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A guide to the groundwater invertebrates of New Zealand

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Cover: Left to right –
Hexabathynella aotearoae, Paracrangonyx compactus, Phreatoicus typicus.
Photographs by Graham Fenwick.
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Abstract

Scarsbrook, M. R.; Fenwick, G. D.; Duggan, I. C.; Haase, M. (2003). A guide to the groundwater invertebrates of New Zealand. ***NIWA Science and Technology Series No. 51.*** **59 p.**

Groundwaters in New Zealand constitute a huge freshwater resource that is managed primarily for human uses (e.g., provision of potable water and water for irrigation). However, these extensive resources also have intrinsic ecosystem values, including a diverse, but poorly known invertebrate fauna. Despite the discovery of this groundwater fauna in the 1880s, research has been sporadic and piecemeal. This guide, structured by taxonomic groups, reviews existing knowledge of the invertebrates of New Zealand's groundwater habitats, which include alluvial and karstic aquifers, cave systems, springs and the hyporheic zone beneath streambeds. Invertebrates that spend their entire lives in groundwater habitats (stygobites), exhibit common morphological and physiological characteristics widely interpreted as adaptations to life in the interstitial spaces of groundwater habitats. The most apparent characteristics are lack of body pigments, a narrow, elongate body form and the absence of eyes.

One hundred and two formally described stygobitic invertebrate species are known to inhabit groundwater habitats in New Zealand. This number is sure to increase dramatically because many habitats have been poorly represented in past sampling work, and several groups are currently the focus of taxonomic reviews.

The most diverse taxonomic group are the Hydracarina (water mites), with 70 species described from New Zealand groundwater habitats. Crustacean groups that are reasonably well known are the Amphipoda (4 species), Isopoda (4 species), and Syncarida (7 species). We provide keys for the identification of these better known crustacean groups. New Zealand also has a significant hydrobiid groundwater fauna, with 10 species already described, and indications of many more awaiting description.

As a result of this review, we have identified significant gaps in the knowledge of our fauna. In particular, our knowledge of groundwater Copepoda is very poor. Copepoda are found in groundwater habitats throughout New Zealand, and the group is an important component of groundwater assemblages overseas. As yet no stygobitic copepod species have been described from New Zealand. Another group deserving immediate attention is the Oligochaeta.

Introduction

In 1882, Charles Chilton first brought the existence of New Zealand's groundwater fauna to the attention of the international scientific community. It was an important discovery, not least because it constituted the first records of subterranean Crustacea from the southern hemisphere. Chilton subsequently described several new genera of groundwater amphipods and isopods (Chilton 1892, 1894), and also described a new southern hemisphere family of isopods (Phreatoicidae). Since Chilton's pioneering work, investigations of our subterranean fauna have been limited and sporadic, and knowledge of our fauna has remained restricted to a few "die-hard" biologists both here and overseas. This oversight is not limited to New Zealand. Groundwaters contain a largely untapped reservoir of biodiversity, which has been largely or totally ignored in calculations of global biodiversity (Gibert et al. 1994). However, New Zealand does lag far behind many other countries in describing and understanding the groundwater "reservoir of biodiversity". Overseas, the extensive biodiversity in groundwaters, particularly in Europe, was highlighted by the seminal work "Stygofauna Mundi" (Botosaneanu 1986). In addition, ecology of groundwaters is becoming well established, with several books now highlighting the importance of groundwater ecosystems (Gibert et al. 1994, 1997) and their linkages with surface waters (Jones & Mulholland 2000). Australia has also recently made significant advances in the description of its groundwater fauna (Humphreys & Harvey 2001).

Groundwaters in New Zealand constitute a huge freshwater resource. It has been estimated that 80% (1.7×10^{12} m^3) of New Zealand's available freshwater resources are held as groundwater (White 2001). The uses to which this resource is put are varied, and include irrigation for agriculture, public water supply, industrial processing, and recreation (e.g., Waitomo caves, Pupu Springs). Geothermal groundwater systems are also used for power generation and heating, and provide a significant recreation and tourism resource. White & Rosen (2001) estimated that 26% of New Zealand's population depend totally on groundwater for drinking water. The value of the resource is growing and demand often exceeds supply in some areas (White et al. 2001).

Worldwide, the resource is also under increasing pressure from a range of contaminants, including organic and inorganic toxic compounds (e.g., pesticides, heavy metals, etc.), nitrogen and phosphorus, and organic matter (including faecal bacteria) from land-based sewage effluent disposal (Notenboom et al. 1999). The same is true in New Zealand. Significant organic contamination occurs in many aquifers (e.g., Sinton 1984, Scarsbrook & Fenwick 2003) and pesticides have been detected in a number of wells (Smith 1993a, 1993b, Close 1996). Investigation of the impact of contaminants on *in situ* community structure indicates quite marked reductions of interstitial invertebrates adjacent to rivers contaminated by heavy metals, with elimination of amphipods and some insects from these habitats (Notenboom et al. 1994). Nothing appears to be known of pollution effects on ecosystem functioning and community recovery following contamination. However, crustaceans, the dominant animals within New Zealand and most other groundwater systems, are among the most sensitive of all aquatic animals to such contaminants (Thomas 1993, Hickey 2000).

We are now entering a phase where perceived values and usage of our groundwater resources are increasing, yet we have a poor understanding of the structure and functioning of groundwater ecosystems. Indeed, groundwaters are almost universally regarded as simply a physical resource, not as part of an ecological, life-sustaining system. A crucial step in providing more effective protection of groundwater resources is to understand the biological component of groundwater ecosystems, and how this component contributes to the health and sustainability of this economically and culturally valuable resource.

In the current work, we provide a preliminary guide to the invertebrates of New Zealand's groundwater habitats. It is structured to provide a source of information on the major groups of organisms known to occur in groundwaters, both here and overseas. What will be apparent to readers of the guide is the severe lack of knowledge with regard to many invertebrate groups. Where possible we have included overseas information to fill gaps in knowledge of our own fauna.

It was not our aim to provide detailed keys for all groups and, indeed, this is impossible at this stage. We hope that more detailed taxonomic and biological information will be available for future incarnations of this guide. It is also our hope that this guide will provide scientists and managers with a gateway to the world to be found beneath our feet and stimulate work on the many interesting aspects of biology, systematics, and ecology that are unexplored.

Groundwater habitats in New Zealand

Groundwater aquifers can be broken into three main types (Mangin 1994): i) aquifers in porous media (e.g., alluvial aquifers), ii) aquifers in fissured media (e.g., fractured basalt), and iii) aquifers in karstic media (e.g., limestone). New Zealand's groundwater resources are distributed predominantly in porous media (White 2001). Porous media aquifers are commonly associated with Quaternary sediments (Creuzé des Châtelliers et al. 1994, White 2001). In New Zealand, the Rangitaiki Plains, Heretaunga Plains, Manawatu Plains, Wairarapa Valley, Waimea Plains, Marlborough Plains, Canterbury Plains, Otago basins, and Southland Plains are examples of aquifer systems in Quaternary sediments.

In contrast to many areas of Europe where karst aquifers are extensive and extremely valuable (e.g., 50% of Austria's population relies on karstic water supply (Maire & Pomel 1994)), New Zealand has limited areas of karst. Areas of uplifted marine limestones, which often form karstic landscapes, are found in relatively small areas in Northland, Waikato, Hawke's Bay, Wairarapa, Nelson, west coast, Canterbury, Otago, and Southland (White 2001). However, these small areas can be extremely rich in groundwater fauna, particularly with respect to hydrobiid snails (Climo 1974, M. Haase unpublished data). The areas are also often associated with important recreation and tourism sites (e.g., Waitomo Caves) because of their usually spectacular landscapes.

Little is known of the ecology of the third type of aquifer system. Fractured rock aquifers are often found in areas of basalt lithology and examples of this occur around Auckland and in North Otago. They can be locally important water resources.

Groundwater and surface waters are not isolated components of the hydrologic system, but instead interact in complex and dynamic ways (Sophocleous 2002). The interactions between surface water and groundwaters provide a range of habitats beyond what we would consider as true groundwaters. For example, springs are areas of concentrated groundwater discharge (Van Everdingen 1991) and often form the headwaters of streams and rivers. Using this definition, we also consider some cave resurgences to be springs. As an ecotone, or area of direct overlap between two ecosystems, springs often exhibit high biological diversity containing species from both ecosystems, along with those peculiar to the zone of interaction (e.g., spring specialists, or crenobites). Another area of direct interaction between the two ecosystems is the hyporheic zone of streams (Orghidan 1959).

Groundwater ecosystems are generally considered to be carbon-limited (Strayer 1994, Poulson & Lavoie 2000). Due to the lack of light, no primary production takes place in groundwater ecosystems. As a result, groundwater food webs are predominantly heterotrophic, with production relying on the input of organic matter from external sources. Most of the organic matter entering groundwater habitats is mineralised by micro-organisms (e.g., bacteria, fungi). The microbes then serve as food for meiofauna (protozoans, nematodes, and copepods) and macrofauna (e.g., amphipods and isopods). Predatory invertebrates (e.g., Dytiscidae, Acari) usually form the top of the food chain, except in some aquifers where vertebrate predators are present. However, there are no known vertebrate stygobites in New Zealand.

Over the last five years, we have sampled groundwaters in several areas of New Zealand. Most of this work has been in alluvial aquifers to date (e.g., Scarsbrook & Fenwick 2003). There has been extensive collecting in several cave systems, particularly those around Waitomo and northwest Nelson. Unfortunately, much of this sampling has been relatively recent or is currently underway and results are not yet published. Consequently, the information presented in this guide is biased towards the fauna of porous media, but work on cave dwellers is in progress.

Groundwater invertebrates

From an ecological perspective, the primary physical characteristic of the groundwater environment is permanent darkness (Gibert et al. 1994). Invertebrates which spend their entire lives in this darkness are called stygobites. The term stygo refers to the River Styx, which, according to Greek mythology, was one of the five rivers of the underworld. Stygobitic organisms are found throughout the world in porous groundwater aquifers (e.g., alluvial aquifers) and karstic areas, and are also found in zones of groundwater/surface water interaction (e.g., springs).

Stygobites of diverse taxonomic groups often exhibit similar morphological and physiological characteristics that can be interpreted as adaptations to life in the interstitial spaces of groundwater habitats (Danielopol et al. 1994a). The most apparent characteristics are the depigmented and vermiform (worm-like) body and the lack of eyes. Compared with related organisms in surface waters, stygobites can have very long lives and developmental stages are often prolonged. In addition, studies have shown that the metabolic rate of stygobites is often reduced relative to closely related surface forms (e.g., Malard & Hervant 1999, Mosslacher 2000). Fecundity may also be reduced, although the increased longevity may mitigate this.

Given the extensive jargon associated with groundwater systematics and ecology, we have tried to maintain some consistency in classifying animals by following the system of Gibert et al. (1994). Briefly, Gibert et al. (1994) provided a comprehensive classification system based on the affinity of invertebrates for groundwater habitats (Figure 1). Organisms are classified as 'stygoxenes' (no affinities to hypogean systems), 'stygophiles' (actively exploit resources of hypogean habitats), and 'stygobites' (specialised subterranean forms found almost exclusively in hypogean habitats). The latter two categories are separated further, so that within the stygophile groups 'occasional' and 'permanent' hyporheos (*sensu* Williams & Hynes 1974), and the organisms termed as 'amphibites' by Stanford & Ward (1993) can be recognised. Within the stygobite group are 'ubiquitous' forms (found in karst and alluvial aquifers and also occasionally at or close to the stream surface), as well as forms restricted to deep alluvial aquifers ('phreatobite'). Stygobites usually show the characteristic morphological features associated with the constant dark of the groundwater environment. Collier & Scarsbrook (2000) discussed the New Zealand fauna in relation to this classification scheme. This guide focuses primarily on stygobites, although some of the fauna associated with hyporheic zones (i.e., stygophiles) are also included.

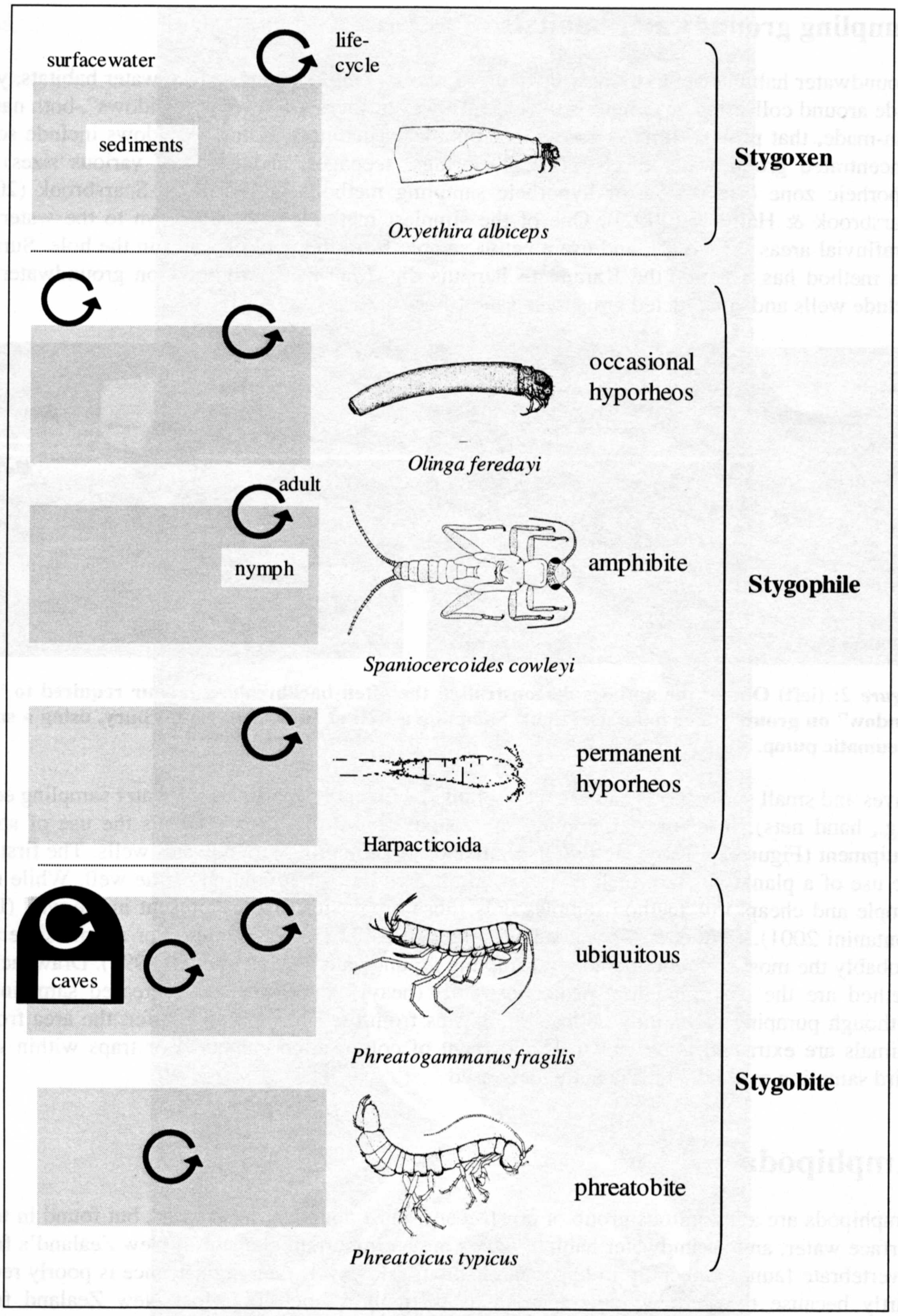

Figure 1: **Classification system after Gibert et al. (1994). Reproduced with permission from Collier & Scarsbrook (2000). The circular arrow refers to an organism's life cycle. The classification system is based on the type of habitat where the life cycle is carried out. For example, a stygoxen does not require phreatic or interstitial habitats for any part of its life cycle, whereas stygobites are found in groundwater habitats at all stages of their life cycle.**

Sampling groundwater habitats

Groundwater habitats are extremely difficult to access. Unlike many surface water habitats, you can't wade around collecting anywhere you please. However, there are several "windows", both natural and man-made, that provide limited access to groundwater habitats. Natural windows include sources of concentrated groundwater discharge (e.g., springs, seepages, and caves of various sizes) and the hyporheic zone (see review of hyporheic sampling methods in Collier & Scarsbrook (2000) and Scarsbrook & Halliday (2002)). One of the simplest methods is to dig down to the water table in parafluvial areas (Figure 2), and use a net to sample from the pool of water in the hole. Surprisingly this method has a name; the Karaman-Chappuis dig. Man-made windows on groundwater habitats include wells and constructed gravel and sand filter-beds.

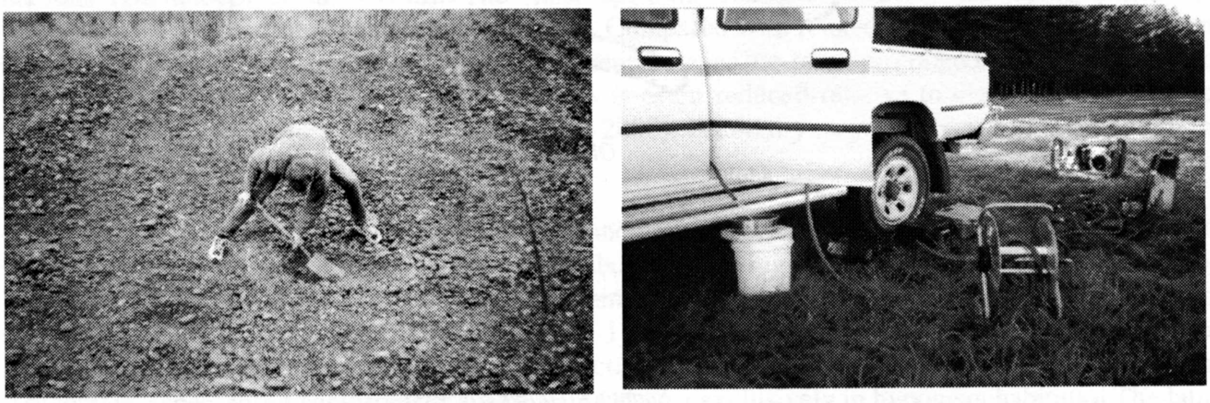

***Figure 2*: (left) One of the authors demonstrating the often backbreaking labour required to "open the window" on groundwater habitats. (right) Sampling a well at Burnham, Canterbury, using a submerged pneumatic pump.**

Caves and small springheads can often be sampled with appropriate surface water sampling equipment (e.g., hand nets). In contrast, sampling of groundwater wells often involves the use of specialised equipment (Figure 2). There are two main methods of sampling groundwater wells. The first involves the use of a plankton net, which is drawn up through the water column of the well. While relatively simple and cheap, this method samples only those organisms that are present in the well (Dumas & Fontanini 2001). Extraction of water from the well using surface-mounted or submersible pumps is probably the most common method of sampling groundwaters (Malard et al. 1997). Drawbacks of this method are the costs and logistical constraints (heavy equipment and increased sampling times). Although pumping potentially collects organisms from the surrounding aquifer, the area from which animals are extracted is unknown. Deployment of colonisation chambers or traps within wells is a third sampling method, but it is not widely used.

