 Mh
Amebocythere? sp? 5078 Dingle 2009 Mh
Keija? hornibrooki Milau, 1993 Po
Keija? sp. Ayress 2006 Po
Munseyella brevis Swanson, 1979 Ld-Rec
Munseyella danaeza McKenzie, Reyment & Reyment, 1993 Ak
Munseyella modesta, Swanson, 1979 Ak-Rec
Munseyella pseudobrevis Ayress, 1995 Ak
Munseyella rectangulara Swanson, 1969 Pl
Munseyella cf. splendida Whatley & Downing, 1983 Ld-Lw
Sarsonsera eocenica (Swanson, 1979) Ld-Rec E
Sarsonsera intermedia Milau, 1993 Po E
PONTOCYTHEIDAE
Argillia acuticunda Whatley & Downing, 1983 Ak
Argillia australiomorpha Whatley & Downing, 1983 Ak
Argillia krithiformae Whatley & Downing, 1983 Ak
Argillia psilis (Brady, 1880) Lhw-Lw
Australocythere sp. Ayress 1995 Ak-Lhw
Maddiella argilliafera (Whatley & Downing, 1883) Ak
Maddiella tumefacta (Chapman, 1914) Lhw-Lw
Maddiella sp. 5047 Dingle 2009 Mh
Pontocythere sp. Ayress 1993 Lw
Propontocythere cf. herdmani (Scott, 1905) Ab-Rec
PROGONOCYTHEIDAE
Majunagella asparapensis Dingle, 2009 E Mh
Majunagella ursoni Dingle, 2009 E Mh
Majunagella sp. 4978 Dingle 2009 Mh
Paranਪtilocythere ericis Dingle, 2009 E Mh
Paran testimocythere sp. 5070 Dingle 2009 Mp
ROCKCALLIDAE
Aracythere chapmani Hornibrook, 1952 Mp-Sw
Aracythere all. chapmani Hornibrook, 1952 Lhw-Lw
Aracythere eocenica (Whatley et al, 1980) Ak
SCHIZOCYTHEIDAE
Apapethoxicythere? colleni Dingle, 2009 Cn
TRACHELBERIDAE
Alagracilus sp. Ayress 1993 Ld-Rec
Alasuthaphile leptidictyous (Ayress, 1995) Ar E
Actinocythereis microgenon Ayress, 1995 Ak-Lw
Actinocythereis thomsoni (Hornibrook, 1952) Dw-Rec
Acanthocythereis? reticulisonosa Ayress, 1993 Ab
Acanthocythereis sp. Ayress 1993 Ab
Alatalberis panaiuda Milau, 1993 Po
Auelcocerith hostizia (Hornibrook, 1952) Dh-Ld
Cletocythereis cf. bradyi Holden, 1967 Pl
Cletocythereis rastromargnata (Brady, 1880) Ak-Rec
Clynochætheris australis Ayress & Swanson, 1991