Amphipoda

Amphipods are a ubiquitous group of crustaceans, most abundant in the seas, but found in terrestrial, surface water, and groundwater habitats. They are an important element of New Zealand's freshwater invertebrate fauna, especially in hypogean habitats. However, their significance is poorly recognised, partly because they are widely regarded as difficult to identify. Most New Zealand freshwater biologists are unfamiliar with this group. Thus, their often smallish size, their perceived morphological complexity (19 pairs of appendages plus other "bits"), reliance on cryptic characteristics (especially mouthpart morphology) for the group's formal taxonomy, and the lack of an authoritative identification guide bringing together illustrations and keys in a single source (although Chapman & Lewis (1976) was a useful start) all serve to dissuade ecologists from attempting to work with them. Also, the groundwater amphipods lack pigmentation (most are shades of white or cream) and eyes are usually reduced or absent (Figure 3), making species even more difficult to distinguish. Their identification is also exacerbated by confusion in the literature over some taxa (Fenwick 2001a).

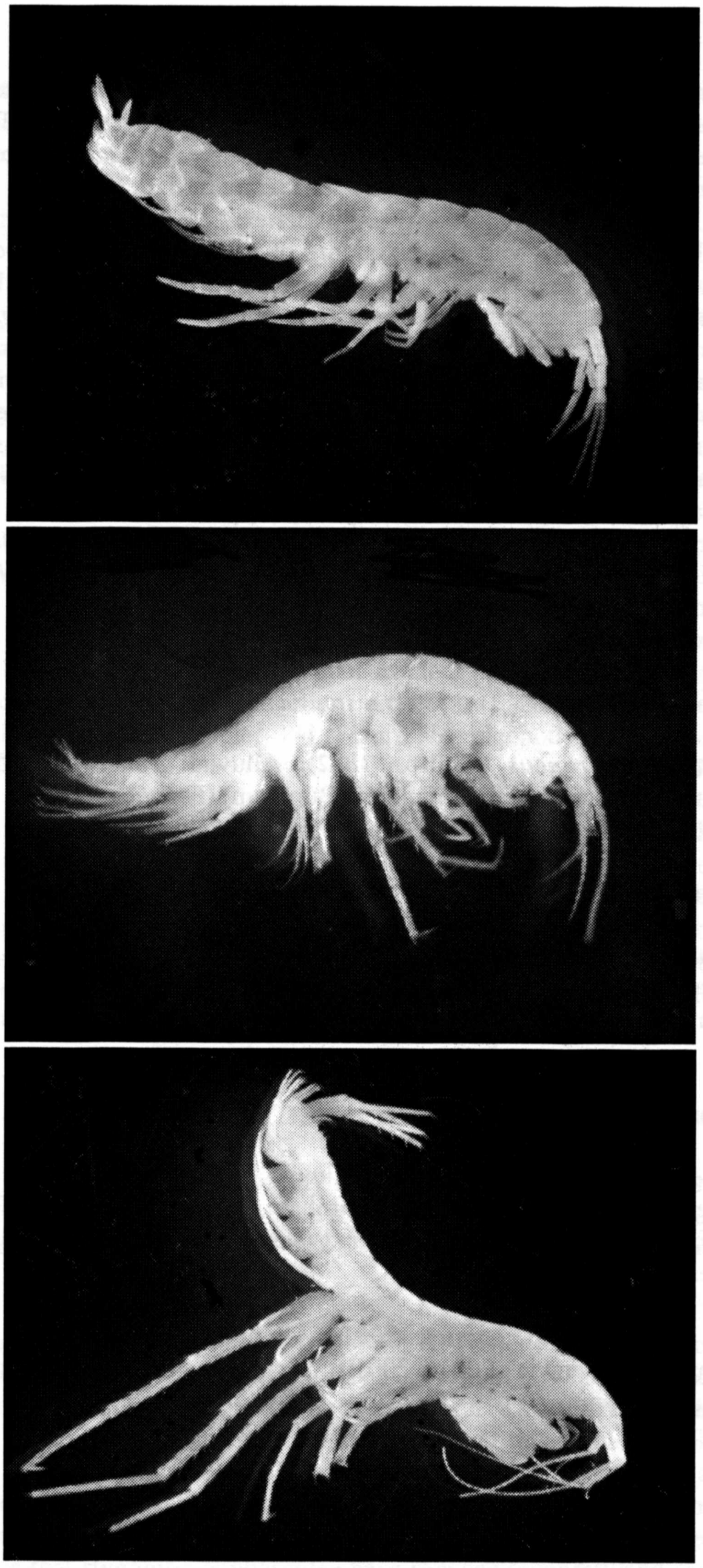

***Figure 3*: Examples of New Zealand's stygobitic amphipod fauna: top, *Paracrangonyx compactus* from the hyporheic zone of the Wangapeka River, Nelson. centre, *Paraleptamphopus* sp. from a well near Templeton, Canterbury. bottom, *Phreatogammarus fragilis* from a well near Winchester, South Canterbury.**

Systematics

Of the four suborders of the Amphipoda, only the Gammaridea is represented in New Zealand freshwater habitats. The Hyperiidea and Caprellidea are exclusively marine. The fourth suborder, the Ingolfiellidea, are very small interstitial animals. Two marine species of ingolfiellids were reported from New Zealand (Schminke & Noodt 1968), but have not been described.

There has been little progress with the taxonomy of groundwater amphipods since the review by Chapman & Lewis (1976). Fenwick (2001a) prepared a full synonymical bibliography for all New Zealand freshwater amphipods, noting confusion within *Paraleptamphopus*. A later paper re-diagnosed the genus *Paracrangonyx*, established *P. winterbourni*, and provided full descriptions of both species (Fenwick 2001b). Chapman (unpublished results) has re-described *Phreatogammarus fragilis* and Fenwick is currently clarifying the genus *Paraleptamphopus* and associated taxa.

Three families are represented among the four described species of New Zealand grpundwater amphipods: Paraleptamphopidae (*Paraleptamphopus subterraneus*), Paracrangonyctidae (*Paracrangonyx compactus, P. winterbourni*), Phreatogammaridae (*Phreatogammarus fragilis*). Work in progress indicates that there are additional undescribed species of *Paraleptamphopus* and *Paracrangonyx* inhabiting groundwater habitats.

Family Paraleptamphopidae

***Paraleptamphopus subterraneus* (Chilton 1882):** Alluvial groundwater, 5–20 m below ground surface; Canterbury Plains (Eyreton, Templeton, Burnham) (Fenwick, 2001a).

Family Phreatogammaridae

***Phreatogammarus fragilis* (Chilton 1882):** Alluvial groundwater to 58 m below ground, also in hyporheic habitats; Canterbury (Eyreton, Templeton, Burnham, Selwyn River, Rakaia River, Winchester) (Fenwick 2001a); unconfirmed records from Marlborough, Nelson, Wellington areas.

Family Paracrangonyctidae

***Paracrangonyx compactus* (Chilton 1882):** Alluvial groundwater to 58 m below ground, also in hyporheos; Canterbury (Eyreton, Templeton, Burnham, Leeston, St Albans) (Fenwick 2001a, 2001b); unconfirmed records from South Canterbury and Otago (Nicholls 1944) and hyporheos of rivers in Marlborough, Nelson and Otago.

***Paracrangonyx winterbourni* Fenwick 2001:** Alluvial groundwater to 20 m below ground; Canterbury (Templeton) (Fenwick 2001a, 2001b); unconfirmed records from hyporheic zone of rivers in Marlborough, and Nelson.

Identification

This guide is an interim tool only. Several undescribed taxa are currently under investigation. The identification key is simplistic, in that it uses characteristics that are easier for non-specialists, rather than truly taxon-specific diagnostic characteristics. Thus, the guide will not necessarily make it easy to detect undescribed species. The main characteristics used to identify amphipods in this key are summarised in Figure 4. The same characteristics are also useful for isopod identification (see Isopoda section).

1 **a.** Accessory flagellum with more than two articles, much longer than articles 1–3 of primary flagellum combined (Figure 5b); telson deeply cleft along mid line in dorsal view, usually conspicuous, with stout spines posteriorly on each lobe (Figure 5a) ***Phreatogammarus fragilis***
b. Accessory flagellum inconspicuous, and with 0–3 articles; accessory flagellum shorter than primary flagellum articles 1–3 combined (Figures 5c–d); telson entire or notched (emarginate), may be small and inconspicuous, no more than two distal spines (Figures 5e–f) **2**

2 **a.** Antenna 1 peduncle articles 1–2 equal in length; accessory flagellum of one article, shorter than primary flagellum article 1 (Figure 5d); peraeopods 5–7 article 2 much wider than articles 3–4 (Figure 5g); pleopods biramous, each ramus with numerous (>20) long setae (Figure 6a) ***Paraleptamphopus subterraneus***
b. Antenna 1 peduncle article 1 longer than article 2 (Figure 4b, 5b); accessory flagellum 2–3 articulate, longer than primary flagellum article 1 (Figure 5c); peraeopods 5–7 article 2 narrow, similar in width to articles 3–4 (Figure 5h); pleopods uniramous, ramus with up to 6 long setae (Figure 6b) ***Paracrangonyx*** **3**

3 **a.** Coxae inconspicuous, widely spaced, not in contact with each other (Figure 6c); pleonites each longer than deep, epimera lacking conspicuous ventral spines (Figure 6c); uropod 3 outer ramus about five times longer than peduncle (Figure 6d) ***P. winterbourni***
b. Coxae conspicuous, closely spaced, in contact or almost in contact with each other (Figure 6e); pleonites each deeper than long, epimera with conspicuous ventral spines (Figure 6e); uropod 3 outer ramus no more than three times longer than peduncle (Figure 6f) ***P. compactus***

Biology

Almost nothing is known of the biology of any of the New Zealand species. Only rarely are gravid females collected, so their life histories remain a mystery. In Canterbury, all four described species co-occur at sites of organic enrichment (Sinton 1984), suggesting an attraction to moderate levels of such contamination.

Overseas there is an extensive literature on stygobitic amphipods. Perhaps one of the best known groups are species of the genus *Niphargus* (family Niphargidae), which is ubiquitous in European groundwater habitats, particularly in the Rhône River basin (Dole-Olivier et al. 1994). In a brief review, Karaman & Ruffo (1986) noted that the 251 species of this genus exhibit various degrees of sexual dimorphism, varying body size, and habitat preferences. *Niphargus* spp. are omnivorous, and are often found feeding on decomposing animal material. In certain species, mud appears to be a crucial dietary requirement for life history completion. Compared with epigean forms, there is considerable evidence that stygobitic Niphargidae have reduced fecundity and can live up to 10 years (Karaman & Ruffo 1986). Gibert & Mathieu (1980) found that stygobite *Niphargus virei* was able to withstand starvation conditions due to storage of lipids. Hervant et al. (1995) showed that *Niphargus rhenorhodanensis* is highly tolerant of severe hypoxia. In New Zealand, the closely related *Phreatogammarus fragilis*, has been collected live from well sediments that were anoxic and full of decomposing phreatoicid isopods, suggesting it too may be tolerant of hypoxic conditions.

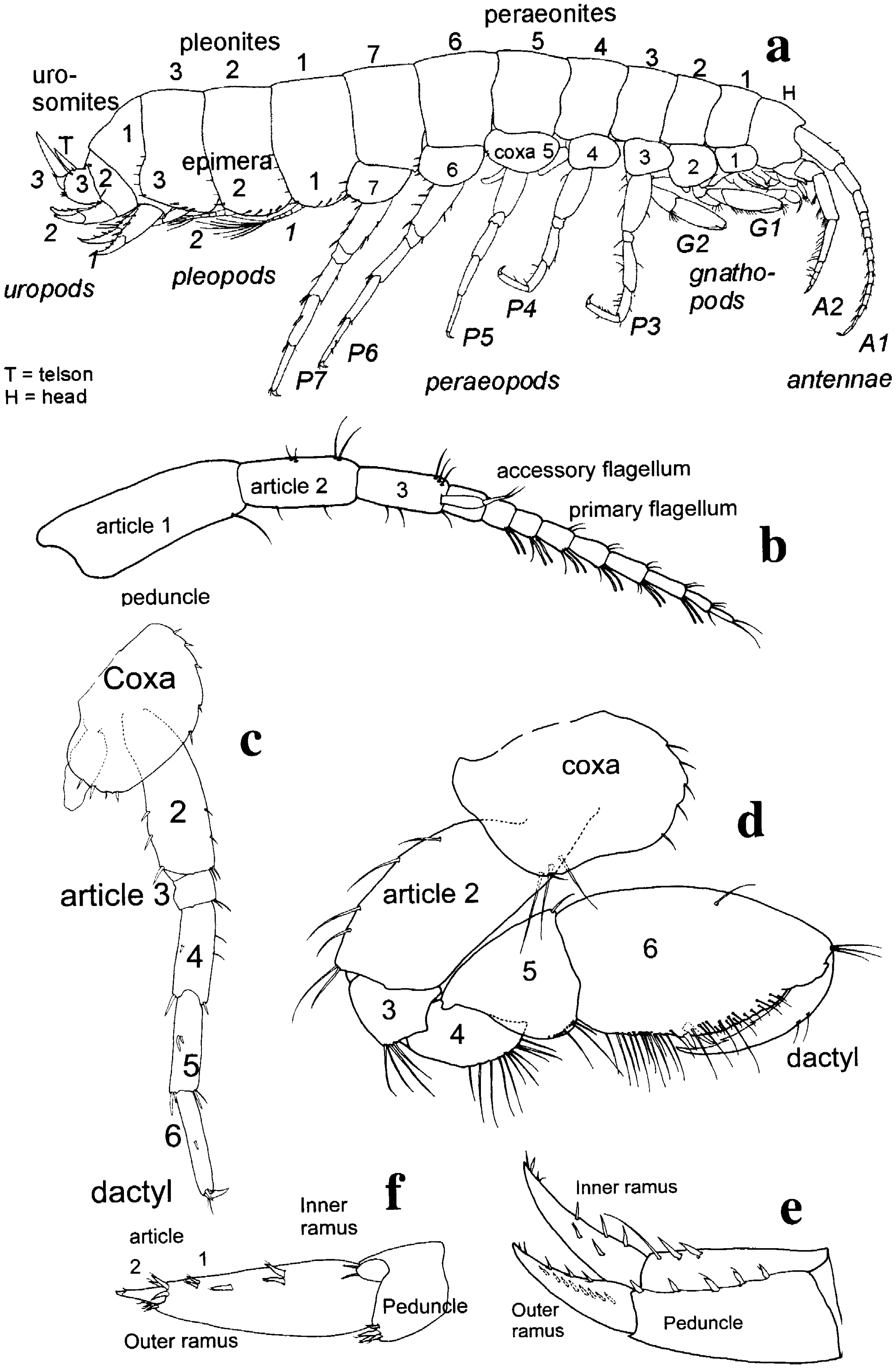

Figure 4: **Amphipod anatomy. a: whole animal; b, antenna 1, medial view; c, peraeopod 7, lateral view; d, gnathopod 1, lateral view; e, uropod 1; f, uropod 3, medial view.**

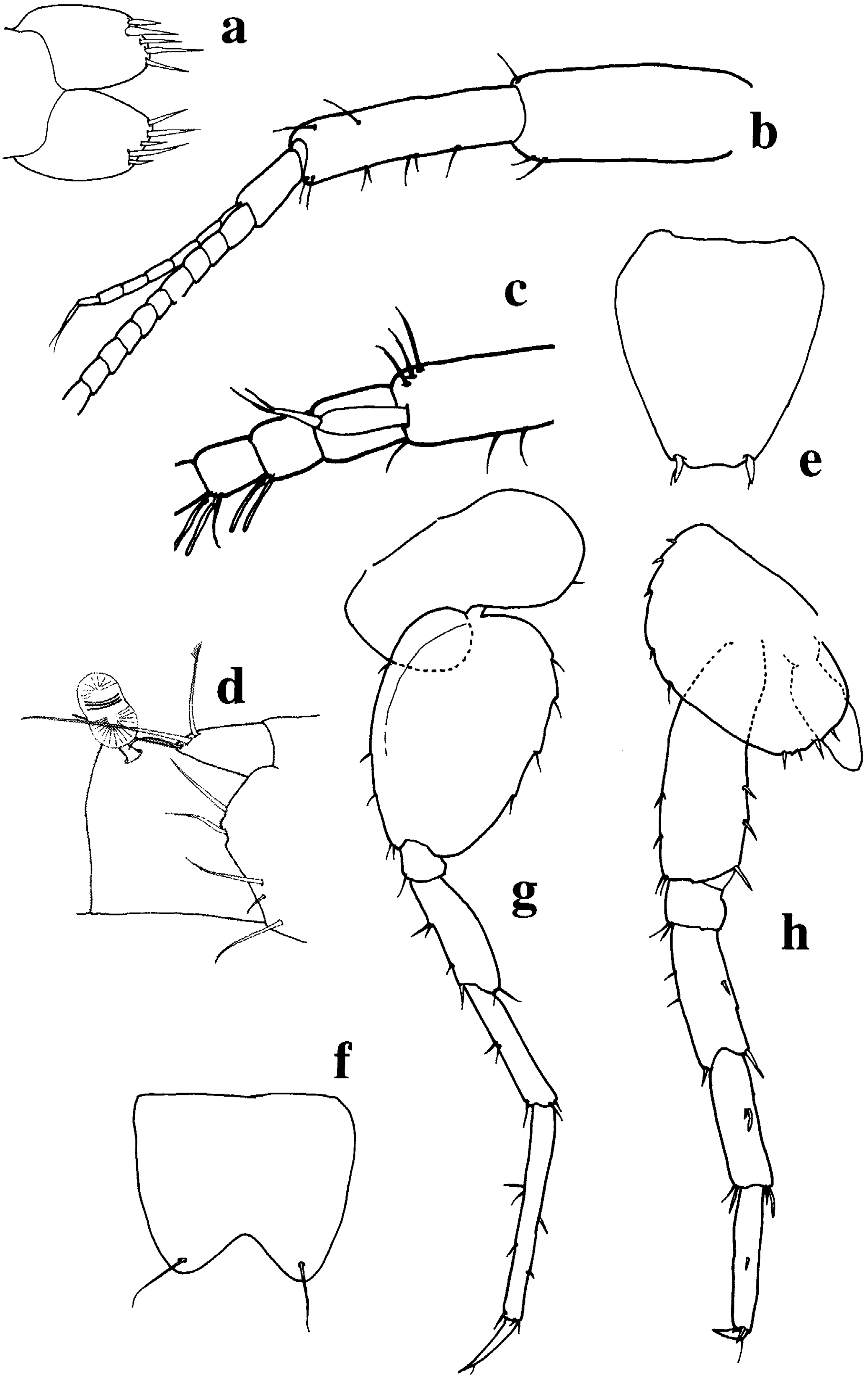

Figure 5: ***Phreatogammarus fragilis***: **a, telson; b, antenna 1.** ***Paracrangonyx compactus***: **c, accessory flagellum; e, telson; h, peraeopod 7.** ***Paraleptamphopus subterraneus***: **d, accessory flagellum; f, telson; g, peraeopod 7.**

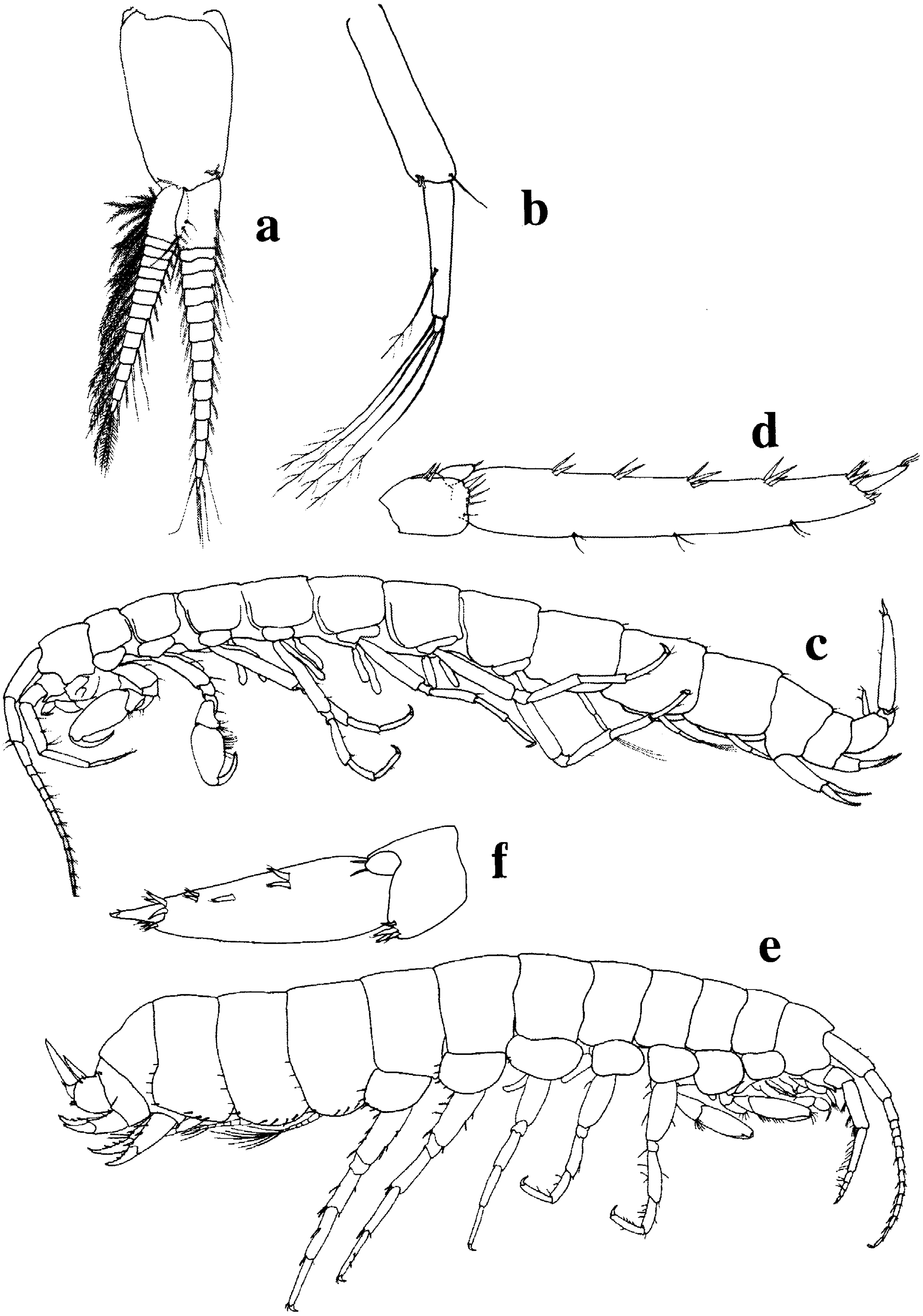

Figure 6: ***Paraleptamphopus subterraneus***: **a, pleopod 2.** ***Paracrangonyx winterbourni***: **b, pleopod 2; c, whole animal; d, uropod 3.** ***Paracrangonyx compactus***: **e, whole animal; f, uropod 3.**

Isopoda

Like amphipods, isopods are predominantly marine crustaceans that live in most marine, terrestrial, and freshwater habitats throughout New Zealand and elsewhere. Isopods are rare in most New Zealand surface waters, except in parts of the South Island (south of Banks Peninsula), Stewart Island, and subantarctic islands. Those living in groundwaters are usually smaller and quite different in overall appearance from each other. The New Zealand surface water isopods belong to two suborders, the Phreatoicidea and the Valvifera, whereas groundwater isopods include representatives of four suborders: Phreatoicidea, Anthuridea, Flabellifera, and the Asellota. Very little is known of the biology of New Zealand freshwater isopods from either epigean or hypogean waters.

Systematics

Phreatoicid isopods are the most diverse of known freshwater isopods in New Zealand. Fossils indicate that the phreatoicid group is very old (325 million years) and their morphology appears to have changed little over time (Wilson & Keable 1999). These elongate isopods range in size from a few millimetres up to over 25 mm long. Typically brown or white, phreatoicids have rounded heads with small or absent eyes, depending on the species (Figures 7b, 7f–7h). Phreatoicids live in freshwater streams, lakes, and in groundwaters in the southern South Island. Only three (*Phreatoicus typicus, P. orarii, Neophreatoicus assimilis*) of the nine described New Zealand species are reported from groundwater, although another three are reported from springs and related microhabitats. All species, except *Phreatoicus typicus*, are so poorly known that they may all prove to be more hypogean than epigean. Few have been collected or reported since Nicholls's (1944) review and description of the New Zealand fauna. All records are from south of central Canterbury, with most species known from Southland and Otago. All three known groundwater dwellers are found in the alluvial aquifers of Canterbury. Additional specimens from Westland are being investigated.

Two species of freshwater Anthuridea are reported from New Zealand, but only one groundwater species is known. *Cruregens fontanus* (Figure 7c), originally described from wells near Christchurch, appears confined to groundwaters and the hyporheos from South and North Canterbury (Winchester, Eyreton) to near Wellington, the Wairarapa, and groundwater in Hawke's Bay.

The Flabellifera are represented in New Zealand by three currently undescribed species from limestone caves in northwest South Island (B. Sket, University of Ljubljana and N. Bruce, NIWA, Wellington, unpublished results). One species was illustrated and photographed in Chapman & Lewis (1976: figure 10.7, plate 7b), although incorrectly labelled as an anthuridean.

Asellotan isopods from New Zealand's freshwaters are very poorly known, and Dr Buz Wilson (The Australian Museum) has tentatively identified specimens from the South Island as belonging to two genera (*Heterias* and *?Mackinia*), both very small (1–3 mm long). Other collections suggest that asellotan isopods are common in interstitial groundwater habitats throughout New Zealand, probably with additional genera and species.

Suborder Asellota: Family Janiridae

***Heterias* sp.:** Otago, Canterbury and Hawke's Bay; hyporheic in streams and rivers. Also commonly found in wells.

***?Mackinia* sp.:** Hyporheic in alluvial rivers and streams in Canterbury and Otago.

Suborder Flabellifera: Family Anthuridae

***Cruregens fontanus* Chilton 1882:** Central (Eyreton, Leeston, Waipara River) and South Canterbury (Orari valley, Winchester) (Nicholls 1944, Hurley 1961), and near Wellington. Also found in a Wairarapa cave (Schminke & Noodt 1968), and in alluvial groundwaters, hyporheic zones, and cave streams.

Suborder Flabellifera: Family Sphaeromatidae

New genus & species: These flattened isopods from northwest Nelson are currently being described. They are found in streams within limestone caves.

Suborder Phreatoicidea: Family Phreatoicidae

***Phreatoicus typicus* Chilton 1883:** Central Canterbury (Eyreton, Templeton, Burnham); shallow to deeper (3–20 m below ground) alluvial groundwater (Wilson & Fenwick 1999).

***Phreatoicus orarii* Nicholls 1944:** South Canterbury (Ashburton, Orari Valley); shallow groundwater (Nicholls 1944).

***Neophreatoicus assimilis* (Chilton 1884):** South Canterbury (Temuka, Winchester); from shallow, alluvial groundwater and springs (Nicholls 1944).

***Notamphisopus benhami* Nicholls 1944:** Stewart Island (Horseshoe Bay); under debris and moss in small streams (Nicholls 1944).

***Notamphisopus dunedinensis* (Chilton 1906):** Otago (Mosgiel, Woodhaugh); from streams (Nicholls 1944).

***Notamphisopus flavius* Nicholls 1944:** Southland (Lumsden, Oreti River bed); from springs and seeps (Nicholls 1944).

***Notamphisopus kirkii* (Chilton 1906):** Foveaux Strait (Ruapuke Island); in freshwater lagoon (Nicholls 1944).

***Notamphisopus littoralis* Nicholls 1944:** Otago (Pounawea) in springs and ditches draining them within 100 m of the shore (Nicholls 1944).

***Notamphisopus percevali* Nicholls 1944:** Otago (Drummond) and Southland (near Invercargill, Otautau); on roots of rushes and amongst plant material in muddy ponds and streams (Nicholls 1944).

Identification

This key was developed from the literature without checking against specimens. Thus, its accuracy cannot be confirmed, especially for the species of *Notamphisopus*; published descriptions and illustrations of these species seem inadequate for reliable identification. The key also includes all phreaticoids because some of the presumed epigean species may well live in groundwaters. Because the key is simplified, combinations of characters are used to increase its reliability. Also, terms like "usually" are used sparingly to facilitate more rapid separation of some species, but it is important to check all characters within these couplets.

1 **a.** Uropods lateral or ventral, not terminal; rod-like or lamellate (Figures 7a–d, 8a–d) 2
b. Uropods terminal, always rod-like, may be long (often lost) or short and inconspicuous; animals usually very small (2–3 mm long) (Figure 7e) **Asellota** (2 undescribed hypogean species)

2 **a.** Uropods ventral, plate-like, hinged ventro-laterally to pleotelson to form opercular plates covering pleopods, not visible in dorsal view (Figure 8a) **Chaetiliidae** (*Austridotea*, epigean)
b. Uropods ventral or lateral, rod-like or flattened, but not forming a ventral operculum covering pleopods (Figures 8b-d) 3

3 **a.** Body cylindrical (Figures 7b–c), not flattened, not capable of rolling into a ball (Figs 7b-c); uropods rod-like or flattened (Figures 8b–d), if flattened, pleotelson almost twice as long as wide (Figure 8b) 4
b. Body flattened, almost limpet-like, capable of rolling into a ball (Figure 7d); uropods lamellate, together with pleotelson forming a tail fan; pleotelson about as wide as long (Figure 7d) **Sphaeromatidae** (3 hypogean species currently being described)

4 **a.** Head rounded, distinct from body; body not evenly cylindrical (Figures 7b, f–h); uropod outer ramus not inserted markedly anterior to inner ramus (Figures 8c–d); uropod rami conical, tapering to a point, margins not evenly setose **Phreatoicidea** 5
b. Head cylindrical, not very distinct from body; body cylindrical, long and very thin (Figure 7c); uropod outer ramus attached more than half its length anterior to insertion of inner ramus (Figure 8b); uropod rami flattened, not conical, tips rounded in dorsal view, with long setae **Anthuridae** (1 hypogean species: ***Cruregens fontanus***)

5 **a.** Peraeon segments 3–4 usually longer than deep (Figures 7b, f); lateral pleotelson ridge anterior to uropod insertion present or absent, lacking spines (Figures 8c, 9c–d); large posteroventral spine on uropod peduncle beneath insertion of uropod rami simple (untoothed) (Figures 8c, 9d) or absent 6
b. Peraeon segments 3–4 usually deeper than long (Figures 7g–h); lateral pleotelson ridge anterior to uropod insertion conspicuous, with 1–4 spines (Figures 8d, 10a–b, e, g); large posteroventral spine on uropod peduncle beneath insertion of uropod rami present, toothed (Figure 8e) ***Notamphisopus*** **8**

6 **a.** Gnathopod article 6 widened distally (Figure 8f), palm with shallow distal excavation, dactyl closing against palm at tip only (Figure 8g); peraeopods 5–7 article 2 not widened (Figs 8h, 9f); pleotelson longer than deep (high) (Figures 8c, 9d) ***Phreatoicus*** **7**
b. Gnathopod article 6 inflated, as wide proximally as distally (Figure 9a); palm excavate proximally, dactyl closing against palm over distal 50% (Figure 9a); peraeopods 5–7 article 2 conspicuously wider at midpoint than basally (Figure 9e); pleotelson about as deep as long (Figure 9c) ***Neophreatoicus assimilis***

7 **a.** Ventral margins of pleon side plates (epimera) lacking an even fringe of setae (Figure 7b); peraeopod 7 article 3 linear, not produced into a posterodistal lobe overhanging article 4 (Figure 8h) ***Phreatoicus typicus***

b. Ventral and posteroventral margins of pleon side plates (epimera) with conspicuous, even fringe of setae (Figures 7f, 9d); peraeopod 7 article 3 slightly widened in middle, with a small posterodistal lobe overhanging article 4 (Figure 10f) ***Phreatoicus orarii***

8 **a.** One large and one small spine or two subequal spines at posteroventral corner of uropod peduncle, beneath insertion of rami (Figure 8e) **9**
b. Only one spine at posteroventral corner of uropod peduncle, beneath insertion in rami (Figure 10a) (epigean?) ***Notamphisopus percevali***

9 **a.** Posteroventral spines on uropod peduncle equal in size (Figure 8d) (epigean?) ***Notamphisopus dunedinensis***
b. Posteroventral spines on uropod peduncle unequal in size (Figure 8e) **10**

10 **a.** Both posteroventral uropod peduncle spines apically toothed or spined (Figure 8e) **11**
b. Only the larger posteroventral uropod peduncle spine apically toothed or spined, smaller spine simple or untoothed (Figure 10g) **12**

11 **a.** Antenna 1 flagellum penultimate article conspicuously longer than preceding articles (Figure 10c); lateral pleotelson ridge anterior to uropod insertion with 3 dorsal spines (Figure 10b) ***Notamphisopus benhami***
b. Antenna 1 flagellum penultimate article not conspicuously longer than preceding articles, all similar in length and width (as in *N. flavius*; Figure 10d); lateral pleotelson ridge anterior to uropod insertion with 1 dorsal spine (Figure 10e) (epigean?) ***Notamphisopus kirkii***

12 **a.** Maxilliped palp penultimate (third) article ovate, almost as wide as long (Figure 10f) ***Notamphisopus littoralis***
b. Maxilliped palp penultimate (third) article longer than wide (Figure 10h) ***Notamphisopus flavius***

Biology

The biology of isopods in New Zealand groundwaters is poorly known. *Phreatoicus typicus* (Figure 11d) ingests and digests bacteria in the vicinity of sewage effluent entering the groundwater (Sinton 1984, Fenwick 1987). These animals extensively browse non-living organic layers that form on sediment particles within aquifers, removing significant quantities of organic carbon from the system (Fenwick 1987). Other groundwater phreatoicids probably feed in much the same way.

With one exception, other groundwater isopods in New Zealand probably also feed on detritus in various forms. The tiny asellotans (Figure 11 a–b) from interstital hyporheic habitats and the larger flabelliferans from caves are probably also detritus feeders, browsing on detritus fragments or films. *Cruregens fontanus* (Figure 11c) may be the exception. This species has large raptorial gnathopods and piercing-sucking mouthparts, suggesting it may be predatory.

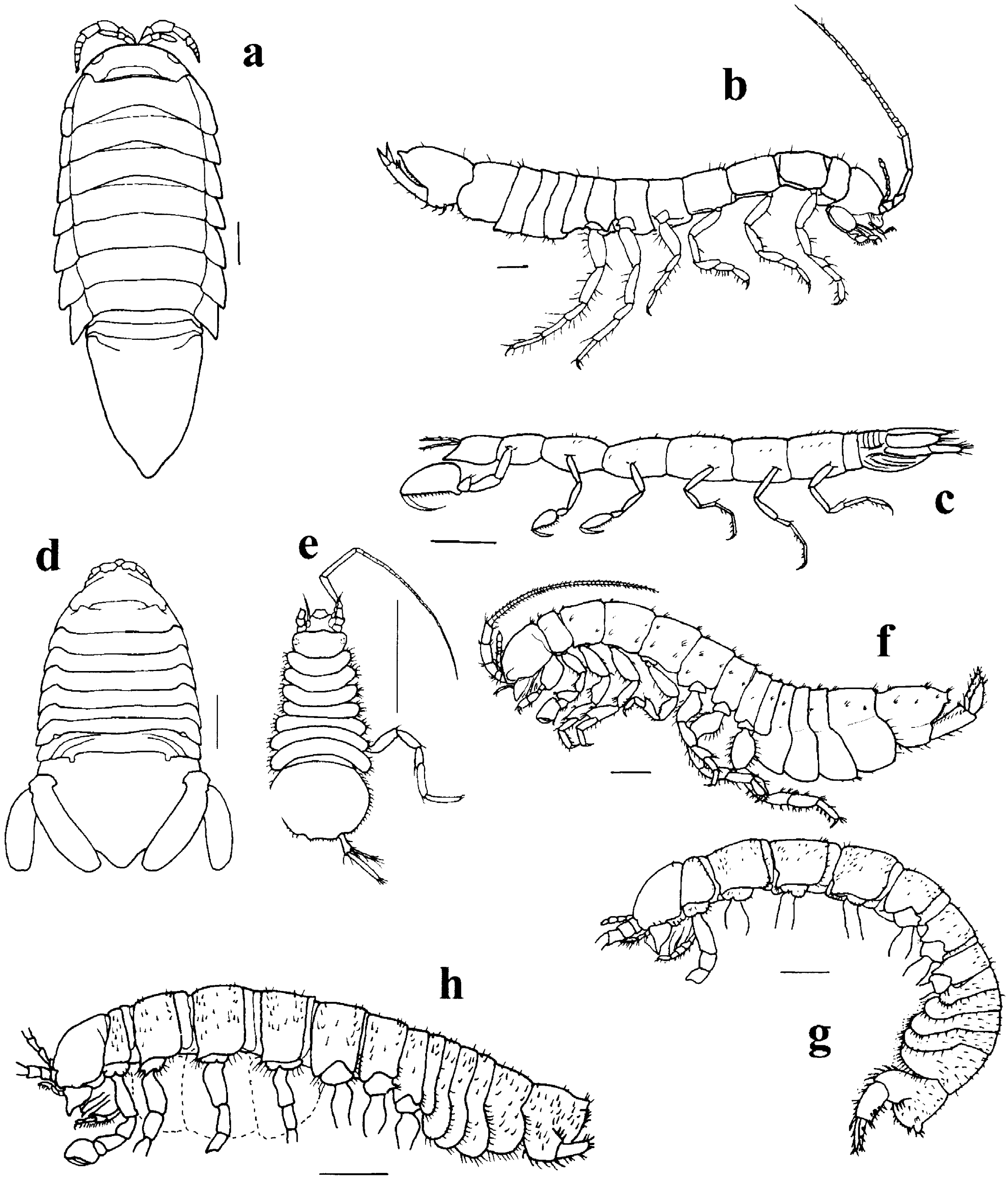

Figure 7: Isopoda: a, Idotheidae: *Austridotea annectens*; b, Phreatoicidea: *Phreatoicus typicus*; c, Anthuridae: *Cruregens fontanus*; d, Sphaeromatidae; e, Asellota: *Heterias* sp. (most appendages missing); Phreatoicidea: f, *Neophreatoicus assimilis*; g, *Notamphisopus dunedinensis* ♂; h, *N. dunedinensis* ♀. (Figures redrawn from: b, Wilson & Fenwick 1999; c, Chilton 1894; e, Roberts 1975; f–h, Nicholls 1944.)