Clynochætheris contigua Hornibrook, 1952 Dw-Pl
Clynochætheris insulae Hornibrook, 1952 Pl-Rec
Clynochætheris planalata Hornibrook, 1952 Dh-Pl
Clynochætheris cf. brevicostata Bate, 1972 Mh
Glocerocythereis? cf. armata Jellinek & Swanson, 2003
Lhw-Pl
Glocerocythereis? cf. brevicosta (Hornibrook, 1952) Lhw-Pl
Glocerocythereis? cf. oculata Jellinek & Swanson, 2003 Lhw-Pl
Glocerocythereis? thomsoni (Hornibrook, 1952) Pl-Rec
Limburgina postaurora Dingle, 2009 E Mh
Marwickocythere is marwicki (Hornibrook, 1952)
Ab-Ar
Marwickocythereis oderomenta Whatley & Millson, 1992 Dw E
Oerttelia semiventer (Hornibrook, 1952) Mm-Ld
Oerttelia cinchica (McKenzie, Reyment & Reyment, 1993) Ak-Lw
Philocenocythereis algaricus Whatley, Millson & Ayress, 1992 Mh-Ab
Philocenocythereis eocenica Whatley, Millson & Ayress, 1992 Dh-Rec
Philocenocythereis planalata (Hornibrook, 1952) Lw-Rec
Philocenocythereis peganplanaltus Whatley, Millson & Ayress, 1992 Lhw
Philocenocythereis reticulatus Whatley, Millson & Ayress, 1992 Ab-Ar
Philocenocythereis sawsoni Whatley, Millson & Ayress, 1992 Ab-Lhw
Philocenocythereis triostatus Whatley, Millson & Ayress, 1992 Dh-Mh
Philocenocythereis sp. 1 Whatley, Millson & Ayress 1992 Lw
Philocenocythereis sp. 2 Whatley, Millson & Ayress 1992 Pl-Ple
Philocenocythereis sp. 3 Whatley, Millson & Ayress 1992 Ple
Philocenocythereis sp. 5 Whatley, Millson & Ayress 1992 Lhw
Philocenocythereis sp. 6 Whatley, Millson & Ayress 1992 Ak
Pinoxicythereis praenuntiusi Milau, 1993 Pf
Protobuntonia laui (Hornibrook, 1953) Ab-Rec
Rayneria? punctata Dingle, 2009 E Mh
Rugocythereis reticulata Ayress, 1993 Ab-Rec
Rugocythereis semiconvex (Hornibrook, 1953) Ab-Lhw
Sectocythereis cf. ornata Bate, 1972 Mh
Sectocythereis? sp. 5044 Dingle 2009 Mh
Taracocythereis conjunctispina Ayress, 1995 Ak-Rec
Taracocythereis planalta (Hornibrook, 1953) ?Dh-Lw
Taracocythereis sp. Ayress 1993 Ab
Trachelberis ayressi Milau, 1993 Po
Trachelberis brevicostata Hornibrook, 1952 Ld-SL
Trachelberis denticulata Milau, 1993 Po
Trachelberis hornibrooki Dingle, 2009 E Mh
Trachelberis julietti Ayress, 1993 Lw
Trachelberis lytleonis Harding & Sylvest-
**PHYLUM ARTHROPODA CRUSTACEA**

Carcocaris minima Chapman, 1934 Ord
Carcocaris arctii Chapman, 1934 Ord

Subclass EUMALACOSTRACA
Superorder PERACARIDA
Order ISOSOPIDA
Suborder VALVIFERA
HOLOGNATHIDAE
Debodea mellite Hiller, 1999 (not Cirolanidae)
UCet E

Suborder CYMOTHOHOIDA
CIROLANIDAE
Palagonia kakaahia Feldmann & Rust, 2006 Wo-Wp E

INCERTAE SEDIS
URIDIDAE
Urdz elandica Buckeridge & Johns, 1996 UJur E

Superorder EUCARIDA
Order DECAPODA
Suborder PLEOCYMATA
Infraorder GLYPHEIDAEA
ERYMIDAE
Gen. et sp. indet. Mp-Mh
GLYPHEIDAE
Glyphya christyi Feldmann & Maxwell, 1999 Ab E
Glyphya stilvilli Feldmann, 1993 Dt E
Glyphyopsis antipodum Glaessner 1960 Hu E
MEOCHIRIDAE
Meocharus marwicki Glaessner, 1960 Kh
Meocharus? sp. Bw, Kh-Op

Infraorder ASTACIDEA
NEPHROPIDAE
Hoplopuria sp. Mp
Metaneophaus notanaeensis Jenkins, 1972 Sw-Tt E
PARASTACIDAE
Paraneophaus fordyci Feldmann & Pole, 1994 Po-Sl E

Infraorder AXIIDAEA
CALLIANASSIDAE
Callianassa auckina Glaessner, 1960 Po E
Callianassa vaikurana Glaessner, 1960 Mh E
Callianassa sp. a Mh
Callianassa sp. b Bt
Callianassa sp. Cn, Mp-Mh
Callianassa sp. Ab, Lwh-Pt, Sw-Tt
Protocalianassa sp. Mp-Mh
CTENOCHELIDAE
Ctenochela cf. maoriana Powell, 1949 Wc
Ctenochela sp. Wc
INCERTAE SEDIS

Infraorder GEBIDEA
UPOGEBIIDAE
Upogethes kowai Feldmann, Schweitzer, Maxwell & Kelley, 2008 Wo E
Upogethes sp. Ar-Lwh

Infraorder ACHELATA
PALINURIDAE
Jasus Remoing Glaessner, 1960 Pj
Linuparvs korora Feldmann & Bearlin, 1988 Ab
Linuparvs sp. Mp-Mh
Linuparvs? sp. Mp-Mh

Infraorder ANOMURA
AEGLIDAE
Haumuruiaeglae glaessneri Feldmann, 1984 Mp-Mh E
GALATHEIDAE
Galathea sp. Wp-Wn
LITHODIDAE
PAGURIDAE
Diaçıanthura ciliifrons (Hyden & Forest, 1980) PI E
Pagurus sp. Tt, Wp, Wn