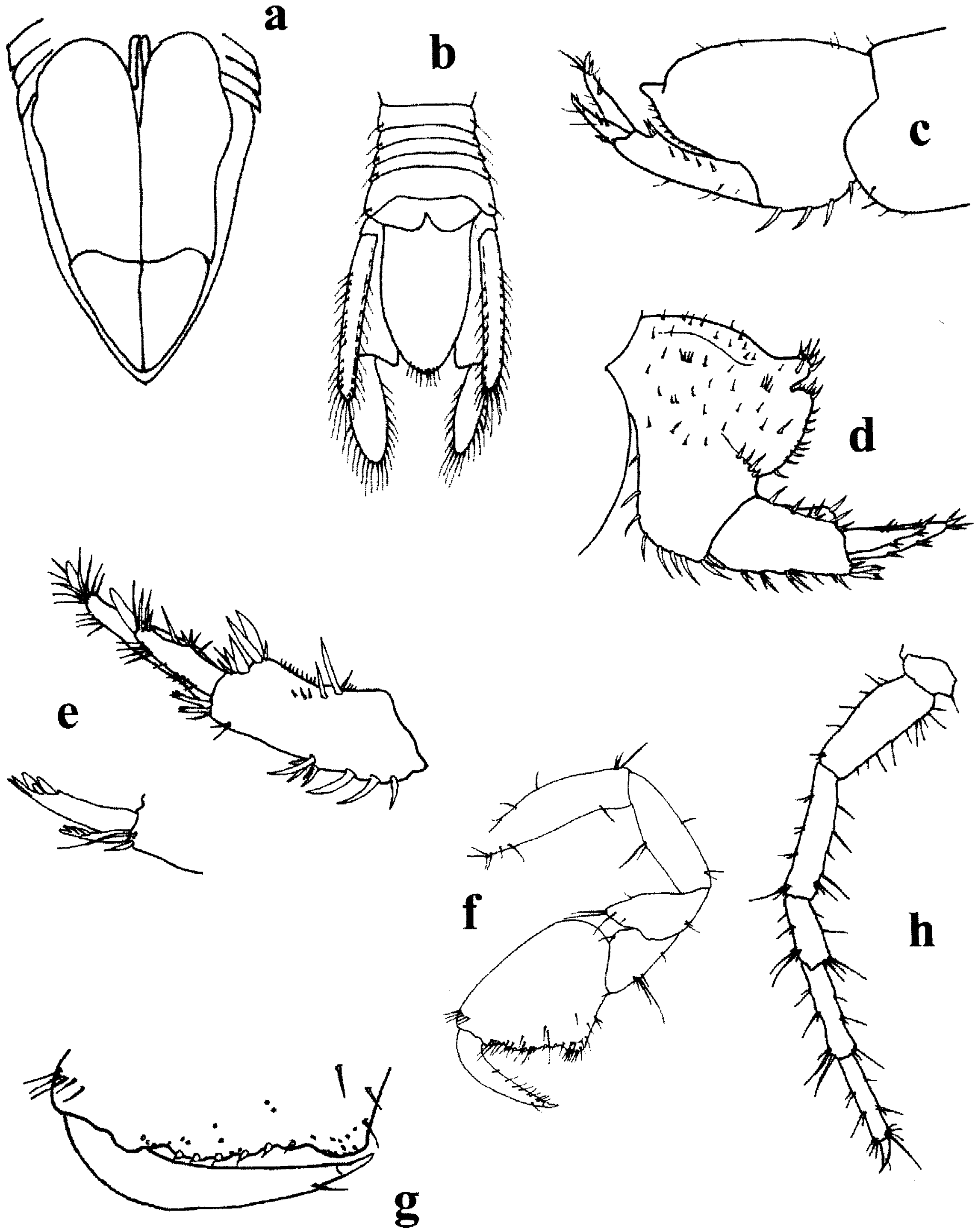

Figure 8: a, ***Austridotea annectens*** **pleotelson ventral view; b,** ***Cruregens fontanus*** **pleotelson, dorsal view; c,** ***Phreatoicus typicus*** **pleotelson, side view; d** ***Notamphisopus dunedinensis*** **pleotelson side view; e,** ***Notamphisopus benhami*** **uropod and inter-ramal spines; f,** ***Phreatoicus typicus*** **gnathopod; g,** ***P. typicus*** **gnathopod palm; h,** ***P. typicus*** **peraeopod 7. (Redrawn from a, Chilton 1894; b, e–g, Wilson & Fenwick 1999; c–d, Nicholls 1944.)**

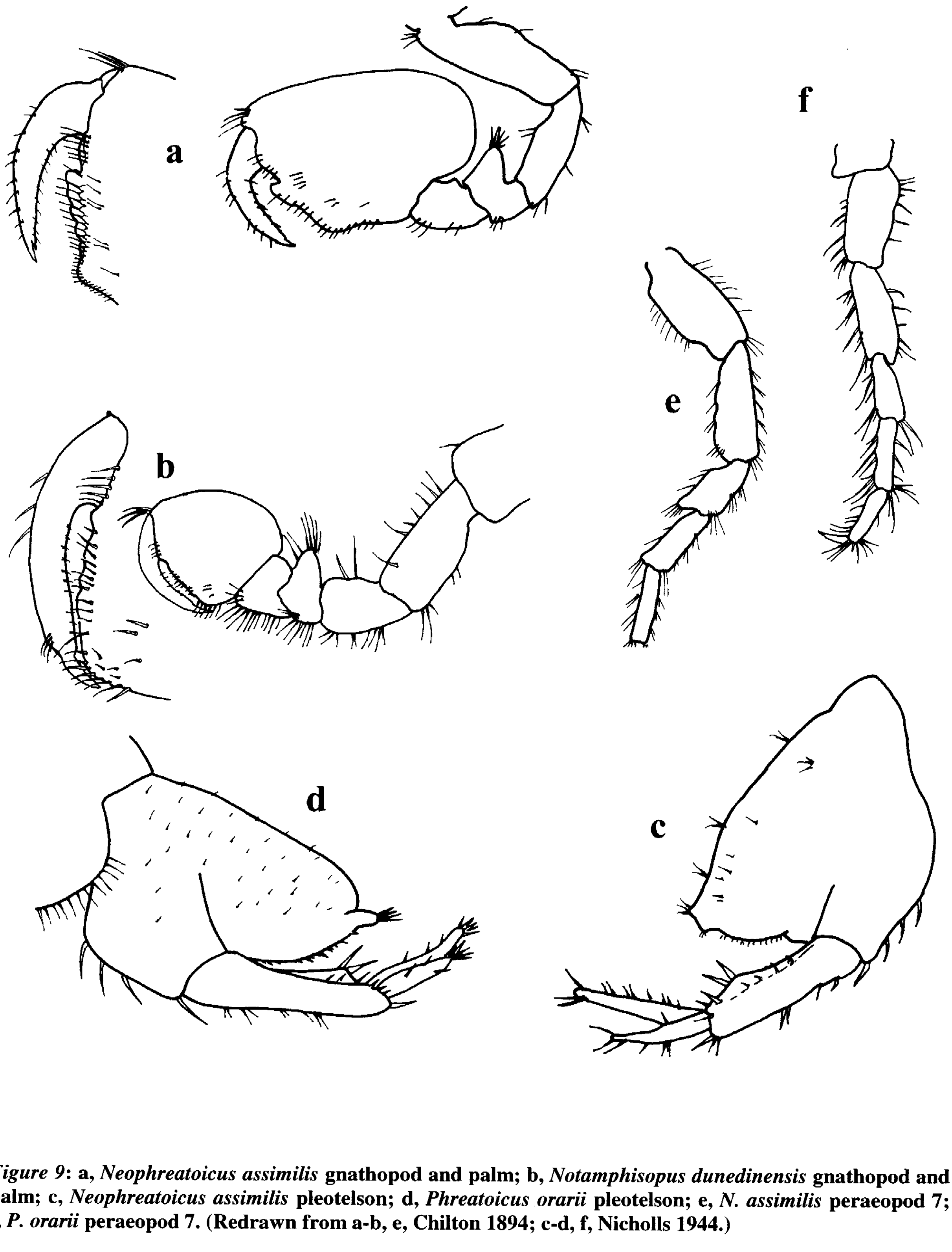

Figure 9: a, *Neophreatoicus assimilis* gnathopod and palm; b, *Notamphisopus dunedinensis* gnathopod and palm; c, *Neophreatoicus assimilis* pleotelson; d, *Phreatoicus orarii* pleotelson; e, *N. assimilis* peraeopod 7; f, *P. orarii* peraeopod 7. (Redrawn from a-b, e, Chilton 1894; c-d, f, Nicholls 1944.)

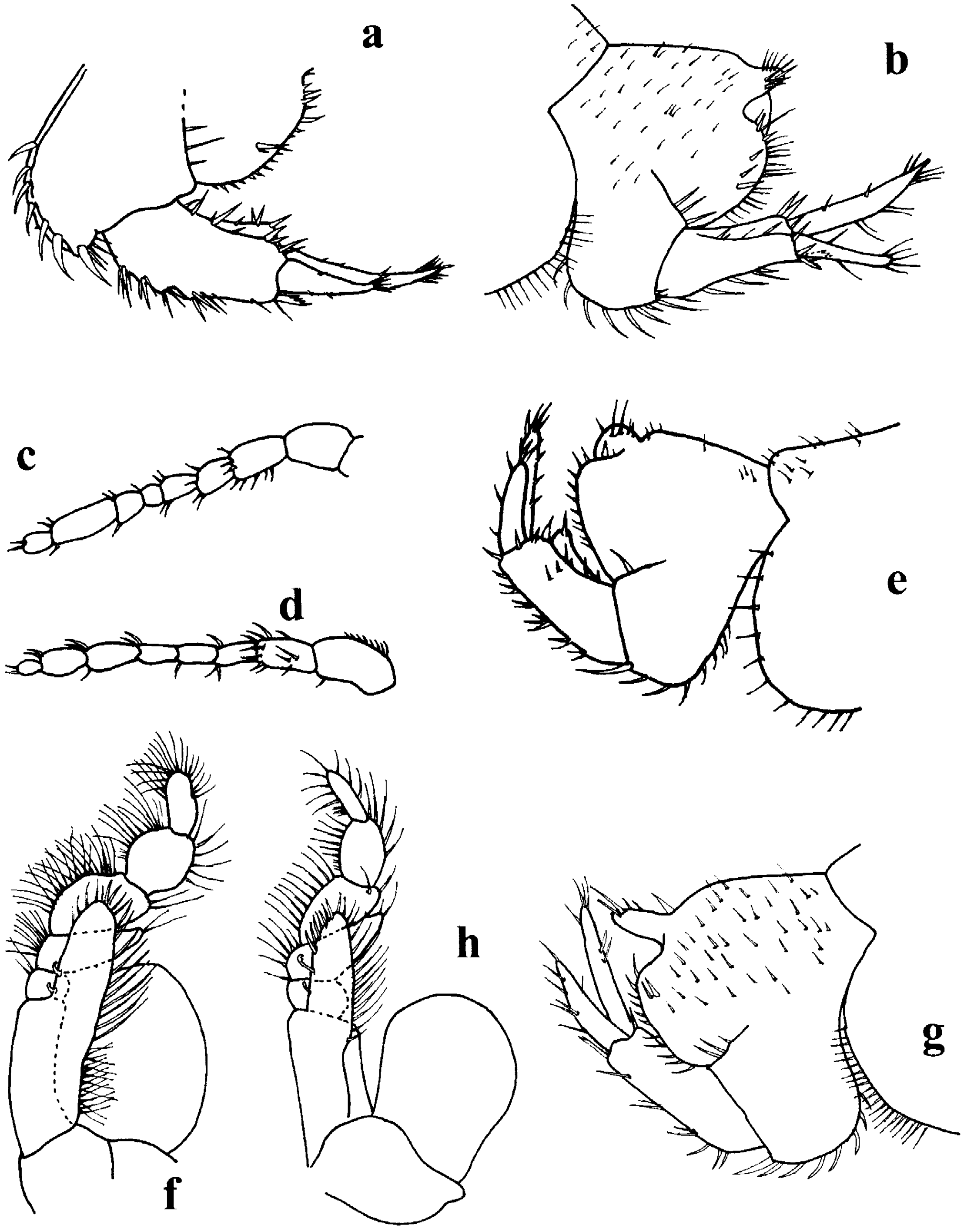

Figure 10: a, *Notamphisopus percevali* pleotelson; b, *N. benhami* pleotelson; c, *N. benhami* antenna 1; d, *N. flavius* antenna 1; e, *N. kirkii* pleotelson; f, *N. littoralis* maxilliped; g, *N. flavius* pleotelson, h, *N. flavius* maxilliped. (All redrawn from Nicholls 1944.)

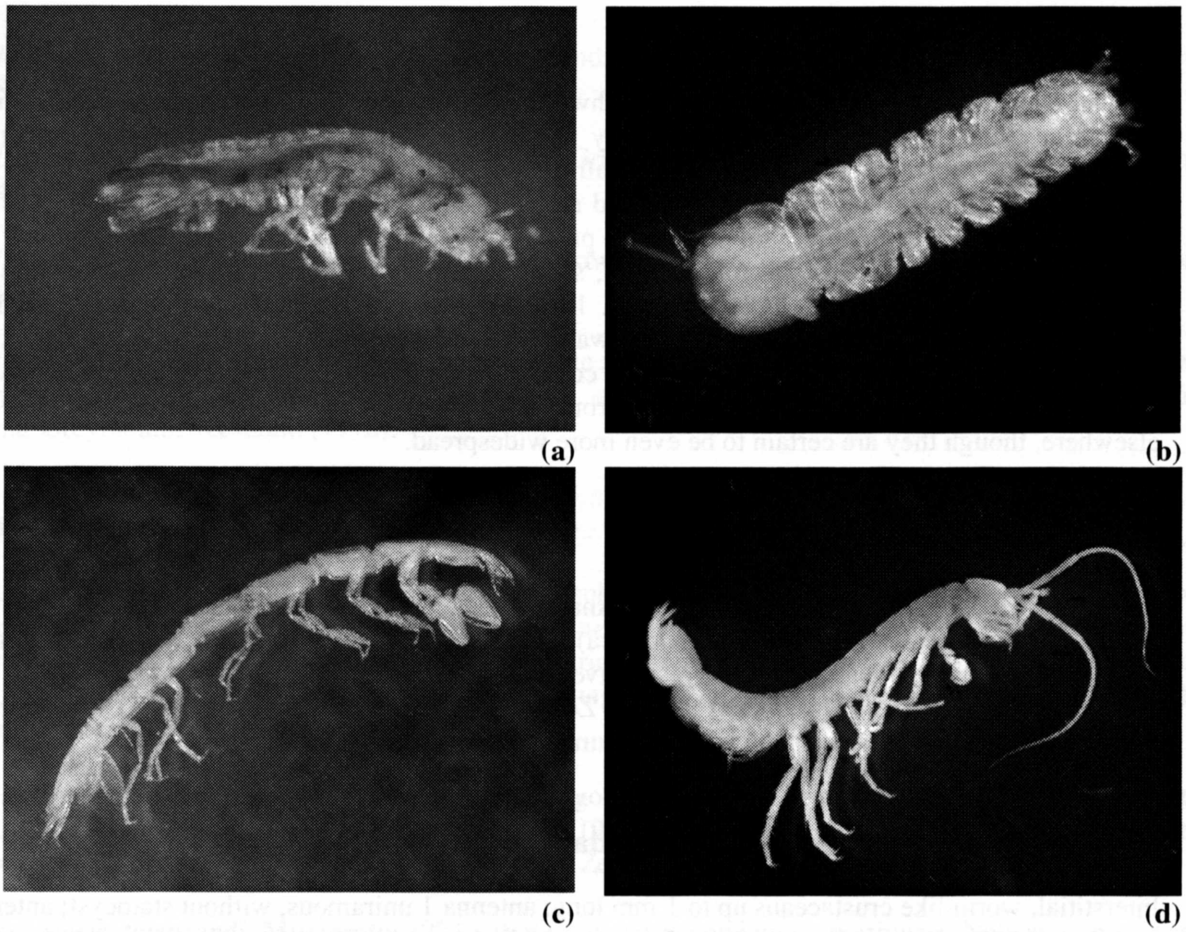

Figure 11: **Janirid isopod from southern Hawke's Bay groundwater wells; a, lateral view; b, dorsal view; c, *Cruregens fontanus* from a South Canterbury well; d, *Phreatoicus typicus* from a Templeton well. All specimens head at right.**

Syncarida

Known from Carboniferous and Permian freshwater deposits, syncarids are primitive malacostracan crustaceans that lack a carapace: their body segments are generally similar to each other and unspecialised. Most are blind and very small (under 5 mm long), amongst the smallest of all crustaceans. Although they are rarely seen and reported, they appear quite abundant wherever found and, with careful searching, are likely to prove widespread and abundant members of most groundwater habitats. In Britain, for example, some have been pumped from alluvial groundwaters and interstitial sands in rivers (Gledhill et al. 1993). Within New Zealand, Schminke (1973, 1978) found syncarids in 36 of 200 (i.e., 18%) freshwater interstitial samples taken through out the country. We have found syncarids among many of our collections from alluvial groundwaters in the Hawke's Bay region, Nelson, Marlborough, and Canterbury. Our sampling has been inadequate to find them elsewhere, though they are certain to be even more widespread.

Systematics

The superorder comprises two extant orders: Anaspidacea (c. 17 described species, up to 50 mm long, Australia, New Zealand, and South America) and Bathynellacea (70+ and 80+ species in the Bathynellidae and Parabathynellidae, respectively; up to 5.5 mm long, worldwide, including New Zealand). Syncarids were discovered in New Zealand by Schminke & Noodt (1968) who collected five species of bathynellans and an unknown number of stygocarid taxa.

Order Bathynellacea: Family Bathynellidae

Interstitial, worm-like crustaceans up to 1 mm long; antenna 1 uniramous, without statocyst; antenna 2 with exopod (scaphocerite); upper lip (labrum) untoothed; mandibular palp prehensile, of 1–3 articles; lower lip with paragnaths; maxilla 1 (maxillule) with two proximal inner plates (endites); maxilla 2 (maxilla) with two or three inner plates; maxillipeds absent; thoracic exopods 1-articulate; 1–2 pairs of pleopods; telson fused to abdominal somite 6 forming a pleotelson.

***Bathynella* sp. Schminke 1973:** One species was reported from the Orari River, Canterbury (Schminke 1973), but not described, presumably because no adult males were present in the collections. Apparently, Schminke's unpublished thesis (1971, not seen) reported an undescribed species of *Bathynella* from New Zealand (Elliot Dawson, pers comm., June 2002), but whether this is the same as his 1973 undescribed species is not known.

Indeterminate genus and species: One species reported from groundwater near Nelson (Schminke 1978), but of uncertain generic status because no males were collected. No description of this species has been published.

Order Bathynellacea: Family Parabathynellidae

Elongate, interstitial-dwelling crustaceans, usually very small, but up to 3 mm long; antenna 1 uniramous, lacking statocyst; antenna 2 lacking exopod (scaphocerite); upper lip toothed or setose; mandibular palp 1-articulate, not prehensile; lower lip lacking paragnaths; maxilla 1 with two basal inner plates; maxilla with 2–3 inner plates; maxillipeds absent; thoracic exopods of one or more articles; pleopods absent or very small; telson and abdominal somite 6 fused into a pleotelson.