Infraorder BRACHYURA
ATELYCLETIDAE
Trichopeltarion greggi DELL, 1969 Sw-Tt E
Trichopeltarion merrinae Schweitzer & Salva, 2000
L Mio E CALAPIDAE
Calappa maxuelli Feldmann, 1993 Po E
CANCIRIDAE
Labocarcinus pustulos Feldmann & Fordyce, 1996 PI E
Metacarcinus novacezelandiae (Hombron & Jacquinot, 1846) Wo-Rec
Metacarcinus cf. novacezelandiae (Hombron & Jacquinot, 1846) Tk, Wp
Metacarcinus sp. Ak, Ld, Wp-Wn
GONEPLACIDAE
Carcinoplax temkoensis Feldmann & Maxwell, 1990 Ak-Ar E
Carcinoplax sp. Wp-Wn
Konnecarcinus maxuellae Feldmann, Schweitzer, Maxwell & Kelley, 2008 Wo E
Ommatocarcinus arenciola Glaessner, 1960 Pl E
Ommatocarcinus cf. arenciola Glaessner, 1960 Pl
Ommatocarcinus cf. Neommatocarcinus huttoni (Filhol, 1886) Wp-Wn
Ommatocarcinus sp. Pl
HOMOLODOMIDAE
Homolodromia novacezelandica Feldmann, 1993 Mp-Mh E
Homolodromia sp. Mp-Mh
MACROPHTHALMIDAE
Macrophthalmus (Hemiplax) hirtipes (Heller, 1862) Wp-Rec E
Hemiplax?major Glaessner, 1960 Wn E
Hemiplax cf. major Glaessner, 1960 Po, Wc
Hemiplax sp. Wn-Wc
MAJIDAE
Actinometacarus chidesgorum Jenkings, 1974 Sc-Tt E
Actinometacarus maculalini Feldmann, 1993 Sw-Tt E
Jacquinotia edwardsi (Jacquinot, 1853) Wp Rec E
Leptomithrax atavus Glaessner, 1960 Tt E
Leptomithrax elongatus McLay, Feldmann & Mackinnon, 1995 Sw E

Leptomithrax garthi McLay, Feldmann & Mackinnon, 1995 Sw-Tt E
Leptomithrax griffini Feldmann & Maxwell, 1990 Ab-Ar E
Leptomithrax irirangi Glaessner, 1960 Wo E
Leptomithrax aff. irirangi Glaessner, 1960 Sw
Leptomithrax aruti Glaessner, 1960 ETr
Leptomithrax cf. urita Glaessner, 1960 Tt
Leptomithrax sp. Tt
Micromithrax? minorisculus Feldmann & Wilson, 1988 Dm-Dh
Notomithrax allani Feldmann & Maxwell, 1990 Ak-Ar E
Notomithrax minor (Filhol, 1885) Wc – Rec Notomithrax sp. Wc
MENNIPIDAE
Galene proavita Glaessner, 1960 PlSc E
Galene sp. Wp-Wn
Menippe sp. Pl
Pseudocarcinus sp. Tk
PORTUNIDAE
Ovalipes cf. catharus (White, 1843) Wn-Wc
Ovalipes sp. A Wp
Ovalipes sp. Wn-Wc
Poropteryx occenta Glaessner, 1980 Ak-Ar E
Portunus sp. Lwh, Lw
Richiouchae graniferum (Glaessner, 1960) Dp-Ar E
Gen. et sp. indet. Dm-Dh, Ab-Ak
PSEUDOOZIDAE
Toroparnesia notonaesens Feldmann, Schweitzer, Maxwell & Kelley, 2008 Wo E
RANINIDAE
Hemionn wavinglandic Glaessner, 1980 Cn E
Laevirinina keyesi Feldmann & Maxwell, 1990 Ak-Ar E
Laevirinina peraromatia Glaessner, 1960 Ab E
Laevirinina poraromatia (Glaessner, 1980) Ak-Ar E
Lyreidus bennetti Feldmann & Maxwell, 1990 Ak-Ar E
Lyreidus elegans Glaessner, 1960 Po-Pl E
Lyreidus waitakiamensis Glaessner, 1980 Ab E
Lyreidus sp. Sw
Gen. et sp. indet. Ab
TORYNOMMIDAE
Exororippe spedeni Glaessner, 1980 Mp-Mh E
Torynomaus flintingii Glaessner, 1980 Mp-Mh E
Torynomaus planata Feldmann, 1993 Mp-Mh E
TUMIDOCARCINIDAE
Tumidocarcinus dentatus Glaessner, 1960 Lwh-Ld E
Tumidocarcinus cf. denticate (Glaessner, 1960) Lwh
Tumidocarcinus giganteus Glaessner, 1980 Pl-Tt E
Tumidocarcinus cf. giganteus Glaessner, 1960 Lw-Po, Sw-Tk
Tumidocarcinus tumidus (Woodward, 1876) Ab-Ld E
Tumidocarcinus cf. tumidus (Woodward, 1876) Lwh-Ld
Tumidocarcinus? sp. Ak-Ld, Po-Sc
VARUNIDAE
Miograpsus papaku Fleming, 1981 Tt E
Developmental stages of New Zealand Decapoda