***Atopobathynella compagana* Schminke 1973:** Shallow groundwater near Nelson (Brightwater and Lee River), Wairarapa (Tauherenikau River), and Victoria (Australia) (Schminke 1973, 1986).

***Hexabathynella aotearoae* Schminke 1973:** Shallow groundwater in rivers; endemic: Westland (Toaroha, Styx (Kokatahi catchment), Poeroa, Waitangi (?), Turnbull Rivers) (Schminke 1973, 1986).

***Notobathynella chiltoni* Schminke 1973:** Groundwater; endemic: South Canterbury (Orari River) (Schminke 1973).

***Notobathynella hineoneae* Schminke 1973:** Groundwater; endemic: Southland (Whakaea and Mataura Rivers) (Schminke 1973, 1986).

***Notobathynella longipes* Schminke 1978:** Groundwater; endemic: near Nelson (Motueka) (Schminke 1978).

***Notobathynella* sp. Schminke 1973:** Indeterminate specimens (adult females, no males) were reported by Schminke from the Lee River, Nelson (1973), a well near Brightwater, Nelson (1978), and from near Greymouth, Westland (1978).

Order Anaspidacea: Family Stygocarididae

Anaspids are confined to the southern hemisphere. In Australia, they occur in surface and groundwaters, with the large *Anaspides tasmaniae* typically found in very shallow, small streams, whereas species of Koonungidae appear to be strictly hypogean (Schminke 1982, 1986). The order contains four extant families (Anaspididae, Koonungidae, Psammaspididae, Stygocarididae) with only the Stygocarididae reported from New Zealand.

Ranging between about 1.4 and 4.2 mm long, Stygocarididae have been reported from southern South America, New Zealand, and Australia (Schminke 1982). Seven species in four genera are known, with two species[1] in different genera known from New Zealand.

***Stygocaris townsendi* Morimoto 1977:** Water in caves, endemic: northwest Nelson (caves near Paturau and Te Hapu) (Morimito 1977, Schminke 1986).

***Stygocaris* sp. 1:** Unreported habitat and location in South Island, New Zealand (Morimoto 1977).

***Stygocaris* sp. 2:** Unreported habitat and location in South Island, New Zealand (Morimoto 1977).

***Stygocarella pleotelson* Schminke 1980:** Shallow groundwater in riverbeds, endemic: Westland (Toaroha, Styx (Kokatahi catchment), Waitangi (?) Rivers) (Schminke 1980, 1986).

Identification

1 **a.** Eight free thoracic segments (no maxilliped present; first thoracic leg same as the others); last thoracic leg biramous (with exopod) or reduced; five free abdominal segments, plus a pleotelson, where the last body segment is fused with the telson (Figures 12a, c, 13d) **Order Bathynellacea 2**

b. First thoracic segment fused to head (may be separated by a transverse groove), leaving seven free thoracic segments; first thoracic leg more robust and setose, directed over mouthparts forming a maxilliped; last thoracic leg uniramous (lacks exopod and epipod), not greatly reduced in size, flexes anteriorly; five free abdominal segments (plus pleotelson) (Figs 12b, 14a, f, g) **Order Anaspidacea 7**

2 **a.** Antenna 2 directed anteriorly (Figure 12c), exopod absent or of one article, bearing a slender, terminally plumose seta (Figure 12d); thoracic legs 1–7 exopods 1-articulate, with dorsal, ventral and terminal setae (Figure 12e); pleopod 1 of two articles (Figure 12f);

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[1] Apparently, Schminke's thesis (1971, not seen) reported an undescribed species of *Parastygocaris* from New Zealand (Elliot Dawson, pers. comm., June 2002).

pleotelson with a pair of dorsal setae (Figure 12c)
Family Bathynellidae (one indeterminate species of ***Bathynella*** from N.Z.)

b. Antenna 2 directed posteriorly (Figure 12a), exopod absent (Figure 12g); thoracic legs 1–7 exopods either 1-articulate and with ventral and terminal setae only (Figure 12h), or of two or more articles (setae on one or both margins) (Figure 12i); pleopod 1 absent or of one article (Figure 12j); pleotelson lacking pair of dorsal setae (Figure 12a)
Family Parabathynellidae 3

3 **a.** Antenna 2 of one article (Figure 13a); uropod peduncle with two equally long spines or a short row of similar spines, distal spine not conspicuously longer and stouter than others (Figure 13b) ***Atopobathynella compagana***

b. Antenna 2 consisting of three or more articles (Figure 12g); uropod peduncle with series of unequal spines, distal spine conspicuously longer and stouter than others (Figure 13c, g) **4**

4 **a.** Seventh pair of thoracic legs missing (Figure 13d); pleotelson produced posteriorly into small triangular (dorsal view) operculum projecting over anus (Figure 13e)
Hexabathynella aotearoae

b. Seventh pair of thoracic legs present (Figure 12a); pleotelson not produced posteriorly into operculum over anus (Figures 13g) ***Notobathynella*** **5**

5 **a.** Inner ramus of uropod with two large, subequal spines mediodistally (Figure 13f)
N. chiltoni

b. Inner ramus of uropod with mediodistal spine distinctly longer and stouter than medial subdistal (Figures 13c, g) **6**

6 **a.** Antenna 2 distal article with four terminal setae (three simple, one plumose) (Figure 13h)
N. hineoneae

b. Antenna 2 distal article with three terminal setae (two simple, one plumose) (Figure 13i)
N. longipes

7 **a.** Rostrum a triangular lobe (Figure 14a); maxilla 1 with a small, 1-articulate palp (Figure 14b); pleopods large, conspicuous, present on all abdominal somites; lamelliform uropod rami form a tail fan with the telson, both uropod rami 1-articulate (Figure 14a)
Family Koonungidae (not reported from N.Z.)

b. Rostrum bi-lobed or rounded; maxilla 1 without a palp (Figures 14c–d); pleopods variously reduced, present on all abdominal somites or absent from abdominal somites 3–4 (Figures 12b, 14f–g); uropod rami not lamelliform, not forming tail fan with telson (Figures 14f, g), outer ramus 1 or 2-articulate, inner 1 or 2- articulate (Figures 14m, n) **8**

8 **a.** Rostrum bilobed, lacking setae (Figure 14c); mandibular palp 3-articulate (Figure 14h); thoracopod 1 not specialised as a maxilliped, with an exopod (Figure 14i); pleopods 3–4 present, greatly reduced (Figure 14g); uropod inner and outer rami 2-articulate (Figure 14g)
Family Psammaspididae (not reported from N.Z.)

b. Rostrum not bilobed or incised (Figures 14d, j); mandibular palp lacking (Figure 14k); thoracopod 1 specialised as a maxilliped, lacking an exopod (Figure 14l); pleopods 3-4 lacking (Figures 12b, 14f); uropod inner ramus 1-articulate (Figures 14m, n)
Family Stygocarididae 9

9 **a.** Rostrum pointed, with a pair of lateral setae (Figure 14d); uropod outer ramus 1-articluate (Figure 14m) ***Stygocarella pleotelson***

b. Rostrum truncate, lacking setae (Figure 14j); uropod outer ramus 2-articulate (Figure 14n)
Stygocaris Three N.Z. species: ***S. townsendi***, two undescribed

Biology

Bathynellans are characteristically small, and are amongst the smallest crustaceans in the world (Figures 15a–b). Most inhabit freshwater, but some occur in slightly brackish habitats, and they are mostly found in cooler conditions. *Thermobathynella adami*, however, lives in very warm (55 °C) water. They typically inhabit interstitial waters in alluvial riverbeds, but have also been recorded from cave waters and from sandy beaches of Lake Tanganyika. Two species from Lake Baikal live at depths of 20–1440 m. Very little is known of bathynellid biology. They are believed to feed on detritus and, possibly, bacteria and fungi (Schminke 1982). Locomotion is thought to be via a combination of crawling and swimming movements and, despite their very small size, development through the six juvenile stages from hatching to adult takes about 9 months at 9 °C for the European species, *Bathynella natans* (Kaestner 1970).

Stygocarids are elongate, worm-like interstitial crustaceans (Figure 15c), mostly found in freshwaters in South America, New Zealand, and Australia. Nothing is known of their biology, but, like bathynellans, they are probably detritus feeders.

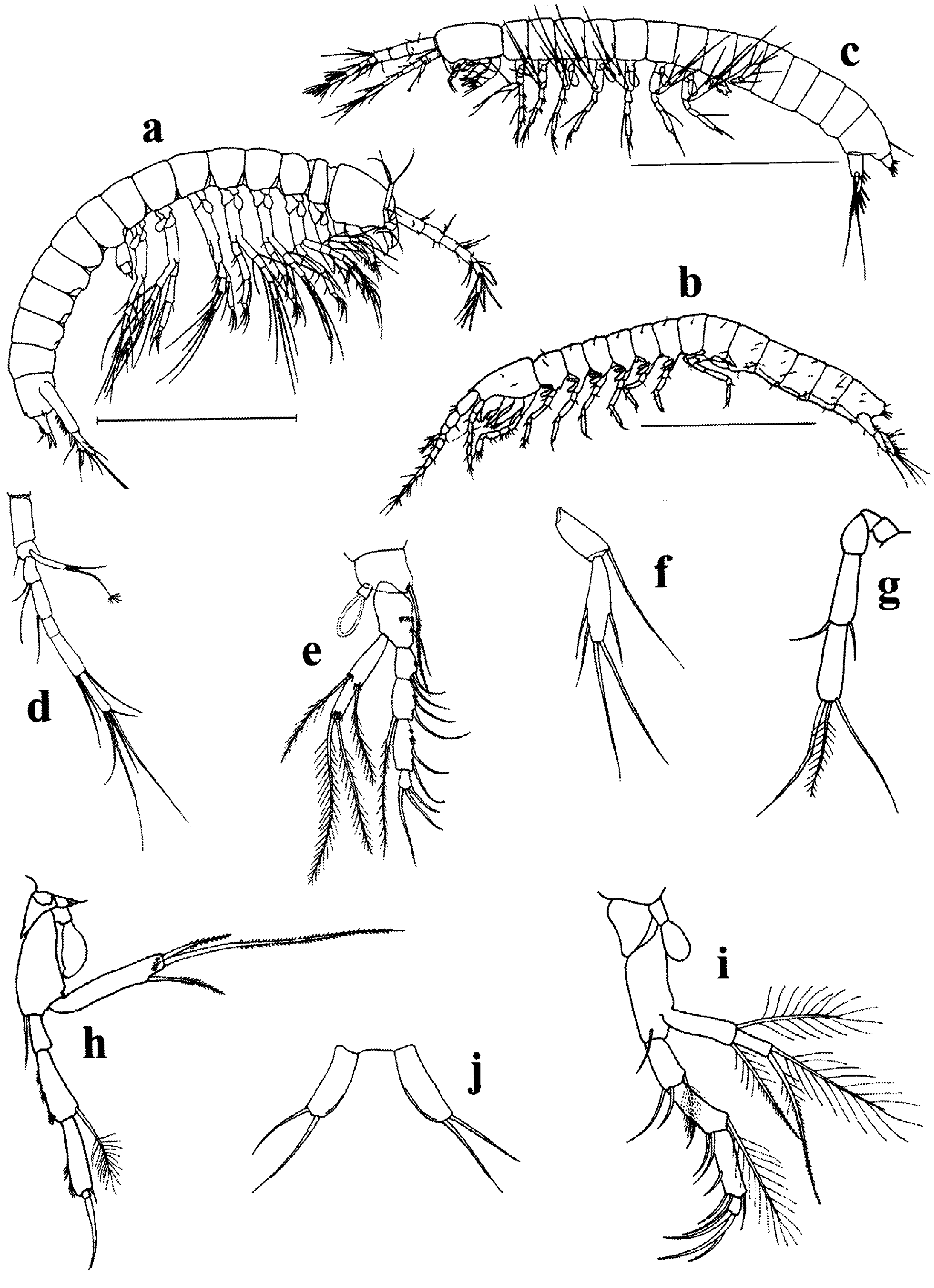

Figure 12: a, *Notobathynella longipes*, whole animal; b, *Stygocarella pleotelson*, whole animal; c, *Bathynella cautinensis*, whole animal; d, antenna 2, *B. cautinensis*; e, thoracopod 1, *B. cautinensis*; f, pleopods 1, *B. cautinensis*; g, antenna 2, *Hexabathynella aotearoae*; h, thoracopod 2, *Atopobathynella compagana*; i, thoracopod 2, *N. longipes*; j, pleopods 1, *Chilibathynella clandestina*. (Sources: a, i, from Schminke (1978); b, redrawn from Schminke (1980); c–f, j, from Noodt (1964); g–h, redrawn from Schminke (1973).)

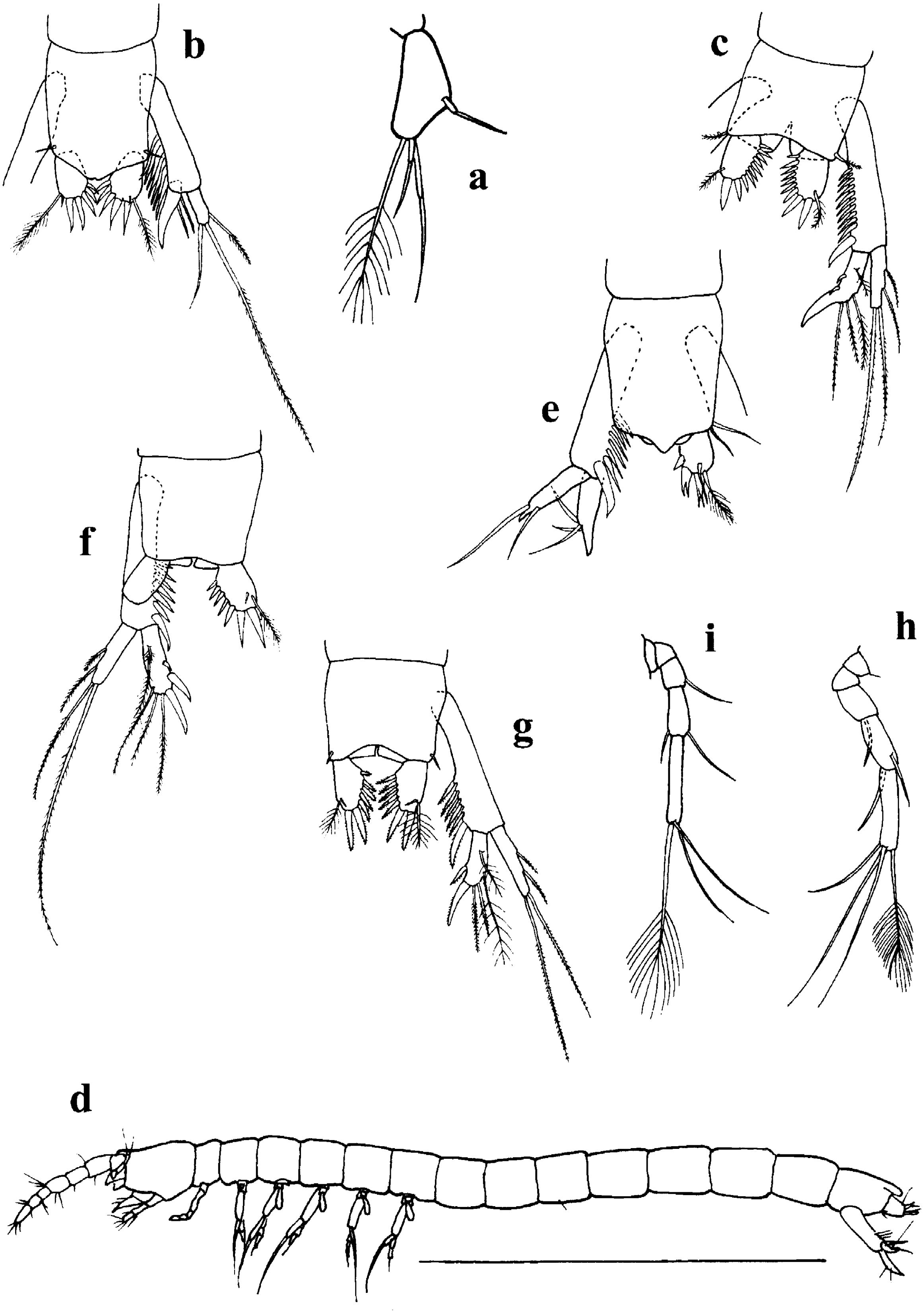

Figure 13: a, antenna 2, ***Atopobathynella compagana***; b, pleotelson, ***A. compagana***; c, pleotelson, ***A. compagana***; d, whole animal, ***Hexabathynella halophila***; e, pleotelson, ***H. aotearoae***; f, pleotelson, ***Notobathynella chiltoni***; g, pleotelson, ***N. longipes***; h, antenna 2, ***N. hineoneae***; i, antenna 2, ***N. longipes***. **(Sources: a–f, h, redrawn from Schminke (1973); g, i, redrawn from Schminke (1978).)**

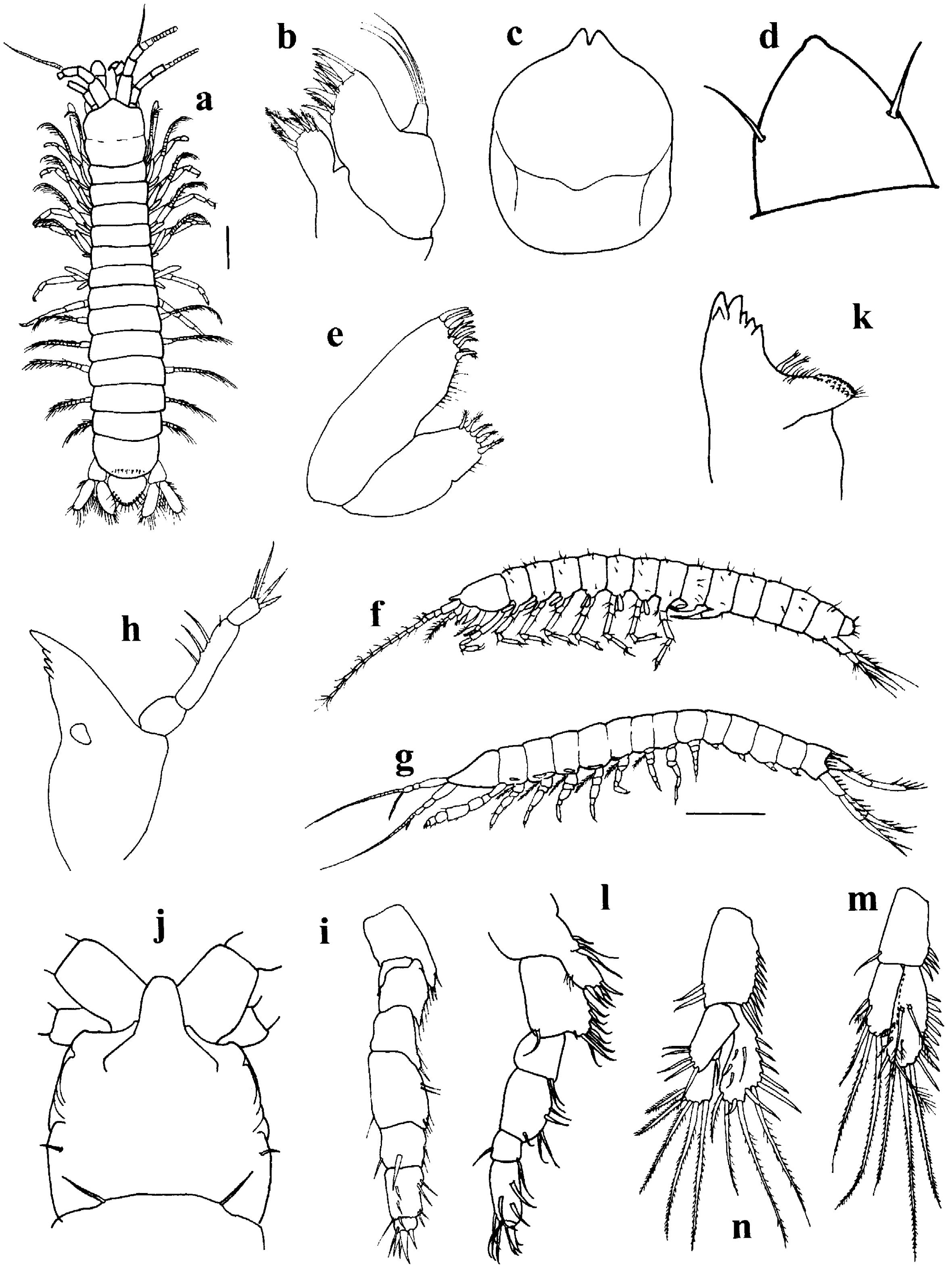

Figure 14: a, whole animal, *Koonunga crenarum*; b, maxilla 1, *K. crenarum*; c, head & rostrum, *Eucrenonaspides oinotheke*; d, head & rostrum, *Stygocarella pleotelson*; e, maxilla 1, *E. oinotheke*; f, whole animal, *Stygocaris townsendi*; g, whole animal, *E. oinotheke*; h, mandible, *E. oinotheke*; i, thoracopod 1, *E. oinotheke*; j, head & rostrum, *S. townsendi*; k, mandible, *S. pleotelson*; l, thoracopod 1, *S. pleotelson*; m, uropod, *S. pleotelson*; n, uropod, *S. townsendi*. (Sources: a–b, redrawn from Zeidler (1985); c, e, g–i, redrawn from Knott & Lake (1980); d, k–m, redrawn from Schminke (1973); f, j, n, redrawn from Morimoto (1977).)