Compiled by W. R. Webber

Following are the larvae and/or pre- or post-larvae described to date, of species listed in the decapod species list above. Species named below are those with one or more developmental stages described in the literature. Names and dates in brackets indicate publications in which larvae are described, not species authorities. However, Jaxea novaezealandiae (Gebiidea) was described in the same paper as the adult and two polychetid species were described from the larva, thus authors in brackets after these names are also the original authorities. Literature sources for the species list below are cited in the References section, above.

PHYLUM CRUSTACEA
Class MALACOSTRACA
Order DECAPODA
Suborder DENDROBRANCHIATA
SERGESTIDAE
Sergestes arcitica [Gurney & Lebour 1940; Wear 1985]
Solenoceridae
Solenocera comata [Gurney 1924; Wear 1985]

Suborder PLEOCYMATIDA
Infrarod STENOPODIDAE
Stenopus hispidus [Gurney 1936, 1942]

Infrarod CARIDEA
Alpheidae
Alpheus euphrasine richardsoni [Packer 1983, 1985]
Alpheus socialis [Packer 1983, 1985]
Alpheopsis aequinoctialis [Packer 1983, 1985]
Atyidae
Paratya curviscrostris [Ch’ng 1973; Wear 1985]
Campylonotidae
Campylonotus rathbuni [Pike & Williamson 1966; Wear 1985]
Congrionidae
Anaptoc lacceri [De Simón 1979; Packer 1983, 1985]
Philocheras australis [Thomson & Anderton 1921; Packer 1983, 1985]
Philocheras chiltoni [Packer 1983, 1985]
Philocheras hamiltoni [Packer 1983, 1985]
Philocheras philoidea [Packer 1983, 1985]
Hippolytidae
Hippolyte bifida [Packer 1983, 1985]
Hippolyte multicolorata [Packer 1983, 1985]
Ogyrididae
Ogyra delph [Packer 1983, 1985]
Palaemonidae
Periclimen es goldrei [Packer 1983, 1985]
Periclimen es (Periclimenes) sp. [Packer 1983, 1985]

Infrarod ASTACIDEA
Nephtyidae
Metanephrops challengeri [Wear 1976]
Parastacidae
Paranephrops planifrons [Hopkins 1967]

Infrarod AXIDEA
Callianassidae
Callianassa filholi [Gurney 1924; Lebour 1955; Wear 1965a]

Infrarod GEBIIDEA
Laomedoniidae
Jaxea novaezealandiae [Wear & Valdöy 1966]
Urogeridae
Acutigebia danaei [Gurney 1924]

Infrarod PALINURA
Palinuridae
Jasus edwardsii [Batham 1967; Lesser 1974]
Sagaminus verreauxii [Lesser 1974; Kittaka et al. 1997]
Polycheilidae
Gen. et sp. indet. (as Eryonuchen fucus) [Bernard 1953]
Gen. et sp. indet. (as Eryonuchen scharfii) [Selbie 1914]
Syllaridae
Ibacus alticrenatus [Atkinson & Boutstead 1982]
Scyllarus sp. Z [Webber & Booth 2001]

Infrarod ANOMURA
Chirostylidae
Gastropycus novaezelandiae [Pike & Wear 1969]
Urothysius n. sp. [Pike & Wear 1969]
Galatheidae
Manida gregaria [Roberts 1973]
Paguridae
Pogurius lectori [Roberts 1971; Wear 1985]
Pogorus novaezelandiae [Greenwood 1966; Wear 1985]
Pogurus traversii [Thomson & Anderton 1921; Wear 1985]
Perecallapogorus edwardsi [Roberts 1972; Wear 1985]
Symppagurus dimorphus [Lemaître & McLaughlin 1992]
Porcellanidae
Petrocheles spinosus [Selbie 1914]
Hippolyte bifida [Packer 1983, 1985]
Hippolyte multicolorata [Packer 1983, 1985]
Nauticaris marionis [Packer 1983, 1985]
Tasmania novaezelandiae [Packer 1983, 1985]
Ozyriidae
Ozyriles delli [Packer 1983, 1985]
Palaemonidae
Palaemon affinis [Lebour 1955; Packer 1983, 1985]
Periclimenes goldrei [Packer 1983, 1985]
Periclimenes (Periclimenes) sp. [Packer 1983, 1985]