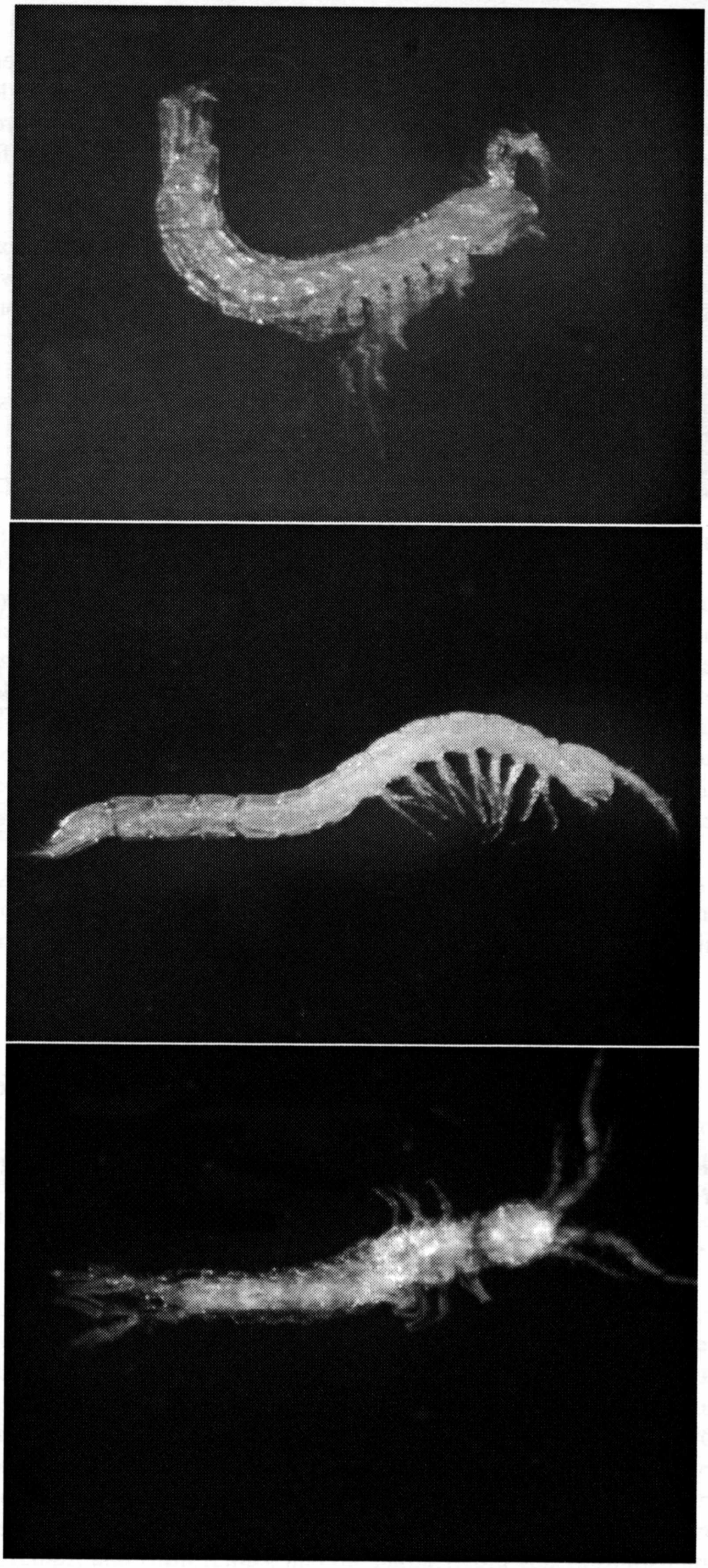

***Figure 15*: top, Parabathynellid from a Canterbury well; centre, Parabathynellid (specimen courtesy of Reece Fowler); bottom, a stygocarid from a southern Hawke's Bay well.**

Copepoda

The Copepoda are a subclass of Crustacea comprising over 10 000 known species (Williamson & Reid 2001). Copepoda are predominantly marine, although 3 of the 10 orders are widespread and abundant in freshwater habitats; Calanoida, Cyclopoida, and Harpacticoida. The first order is common in the plankton only, whereas the latter two are common in benthic habitats of surface waters, and form important components of many groundwater communities.

Harpacticoid and cyclopoid species can be distinguished from one another by examining the length of the antennae, general body shape, and number of egg sacs on the females when these are carried (Chapman & Lewis 1976). The harpacticoids have antennae that do not extend beyond the cephalothorax, the urosome is typically similar in width to the metasome, and the egg sacs of freshwater species are single (Figure 16). By contrast, the cyclopoids (Figures 16–17) have antennae that extend beyond the cephalothorax (but not beyond the metasome), the urosome is narrower than the metasome, and the egg sacs of females are paired.

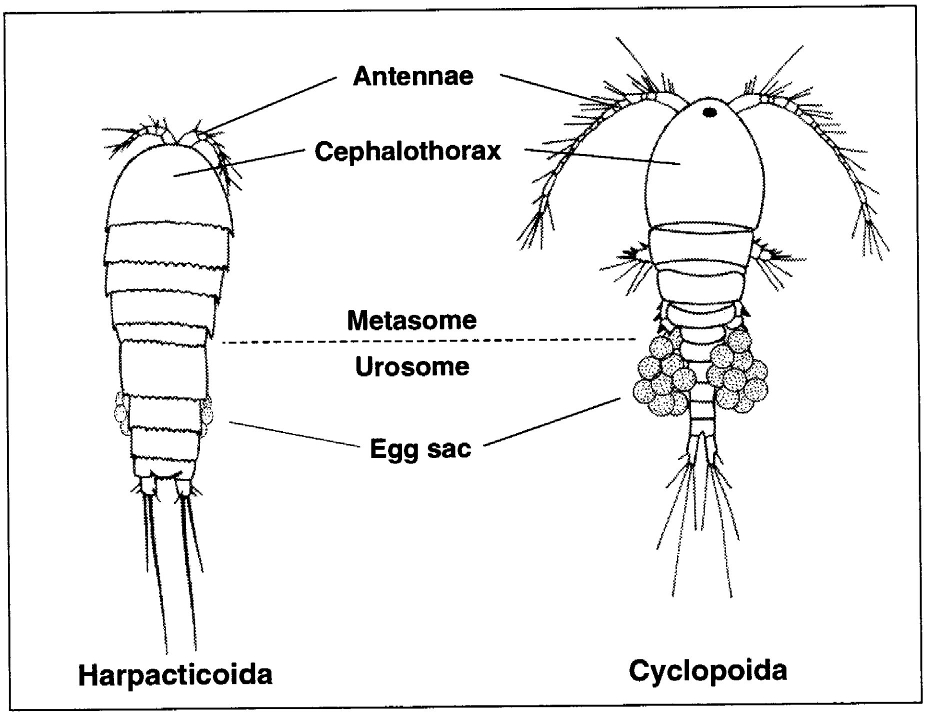

Figure 16**: General morphology of harpacticoid and cyclopoid copepods showing the major distinctions (after Chapman & Lewis (1976) and Shiel (1995)).**

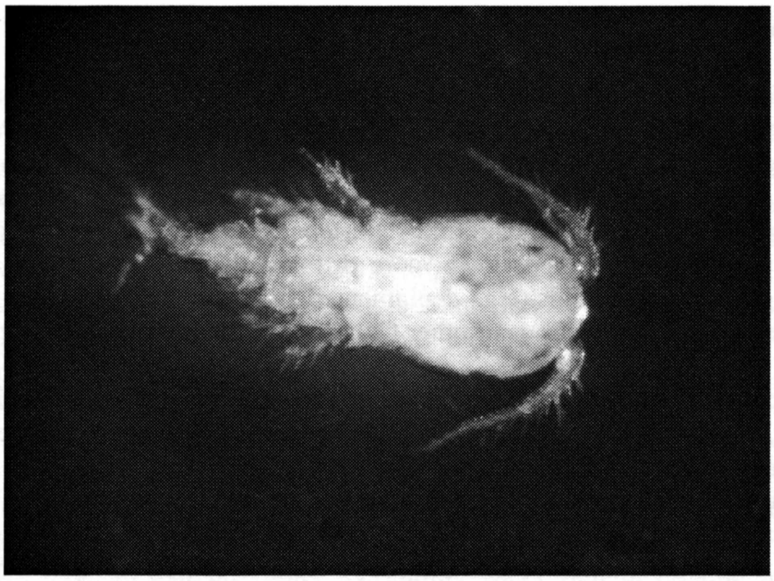

Figure 17: **Dorsal view of a cyclopoid collected from a groundwater well at Burnham, Canterbury.**

Unfortunately, published New Zealand studies that have collected copepod material from hyporheic and groundwater habitats have generally failed to distinguish between Harpacticoida and Cyclopoida. For example, Scarsbrook & Fenwick (unpublished data) found copepods to be major components of the fauna at most of the 17 groundwater wells sampled in Hawke's Bay and Canterbury, but there is no indication of the relative abundance of harpacticoids and cyclopoids. It is also unknown what proportion of the copepod fauna was actually stygobite, versus epigean. Boulton et al. (1997) did distinguish between cyclopoids and harpacticoids in hyporheic samples from five small Waikato, North Island, streams. They found harpacticoids to be more common than cyclopoids.

To date, no New Zealand study has attempted to identify groundwater copepods at a finer level of taxonomic resolution. This is a serious gap in our knowledge of groundwater communities. We must therefore rely on overseas work to provide information on the diversity of these important groups in groundwaters.

Cyclopoida

Lescher-Moutoué (1986) noted that of the roughly 670 species of cyclopoids described from continental freshwaters, about 23% (150) are considered hypogean. However, it is often difficult to characterise species as either hypogean or epigean, without detailed study of life history and distribution, although the absence of ocular pigments can be a reliable indicator of hypogean habits (Lescher-Moutoué 1986).

There are several cyclopoid species recorded from Australian hyporheic habitats, which, because of the faunal affinities between New Zealand and Australia, may also occur in hypogean habitats in New Zealand. This group includes *Australocyclops similis*, *Macrocyclops albidus*, and a possible *Mixocyclops* species (Cooling & Boulton 1993). Of these, *M. albidus* is common in New Zealand ponds and from the littoral zone and benthos of lakes (Chapman & Lewis 1976). The cyclopoids *Eucyclops serrulatus*, *Acanthocyclops robustus*, *A. vernalis*, and *Paracyclops fimbriatus* have all been recorded in hyporheic habitats elsewhere (Dole-Oliver et al. 2000), and have been recorded from New Zealand waters also (Chapman & Lewis 1976). In addition, the cyclopoid genera *Tropocyclops, Diacyclops*, *Microcyclops*, and *Halicyclops,* and the harpacticoid genera *Bryocamptus* and *Attheyella*, are known from interstitial habitats elsewhere (Dole-Oliver et al. 2000) and have representatives recorded from New Zealand (Chapman & Lewis 1976). These taxa are apparently all common to both hyporheic and epibenthic habitats and can, therefore, be classified as stygophiles rather than stygobites.

Harpacticoida

There are 34 families of harpacticoid copepods, with most found in marine habitats (Rouch 1986). Only four families (Gelyellidae, Phyllognathopodidae, Chappuisidae, and Parastenocarididae) are considered wholly freshwater, with other freshwater species belonging to families of mostly marine origin. Rouch (1986) noted a dozen families with known stygobitic species, mostly within three families (Ameiridae, Canthocamptidae, and Parastenocarididae). Determining whether harpacticoid species are hypogean or epigean is even more difficult than for cyclopoids, because the inherent characteristics of the harpacticoids (e.g., depigmented eyes, small size, reduced appendages) are those that are often regarded as adaptations of other Crustacea to the groundwater environment.

Rouch (1986) commented that compared with the growing literature on harpacticoids in other regions, Australia and New Zealand are practically *terra incognita*. Chapman & Lewis (1976) noted the presence in New Zealand of two described species of Phyllognathopodidae, at least 19 species of Canthocamptidae, a single genus of the predominantly marine Diosaccidae, and a number of species in the genus *Nitocra* (Ameiridae). One of the phyllognathids, *Phyllognathopus volcanicus* is found interstitially in the sands of lakeshores in the Taupo-Rotorua region (Chapman & Lewis 1976).

Identification

Many New Zealand freshwater cyclopoids and harpacticoids have, in the past, been considered to be species of cosmopolitan taxa. However, for many taxa it is becoming accepted that this apparent cosmopolitanism is not real, but due to uncritical use of northern hemisphere taxonomic work. Many New Zealand and Australian freshwater taxa have thus been "lumped" with northern hemisphere identities when some are good endemic species (Green & Shiel 1992, Shiel 1995). Many of the New Zealand copepod species recorded to date and, in particular, the cyclopoids, may be hidden under cosmopolitan names. More detailed studies of the fauna are needed to clarify the extent of endemism.

Given the absence of detailed taxonomic treatment of the New Zealand groundwater copepods, the identification of many New Zealand species is currently difficult. In addition, the harpacticoids can be particularly difficult to identify because this involves extensive dissection and removal of all the appendages, including the mouthparts (Chapman & Lewis 1976). This is not a trivial exercise because the adults of most cyclopoid and harpacticoid species are very small (c. 1 mm). However, a key to the identification of New Zealand freshwater cyclopoid and harpacticoid species based on our current understanding was given by Chapman & Lewis (1976), although any identifications of species considered cosmopolitan should be treated with caution. Barclay (1969) and Lewis (1972a, 1972b) provided good descriptions of some New Zealand harpacticoid species.

Ostracoda

Ostracods occur in almost every conceivable habitat in marine, estuarine, and fresh waters. In freshwaters, their habitats include streams, rivers, lakes, springs, caves, groundwaters, temporary ponds, moist organic mats (e.g., among mosses), and even the axial cups of plants like bromeliads (Delorme 2001). Most ostracods are benthic dwellers, living on sediment surfaces, on plants, or interstitially within sediments, where most feed on detritus, although some are herbivores and a few are carnivorous (Delorme 2001). Some are good swimmers, using long, swimming setae on their two antennae for propulsion. Many, however, are truly benthic, having replaced long swimming setae on their antennae with stouter setae or claw-like spines more suited to crawling over the bottom or between sediment particles.

Ostracods are present in all groundwater habitats from fractured rock aquifers, to karst and alluvial aquifer systems, as well as in hyporheic and parafluvial habitats within rivers. Research indicates that species have quite distinct distributions and, apparently, habitat preferences, with highest biodiversity adjacent to rivers and lower diversity in alluvial aquifers more distant from surface rivers (Ward et al. 1994). Other studies indicate that proximity to running water rich in organic matter is important (Rogulj et al. 1994, Rouch & Danielopol 1997). Their distributions are more complicated than simple proximity to rivers or concentration of organic content, however. There appear to be few meaningful correlations between ostracod abundances and individual physical factors (organic content, alkalinity, calcium, oxygen concentration) (Rogulj et al. 1994). Instead, differences in habitat stability in terms of complexes of physico-chemical factors (e.g., water temperature and organic content) and the upwelling or downwelling nature of interstitial flows seem important, with some taxa more common in variable habitats and others more abundant where conditions are more constant (Rogulj et al. 1994, Ward & Palmer 1994).

Worldwide, more than 300 species of ostracods live exclusively in the hypogean habitats (Danielopol & Hartman 1986). Truly hypogean or stygobitic ostracods are recognised by their morphological and/or ecological characteristics. For example, some subsurface ostracods have extremely elongated or triangular and trapezoidal carapaces, sometimes with large dorsal protruberances (see Figure 18). Most hypogean ostracods belong to the Podocopida with many of the common groundwater taxa being largely cosmopolitan in occurrence (Danielopol et al. 1994b). Thus, the Candonidae is regarded as the most diversified family worldwide (Danielopol & Hartman 1986). The second most important hypogean ostracod family is the Cyprididae, with others, such as the Limnocytheridae, Entocytheridae, and Cyclocypridae, also represented.

Ostracods are widely distributed in epigean freshwaters in New Zealand (Chapman & Lewis 1976), as elsewhere in the temperate and tropical world, but hypogean faunas have received almost no attention. There are no hypogean species described from New Zealand, but several have been collected from these habitats in both North and South Islands.

Identification

Although ostracods are a diverse group and have been studied by both zoologists and palaeontologists, their taxonomy is confused. Some of this confusion arises because paleontologists developed a taxonomy based on shell characteristics that are preserved in fossils, whilst zoologists worked with appendages (soft parts), primarily because these structures provide clues to homologies with other crustacean groups, as well as a greater number of valid taxonomic characters. The two approaches have never been fully reconciled and synthesised. Thus, familial and generic diagnoses are widely scattered and the few published keys to extant faunas tend to be incomplete. Perhaps most frustrating is that these keys often use different characters within couplet alternatives and few of the key characters are illustrated adequately.

A number of keys may be useful for identifying our fauna. Chapman & Lewis (1976), Chapman (1963), and Barclay (1968) are the best guides to the New Zealand epigean ostracod fauna. The keys of Pennack (1978) and Williams (1980) to the epigean freshwater ostracods of the United States and Australia, respectively, may also be useful. Delorme's (2001) more recent key to the subfamilies and genera of US podocopid ostracods is extremely useful, as well as presenting some taxonomic notes and a classification of the Order Podocopida.

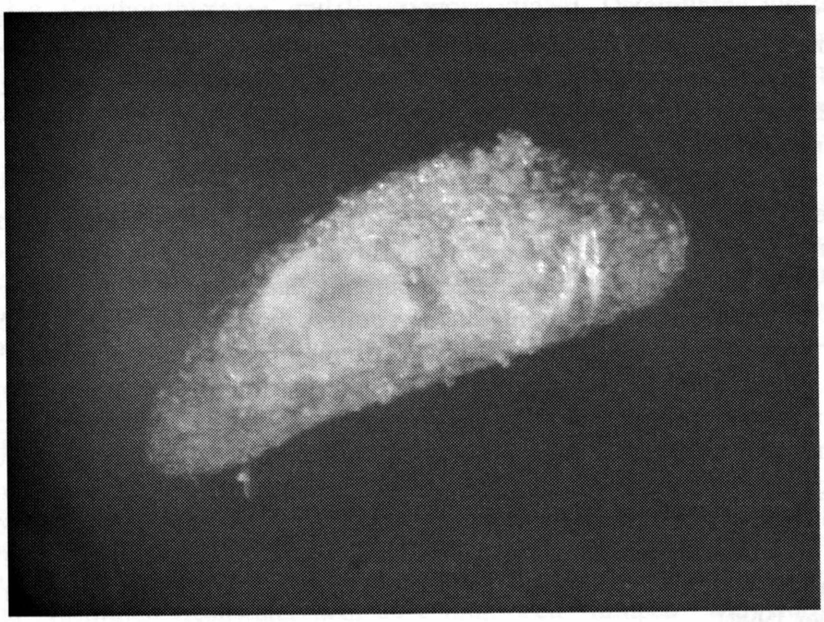

***Figure 18*: An unidentified ostracod collected from a South Canterbury well showing the elongated form often associated with stygobitic species.**

Mollusca

Worldwide, most stygobitic species of molluscs and all groundwater molluscs of New Zealand belong to the prosobranch gastropod family Hydrobiidae (e.g., Bole & Velkovrh 1986). The stylommatophoran gastropod *Hydrophrea academia*, ascribed to the stygofauna of New Zealand by Climo (1974), turned out to be synonymous with the introduced *Helicodiscus singleyanus*, a terrestrial contaminant of Climo's material (Barker 1999). The family Hydrobiidae is represented on all five continents and, with far more than 1000 described species, is the most speciose family of freshwater gastropods. Only a few species live in brackish waters or marine habitats. Most species live in springs and seepages. Hydrobiids are generally small (2–5 mm). Because of their small size, they are pre-adapted to colonise the interstitial spaces of porous and karstic aquifers. There are true groundwater species that have lost their pigment and eyes, and there are surface species, which occasionally have populations living in the groundwater. Because of their small size, very little is known about hydrobiids and every year unknown species are described, even from densely populated, urban areas (e.g., Haase 1993, 2000). Although the family as a whole is widespread, the species very often are not. Many hydrobiids have very restricted ranges. In some cases, the degree of endemism is extremely high, to the extent that a species may occur only in a single valley or even a single spring. This implies that hydrobiid spring and groundwater snails have a very low potential for dispersal.

A few experimental studies (Brendelberger 1992, 1995, Oswald et al. 1991) have identified blue green algae, bacteria, fungi, and green algae, such as diatoms, as the main sources of food of hydrobiids. The ability to live on bacteria and fungi is another prerequisite for the colonisation of the groundwater. It appears that stygobitic hydrobiids can manage to live under almost anoxic conditions (Pospisil 1989). Most species of hydrobiids are probably annual. Only a few marine species exhibit the primitive life cycle including a free larval stage. Most species develop within the egg capsule, still exhibiting the larval stage, and hatch as juvenile snails. Interestingly, ovoviviparity appears to be a quite common mode of reproduction among the species occurring in New Zealand.

Currently, 17 species belonging to 7 genera of hydrobiids are recognised in New Zealand (Climo 1974, 1977), 10 of which are true stygobites (Table 1; see Figure 19 for examples). These species are unpigmented but most of them retain their black eye spots. This suggests that colonisation of groundwater habitats may have occurred relatively recently, in evolutionary terms.

Climo (1974) provided a key to the hydrobiids of New Zealand based on characters of shell, operculum, radula, and their habitat and distribution. This key may work well with this set of species. However, an initial review of museum collections and recent fieldwork (M. Haase, personal observations) indicates that the hydrobiid fauna of New Zealand, including phreatic species, is much more diverse. Because of the small size of these snails and the considerable extent of convergent evolution known from other studies, the characters used by Climo (1974) will almost certainly prove insufficient for unambiguous species identification. Anatomical characters, including the genitalia of both sexes and the digestive system, will also have to be used. In addition, genetic methods, such as allozyme electrophoresis or sequencing of DNA, have proved to be powerful tools in discriminating species and higher taxa and in assessing their relationships (e.g., Haase 1994, Ponder et al. 1994, Hershler et al. 1999).

***Table 1*: Names, habitats, and type locality of 10 described species of stygobitic hydrobiid snails from New Zealand. (Climo (1974) included *Opacuincola troglodytes* in his list of subterranean mollusca. Subsequent work suggests that this is not a true stygobite.)**

Species	Localities
Opacuincola caeca	Caves (Takaka Valley, Nelson)
O. kuscheli	Caves (West of Nelson)
Catapyrgus spelaeus	Caves (West of Nelson)
Kuschelita mica	Wells (Waimea Plains)
K. inflata	Well (Heretaunga Plains)
Potamopyrgus manneringi	Seepages (Waikaretu, Waikato)
P. subterraneus	Well (Ashburton)
P. gardneri	Seepages (Parakau, Northland)
Hadopyrgus anops	Wells and caves (Nelson area)
H. brevis	Wells (Waimea Plains)

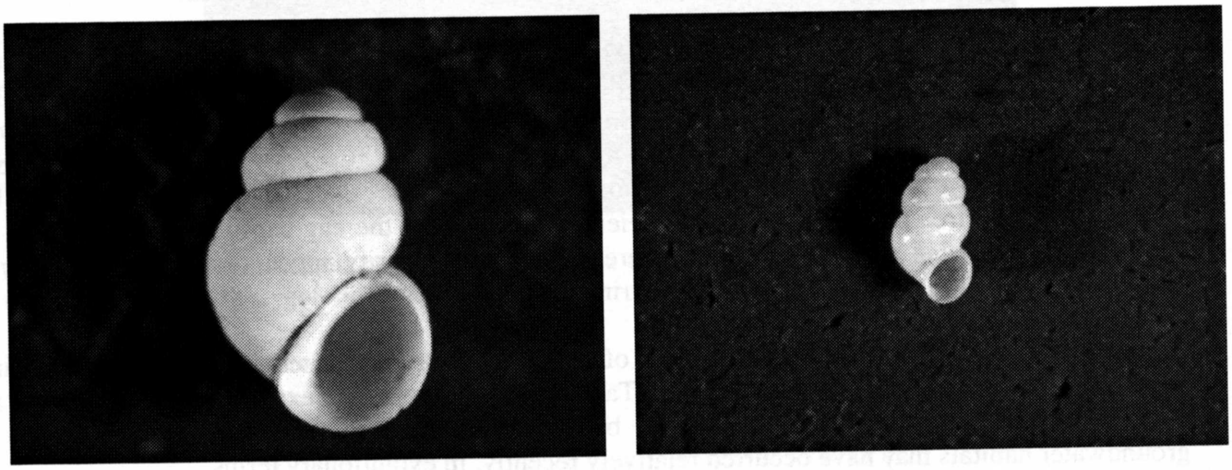

***Figure 19*: Specimens of two stygobitic hydrobiid snails from New Zealand. left, *Opacuinicola* sp.; right, *Catapyrgus spelaeus*.**

Coleoptera

Of the more than 300 000 different species of beetles described worldwide, only about 9500 are aquatic in their adult and/or larval stages. Of these, only around 15 species are known as true stygobites (Spangler 1986). Stygobitic beetles belong to four families (Dytiscidae, Noteridae, Hydrophilidae and Elmidae) and may be distinguished from the surface-inhabiting forms by several features. Firstly stygobites have vestigial eyes or, more commonly, a complete absence of eyes. They usually exhibit greatly reduced, or complete lack of, pigmentation. Exoskeletons are usually thin and soft, and metathoracic wings are often absent or vestigial. Larvae of stygobitic beetles generally lack ocelli (Spangler 1986).

The Dytiscidae have the greatest diversity of stygobitic forms. Spangler (1986) noted nine described species in eight genera. There are three described species of phreatic dytiscids (Hydroporinae: Dytiscidae) in New Zealand. *Phreatodessus hades* and *Kuschelydrus phreaticus* were both described by Ordish (1976) from specimens found in wells in the Nelson City–Waimea River area, including the Maitai River valley. A third species, *Phreatodessus pluto*, was described by Ordish (1991) from a single female from a well at Seadown, South Canterbury. Dr G. Kuschel collected this material during extensive surveys around the Nelson region and other parts of the country in the early 1970s. Despite more recent and extensive sampling of groundwater wells in Canterbury, Nelson, Hawke's Bay, and South Canterbury, only one dytiscid specimen (*Kuschelhydrus phreaticus*) has been obtained (M. Scarsbrook & G. Fenwick, personal observations). This may be due to differences in sampling method between Kuschel and ourselves. Overseas, baited traps have been successful for collecting phreatic dytiscids (Spangler 1986), and this method is worth trialling here to obtain further specimens.

The described New Zealand species are small (5 mm long or less), and lack pigmentation and eyes (Figure 20). Other distinguishing features are a marked atrophy of the wings, including loss of venation, and the presence of long erect setae on the pronotum and elytra (Ordish 1976). Both genera have characteristics diagnostic of the tribe Bidessini. In New Zealand there are two epigean genera in this tribe, *Liodessus* and *Huxelhydrus*.

Adults of the two described New Zealand stygobitic genera are distinguished by the following features.

Phreatodessus: Head evenly rounded in dorsal aspect (Figure 20a). Pronotum constricted posteriorly. Body strongly constricted at junction of pronotum and elytra, not parallel-sided. Length 2.2–2.5 mm, width 0.8–1.0 mm. Larvae of *Phreatodessus hades* have been described from material from a single well in West Nelson. Larvae are 2.2. mm in length (3rd instar). Ocelli are absent. Adults of the two species of *Phreatodessus* are distinguished by geographic range and size of antennal segments. *P. hades*, from Nelson, has antennal segments of approximately uniform size, whereas *P. pluto*, from Canterbury, has antennal segments 3–5 that are smaller than the remainder.

Kuschelydrus: Head not rounded in dorsal aspect (Figure 20b). Pronotum not constricted posteriorly, body parallel-sided. Length 1.5–1.6 mm, width 0.5 mm.

Surface-dwelling dytiscids usually pupate out of water and, presumably, stygobitic dytiscids also pupate out of water in their subterranean habitats (Spangler 1986). If this is the case, pupating dytiscids may be at threat from fluctuating groundwater levels, as may occur under intense irrigation regimes. The saturation of pupation sites may lead to death of the pupa.

Ordish (1976) noted that there is nothing in the structure of the mouthparts to suggest that our phreatic species depart from the normal carnivorous habit of the Dytiscidae. Overseas, phreatic dytiscids have been observed feeding on both live copepods and dead isopods and amphipods.

Elmidae are commonly encountered in hyporheic samples, but as yet no true stygobitic forms have been discovered. There are several known genera of true groundwater Elmidae around the world (Spangler 1981, 1986).

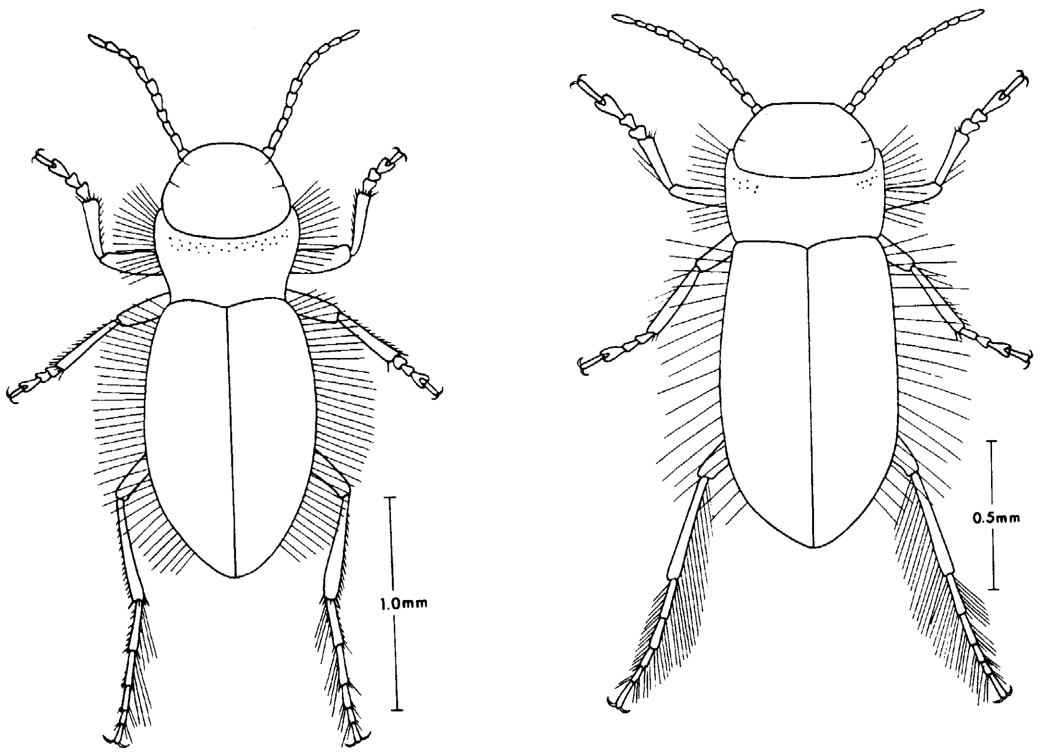

Figure 20: **left, *Phreatodessus hades*; right, *Kuschelydrus phreaticus*. Redrawn after Ordish (1976).**

Acari

Several groups of Acari have made the transition to a fully aquatic lifestyle, including all of the Hydracarina and Halacaroidea, as well as many species of the Oribatida, Astigmata, and Mesostigmata (Harvey 1998). In New Zealand, only the Hydracarina and Halacaroidea have so far yielded described stygobitic species. Indeed, there is only a single described halacarid mite from groundwaters in this country (*Lobohalacarus subterraneus* Bartsch 1995), so the overwhelming majority of our stygobitic mite fauna belongs to the Hydracarina (water mites).

We deal very superficially with the Acari in this guide, and refer readers to more substantial works for detailed information. Harvey & Growns (1998) provided a simple guide to the identification of Australian water mite families and we recommend this as a starting point for work with aquatic mites. An interactive guide to families and subfamilies of water mites in Australia is available at www.lucidcentral.com. A more general key to freshwater arachnids (spiders and mites) is also available.

Hydracarina

The Hydracarina is the most diverse group of the Acari in freshwaters (Di Sabatino et al. 2000). There are currently over 5000 species grouped into eight superfamilies (Di Sabatino et al. 2000). Schwoerbel (1986) recorded 471 species from groundwaters around the world, but, the actual number now exceeds 500 (Cook 1991). Seventy stygobitic water mite species have been described from New Zealand (Table 2). Therefore, it appears that New Zealand is particularly rich in stygobitic water mites, having at least 10% of the world's described fauna.

The life cycle of the Hydracarina is unique among the Acari, with a parasitic/phoretic larva, two pupa-like resting stages, and free-living predaceous deutonymphs and adults. All Hydracarina are predators at deutonymph and adult stages. Schwoerbel (1986) suggested that the life cycle requirements of Hydracarina might limit them to relatively shallow hyporheic habitats, where the insects, which form the hosts of the parasitic larval Hydracarina, can be found. However, Cook (1991) described a rich Hydracarina fauna in groundwater wells near Nelson, suggesting that life history in some groups does not necessarily require insect hosts. It should be noted, however, that two insect species (Dytiscidae) occur in New Zealand groundwater wells. Cook (1991) suggested that an alternative strategy may be to provide eggs with sufficient food resources to allow the bypassing of the larval stage. Cook (1991) observed such a large egg within a single *Taintaturus stoutae* female.

It seems likely that water mites have few natural enemies, probably because of distasteful and unpalatable substances secreted by the idiosomal glands (Di Sabatino et al. 2000).

In the water mites, adaptations to a phreatic or hyporheic habitat include tendencies to miniaturisation, to develop an extensive exoskeleton (sclerotisation) in membranous species, lack of pigmentation and reduced or absent eyes (Schwoerbel 1986). A reduced fecundity and negative phototaxis occur in some species.

Based primarily on collections made around New Zealand in 1982, Cook (1983) described 93 water mite species from running waters, a large number of which were found to be hyporheic. Using known characteristics of hypogean taxa (i.e., loss of integumental pigmentation and reduction or complete loss of eye pigment) 36 species were designated as hyporheic/interstitial (i.e., stygobite). Sampling was limited to the top 45 cm of stream beds. Recent extensive sampling of the hyporheic zone of several Otago streams has found a highly diverse hydracarinid mite fauna to depths of 50 cm (Dean Olsen, personal communication).

From material collected by G. Kuschel from several Nelson wells, Cook (1991) described 27 species, 21 of which were new to science, including 8 new genera and 1 new family. Cook (1991) found little duplication between species occurring in the wells and those previously reported by Cook (1983) in the more superficial hyporheic zone of New Zealand streams, suggesting that relatively distinct faunas inhabit these two types of ground waters. The rich diversity of water mites in groundwaters of New Zealand is second only to that of Japan. Of particular significance is the subfamily Notoaturinae (Cook 1991). Members of this subfamily occur in both superficial and interstitial waters in major regions that were part of Gondwanaland. Slightly over 100 species are known, with well over half that number (58) collected in New Zealand. Of this latter number, 23 species occur only in the subterranean waters. The New Zealand members of the subfamily are distinct from those of other regions, suggesting radiation since the split from Gondwanaland. In New Zealand, the Notoaturinae, with the exception of *Colubaturus diamphida*, may be characterised by their possession of a dorsal shield composed of six sclerites (see Figure 21); a single anteromedial plate; a single posteromedial plate and two pairs of lateral platelets (Cook 1991).