Infrarod BRACHYURA
Atelocyclidae
Trichopetalium fontasticum [Wear & Fielder 1985]
Belliliidae
Heteroniscus rotundifrons [Wear & Fielder 1985]
Cancridae
Metacarcinus novaezelandiae [Wear & Fielder 1985]
Cymonomidae
Cymonomes huttoniae [Wear & Fielder 1985]
Dromiidae
Metadromia wilsoni [Wear & Fielder 1985]
Goneplacidae
Neommatocarcinus huttoni Wear & Fielder 1985
Grapsidae
Leptograpsus variabilis [Wear & Fielder 1985]
Planes major [Wear & Fielder 1985]
Planes marinus [Wear & Fielder 1985]
Homolidae
Dipanopus petteri [Williamson 1965; Wear & Fielder 1985]
Homola orientalis [Wear & Fielder 1985]
Hymenosomatidae
Amarinus laevicristatus [Wear & Fielder 1985]
Elama longirostris [Wear & Fielder 1985]
Elama momona [Wear & Fielder 1985]
Elama producta [Wear & Fielder 1985]
Halicarcinus cookii [Wear & Fielder 1985]
Halicarcinus inominitatus [Wear & Fielder 1985]
Halicarcinus planatus [Wear & Fielder 1985]
Halicarcinus varius [Horn & Harms 1988]
Halicarcinus whitei [Wear & Fielder 1985]
Hymenosoma depressum [Wear & Fielder 1985]
Neobarnaculus pubescens [Wear & Fielder 1985]
Iachidae
Acharus curviscrostris [Wear & Fielder 1985]
Cyclopora lamellata [Wear & Fielder 1985]
Inachidae
Pyronata tuberculata [Webber & Wear 1981; Wear & Fielder 1985]
Latreillidae
Ephalana australiensis [Wear & Fielder 1985]
Leucosiidae
Bellanilia chesmanii [Wear & Fielder 1985]
Macrophthalmiidae
Macrohalimus (Hemiplax) hierites [Wear & Fielder 1985]
Majidae
Eurynolambris australis [Webber & Wear 1981; Wear & Fielder 1985]
Iepsonia edwardsi [Webber & Wear 1981; Wear & Fielder 1985]
Leptomithrax longimanus [Webber & Wear 1981; Wear & Fielder 1985]
Leptomithrax longipes [Webber & Wear 1981; Wear & Fielder 1985]
Leptomithrax tuberculatus mortensi [Wear & Fielder 1985]
Notomithrax minor [Webber & Wear 1981; Wear & Fielder 1985]
Notomithrax peroni [Webber & Wear 1981; Wear & Fielder 1985]
Notomithrax ursus [Webber & Wear 1981; Wear & Fielder 1985]
Oziidae
Ozius truncatus (Wear & Fielder 1985)
Pilumnidae
Pilumnopus serratipennis [Wear & Fielder 1985]
Plumousus lumpsus [Wear & Fielder 1985]
Plumousus novaezelandiae [Wear & Fielder 1985]
Pinnothieridae
Neommatocarcinus novaezelandiae [Wear & Fielder 1985]
Plagiisiiidae
Plagosa chabrus [Wear & Fielder 1985]
Portunidae
Liocarcinus corrugatus [Wear & Fielder 1985]
Nectocarcinus antarcticus [Wear & Fielder 1985]
Ouralpeps cutharbus [Wear & Fielder 1985]
Portunus pelagicus [Wear & Fielder 1985]
Scylla serrata [Wear & Fielder 1985]
Raninidae
Lyridus tridentatus [Wear & Fielder 1985]
Vartnidae
Austrohelice cressa [Wear & Fielder 1985]
Cyclograpsus insularum [Wear & Fielder 1985]
Cyclograpsus laevicristatus [Wear & Fielder 1985]
Hemigrapsus crenulatus [Wear & Fielder 1985]
Hemigrapsus sexdentatus [Wear & Fielder 1985]