Table 2: **List of described sygobiont water mites (Hydracarina) from hyporheic (H), phreatic (P), and cave (C) habitats in New Zealand.**

Super Family: Family	Genus & species	Habitat
Hydryphantoidea		
Hydryphantidae	*Euwandesia tenebrio*	H (Cook 1983)
Lebertioidea		
Anisitsiellidae	*Zelandotonia orion*	P (Cook 1992)
Limnesiidae	*Limnesia birgelda*	H (Cook 1983)
	L. testacea	H (Cook 1983)
	L. halcarda	H (Cook 1983)
	L. crowelli	H (Cook 1983)
Stygotoniidae	*Stygotonia ambigua*	P (Cook 1992)
Hygrobatoidea		
Hygrobatidae	*Notohygrobates kathrynae*	H (Cook 1983)
	Hopkinsobates suzannae	H Cook (1983), Schwoerbel (1984)
	Aciculacarus amilis	H (Cook 1983)
	Zelandobates imamurai	H (Schwoerbel 1984)
Pionidae	*Schminkea pacifica*	H (Schwoerbel 1984), P (Cook 1992)
	Twinforksella tura	P (Cook 1992)
Aturidae: Notoaturinae	*Planaturus setipalpis*	H (Cook 1983)
	P. lundbladi	H (Cook 1983)
	P. rugosus	P (Cook 1991)
	Taintaturus hopkinsi	H (Cook 1983), P (Cook 1991)
	T. accidens	H (Cook 1983)
	T. abditus	H (Cook 1983)
	T. projectus	H (Cook 1983)
	T. zelandicus	P (Cook 1991)
	T. livingstoni	P (Cook 1991)
	T. brevipalpis	P (Cook 1991)
	T. lembus	P (Cook 1991)
	T. stoutae	P (Cook 1991)
	Abelaturus cornophorus	H (Cook 1983)
	A. ogalus	P (Cook 1991)
	Omegaturus longipalpis	H (Cook 1983)
	Neotryssaturus pallidus	H (Cook 1983)
	Pseudotryssaturus planus	H (Cook 1983)
	P. anchistus	H (Cook 1983)
	Evidaturus exilis	H (Cook 1983)
	E. scopticus	H (Cook 1983)
	Piotaturus alvecaudatus	H (Cook 1983), P (Cook 1991)
	P. bovalus	H (Cook 1983)
	Paratyssaturus minutus	H (Cook 1983)
	P. zodelus	H (Cook 1983)
	P. morimotoi	C (Imamura 1979)
	P. cantermus	P (Cook 1991)
	Uralbia gracilipes	H (Cook 1983)
	U. parva	H (Cook 1983)
	U. projecta	H (Cook 1983, Schwoerbel 1984)
	U. filipalpis	H (Schwoerbel 1984)
	Zelandalbia imamurai	H (Cook 1983, Schwoerbel 1984)
	Z. hopkinsi	C (Imamura 1978)
	Z. acuta	P (Cook 1991)
	Hestaturus ovalis	P (Cook 1991)
	Bleptaturus magnipalpis	P (Cook 1991)
	Colubaturus diamphida	P (Cook 1991)
	Zelandopsis aturoides	H (Schwoerbel 1984)
	Z. morimotoi	C (Imamura 1977)

Arrenuroidea		
Momoniidae	*Neomonomomonia torquipes*	H (Cook 1983)
	N. hopkinsi	H (Cook 1983)
	N. benova	H (Cook 1983)
	N. paramecia	H (Cook 1983, Schwoerbel 1984)
	N. rotunda	H (Schwoerbel 1984), P (Cook 1992)
	Partidomomonia polyplacophora	H (Cook 1983)
	P. ramseyi	P (Cook 1992)
	Momonia hopkinsi	H (Schwoerbel 1984)
Mideopsidae	*Nudomideopsis nobilis*	P (Cook 1992)
	N. kuscheli	P (Cook 1992)
	N. parva	P (Cook 1992)
	Paramideopsis kyphus	P (Cook 1992)
	Kuschelacarus ovalis	P (Cook 1992)
	Mideopsis forkensis	C (Imamura 1977)
	Guineaxonopsis serratipalpis	H (Cook 1983)
	G. ramsayi	H (Cook 1983)
	G. confusus	H (Schwoerbel 1984)
Arrenuridae	*Arrenurus zelandicus*	H (Cook 1983), P (Cook 1992)
Athienemanniidae	*Anamundamella zelandica*	P (Cook 1992)

Halacaridae

Freshwater halacarid mites have very different morphological, biological, and ecological characteristics from the Hydracarina (Di Sabatino et al. 2000). Halacarids originated from marine littoral ancestors that secondarily invaded freshwaters, mainly through groundwaters. The halacarid fauna comprises two families, 21 genera, and about 60 worldwide species. Halacarids usually have a 1 year life-span, with only one generation per year. They go through one larval and one to three nymphal stages (Bartsch 1986).

Bartsch (1995) described *Lobohalacarus subterraneus* from Livingston's well, at Brightwater near Nelson. The genus *Lobohalacarus* is worldwide in distribution, and members of the genus are found in a variety of habitats, including hyporheic habitats. The most obvious characters, such as extensive armouring, enlarged articular membranes, and very delicate, long claws, are thought to be associated with, or adaptations to, the conditions of the groundwater habitat.

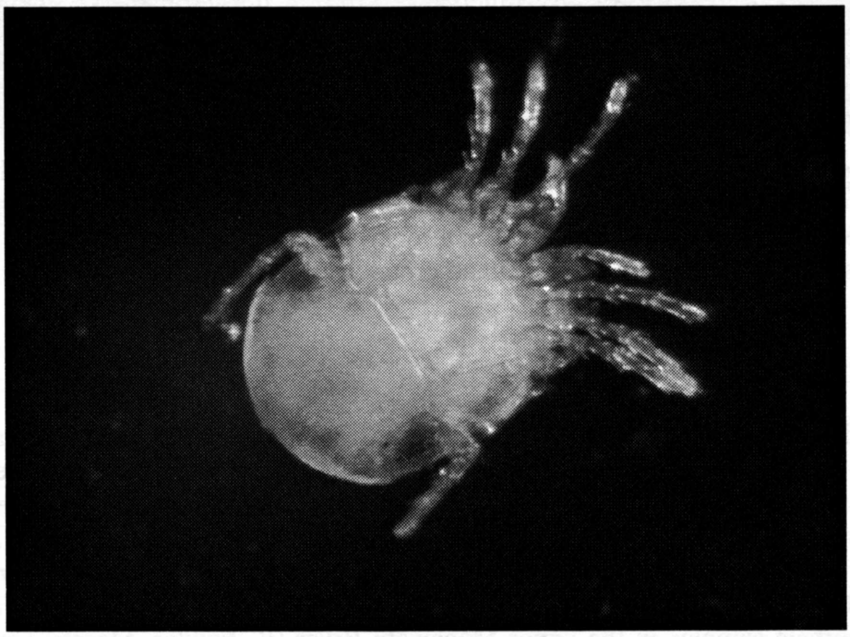

***Figure 21*: Notoaturinid mite from a South Canterbury well.**

Worms and flatworms

Oligochaeta

In Australasia, the Oligochaeta are represented in freshwaters by the families Aeolosomatidae, Haplotaxidae, Lumbriculidae, Phreodrilidae, Naididae, and Tubificidae (Brinkhurst 1971). Of these families, the Naididae appear to be poorly represented in Australia, with particularly low diversity in Tasmania (Pinder 2001). In contrast, New Zealand has at least nine naidids (twice that of Tasmania), despite its greater isolation (Pinder 2001).

The family Phreodrilidae is particularly diverse in Australia with more than 50 species. There are seven species in New Zealand, with two of these recorded from groundwaters. *Phreodrilus subterraneus* is a true stygobite, whereas *P. beddardi* appears to be a stygophile, because it has been recorded in surface and groundwaters (Pinder & Brinkhurst 1997). Beddard (1892) first described the family based on two individuals of *P. subterraneus* collected from a well near Ashburton, Canterbury. The Phreodrilidae are mostly sediment-dwelling freshwater oligochaetes that occur in Australia, South America, Africa, New Zealand, and Sri Lanka, as well as many southern oceanic islands (Pinder & Brinkhurst 1997). This global distribution indicates a Gondwanan origin, with evidence of a more recent dispersal (Pinder 2001).

In a review of the stygobitic oligochaete fauna of the world, Juget & Dumnicka (1986) noted 66 species in seven families (Aeolosomatidae, Potamodrilidae, Haplotaxidae, Lumbriculidae, Dorydrilidae, Tubificidae, and Enchytraeidae). More recently, Giani et al. (2001) reported 57 species that can be classified as stygobites in southern Europe alone, suggesting the global diversity far exceeds initial estimates (e.g., Juget & Dumnicka 1986). Indeed, Giani et al. (2001) estimated that, when records from other areas of the world (e.g., North America, Africa, Europe) are added, a total of 96 stygobitic freshwater oligochaetes are known in the world (they excluded Australasia from their estimate for some reason). It should be noted that it is often difficult to make a clear separation between stygobitic and stygophilic oligochaetes. For example, the features that distinguish stygobitic crustaceans from epigean forms, such as absence of eyes, lack of pigmentation, and elongation of body, do not distinguish between stygobitic and epigean oligochaetes. Giani et al. (2001) noted that very few species of Naididae are stygobites.

Groundwater habitats have played an important role in the evolution of freshwater oligochaetes. Indeed, Lafont (1989) suggested that groundwater might have been the primary source of colonisation of all freshwater oligochaete ancestors. Whether this is true or not, groundwater habitats are a rich source of oligochaete diversity, and many of the more "interesting" species in Australasia seem to be predominantly groundwater-dwelling forms (Brinkhurst 1971).

Sampling in New Zealand groundwaters has shown oligochaetes to be quite widespread. Sinton (1984) found oligochaetes in most of the wells he sampled near Templeton, Canterbury. We have found an unidentified haplotaxid species at Templeton, and have collected specimens of Naididae (Figure 22) from several other locations in Hawke's Bay, Canterbury, and South Canterbury. There is much work to be done on this important group in New Zealand groundwaters.

Polychaeta

Hartmann-Schröder (1986) listed three stygobitic species of *Namanereis* (Namanereinae: Nereidae), one from caves of Papua New Guinea (*N. beroni*), another from subterranean waters of several Caribbean islands (*N. hummelincki*), and a cosmopolitan species (*N. pontica*). A general feature of these stygobitic species is a reduced body size, reduced size and number of appendages, and absence, or reduction, of eyes. New Zealand has one described freshwater polychaete, *Namanereis tiriteae* (Winterbourn 1969). It is relatively small and lacks eyes (Figure 22). These features, along with its collection in hyporheic samples in the upper Manawatu River (R. Fowler, Massey University, pers. comm.), suggest it should be added to the list of stygobitic polychaetes. In a recent revision of the

Namanereidinae, Glasby (1999) placed *N. tiriteae* within the same clade as the known subterranean species of *Namanereis*. Nothing is known of the biology of *N. tiritiae*.

Hirudinea

All known stygobitic species of Hirudinea belong to the family Erpobdellidae (Sket 1986). Troglobitic species or populations have been found in the northeast Mediterranean region, Japan, and Texas (Sket 1986). New Zealand has two recorded freshwater species of Erpobdellidae (Mason 1976): *Dina maoriana* Mason, known from the Opihi River, South Canterbury, and *Barbronia weberi* (Blanchard), which has been found in manmade fish ponds and aquaria in Hawke's Bay. There are no known records of stygobitic leeches in New Zealand.

Platyhelminthes

Worldwide there is a substantial stygobitic flatworm fauna (Gourbault 1986). As in many other groups, stygobitic species are recognised by a reduction in pigmentation and a loss or reduction of eyes.

Sinton (1984) found turbellarians in some wells near Templeton, Canterbury. The samples were sorted live, suggesting these turbellarians were aquatic rather than terrestrial contaminants. Sinton (1984) used a phreatobiological net, which closely fitted the internal diameter of the well, and may have been a more appropriate sampling technique for this tightly adhering species than pumping. We have carried out reasonably extensive pump sampling of wells at Templeton, and elsewhere in New Zealand, and have collected no further turbellarians.

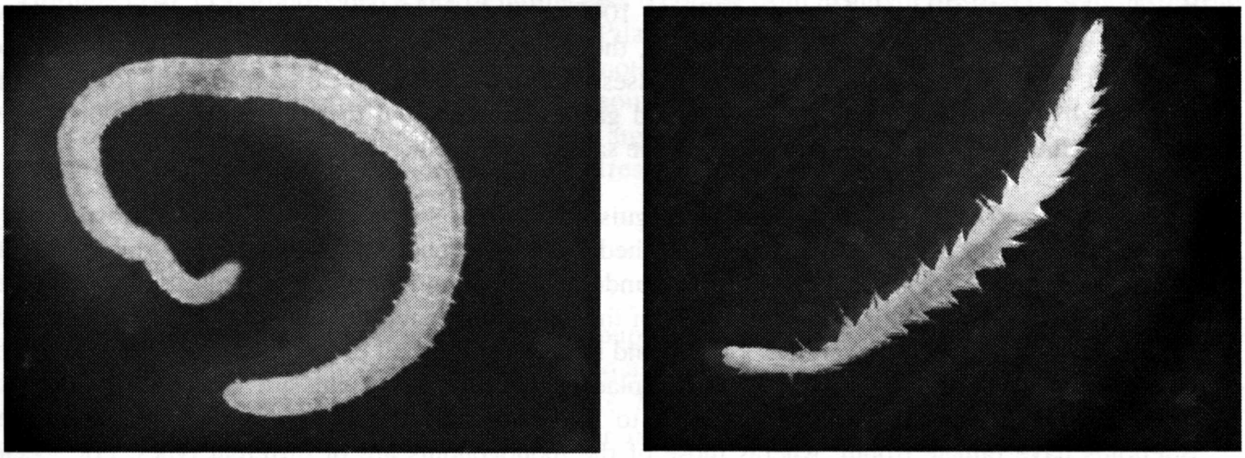

***Figure 22*: left, Naidid oligochaete from a South Canterbury well. right, *Namanereis tiriteae* (specimen courtesy of Reece Fowler).**

Other groups (Meiofauna)

Rotifera

Although there have been a number of recent studies of rotifers from New Zealand littoral and planktonic habitats (e.g., Duggan et al. 1998, 2002), their taxonomic composition from groundwaters has been neglected to date. Studies of hyporheic fauna in New Zealand have generally used mesh sizes greater than the 40 μm required for collection of rotifers. However, one recent study by Ryan (2001), examined rotifer species composition from the interstitial waters of the Whangamarino wetland, which is perhaps likely to show some affinities with true groundwater taxa.

In Europe, rotifers of the classes Monogononta and Digononta (bdelloids) are both highly abundant and diverse in groundwater habitats (e.g., Schmid-Araya 1995, 1998, Robertson et al. 2000). Robertson et al. (2000), examined the diversity of invertebrates from seven European streams, and noted that the rotifers typically dominate these systems. In a review of lotic rotifer species, Ricci & Balsamo (2000) noted that few species were exclusive to the hyporheic, but were also common inhabitants of the epibenthos and periphyton (cf. Duggan et al. 1998, 2001). Many of the species listed are apparently cosmopolitan in distribution, and thus a high proportion has previously been recorded from New Zealand. Fifty-four of the 114 monogonont rotifer species on this list, and 32 of the 40 bdelloids, have been recorded here (cf. Shiel & Green 1996, Duggan et al. 1998). Most of the species recorded are typical inhabitants of vegetated habitats here (Duggan et al. 1998, 2001). It is not known if there is an endemic rotifer component in groundwater habitats in New Zealand. In common with New Zealand planktonic and periphytic rotifer communities, and with the Whangamarino wetland study of Ryan (2001), the groundwater community is also likely to have affinities with the Australian fauna.

Rotifers are small (ranging between 100 and 1000 μm long), unsegmented, bilaterally symmetrical animals with two distinctive features. Firstly, the apical head region, called the corona, is ciliated. Secondly, a muscular pharynx, the mastax, possesses a hard set of jaws called the trophi. Rotifers may superficially resemble ciliated protozoans and gastotrichs although these organisms do not possess trophi and their ciliation is not distributed in the same way (Wallace & Snell 2001).

Monogonont and digonont rotifers are distinguished by their single or paired ovaries, respectively. However, they can be more easily distinguished by the morphology of the trophi, which are hard cuticularised "teeth". These can be observed under a compound microscope by placing the specimen on a slide under a coverslip. Some "erosion" of the body may be required to observe the trophi. To do so, a coverslip is fixed to the slide at the top and bottom using small drops of nail varnish, and a drop of sodium hypochlorite (NaOCl, 5–10%) is placed on the left or right side of the coverslip. The sodium hypochlorite can be drawn through to the other side of the coverslip using filter paper. Bdelloids have ramate trophi, wheras those of the monogononts are of different types. For species identifications, bdelloids must be identified alive, because their morphology is generally distorted by fixatives.

Simple keys to genera are provided by Turner (1999) and Ricci & Melone (2000). Shiel (1995) and Donner (1965) provide useful keys to the species recorded from New Zealand and Australian waters. Most species of monogonont rotifers recorded from New Zealand to date can also be identified using Shiel (1995). Other species can be identified using Koste (1978) or the series Guides to the microinvertebrates of the continental waters of the world (e.g., Segers 1995, De Smet & Pourriot 1997).

Tardigrada

The Tardigrada are a phylum of small invertebrates (up to about 500 μm), commonly called "water bears". Tardigrades have been considered to be closely related to a number of groups in the past, including nematodes, rotifers and annelids, although recent molecular studies show them to be a sister group of the arthropods (Garey et al. 1996, 1999). Tardigrades are one of the lesser known phyla of invertebrate animals due to difficulties with both collecting and culturing, although about 800 species have been described to date from marine, terrestrial, and freshwater habitats (Nelson 2001). Approximately 50 to 70 of these species have been recorded from the meiobenthos of lotic habitats (Nelson & Marley 2000). Three classes of Tardigrada are recognised: Heterotardigrada, Mesotardigrada, and Eutardigrada (Nelson 2001). The Heterotardigrada comprises mainly marine and armoured terrestrial taxa, and Mesotardigrada is known only from a hot spring in Japan, since destroyed by an earthquake (Nelson 2001). The Eutardigrada encompasses most of the freshwater species. Heterotardigrada are mainly distinguished from the Eutardigrada by having a number of paired sensory appendages on their head regions and over their bodies (see Nelson, 2001 for diagrams). The New Zealand Heterotardigrada comprises some species from the genus *Echniscus* (Horning et al. 1978), which may be found in freshwaters (Nelson 2001). Three genera of Eutardigrada are exclusively freshwater *Dactylobiotus*, *Psuedobiotus*, and *Thulinia* (Nelson 2001), although none of these genera appear to have been recorded in New Zealand to date. Other known aquatic genera from New Zealand are *Hypsibius*, *Isohypsibius*, and *Macrobiotus*. Little is known of the biogeographical distributions of tardigrade species, mainly due to a paucity of data and the uncertainty of identifications, although many species appear to be cosmopolitan (Nelson & Marley 2000).

Tardigrades have a bilaterally symmetrical body with four pairs of lobopodous legs that typically terminate in claws. Mature adults are typically between 250 and 500 µm, although some are larger (Nelson & Marley 2000, Nelson 2001). Tardigrade taxonomy is based primarily on the morphology of the claws, buccal-pharyngeal apparatus, cuticle, and eggs. Nelson & Marley (2000) illustrated the claws and buccal-pharangeal apparatus of the major genera of eutardigrades typically found in freshwater habitats.

Horning et al. (1978) provided a key of tardigrades recorded from mainly terrestrial or semi-terrestrial habitats in New Zealand, and Pilato (1996) and Pilato & Binda (1996, 1997) provided further records and redescriptions. However, Nelson (2001) noted that the distinction between freshwater and terrestrial species is sometimes unclear because some species can live in a wide range of habitats. For example, species recorded from moist mosses are often found in aquatic habitats. Nelson (2001) provided a key to the genera of North American freshwater and terrestrial species.

Nematoda

Nematodes are the most abundant meiofaunal group, comprising some 100 000 species (Eder 1986). It is worth noting that morphological adaptations to a stygobitic way of life in other meiofaunal groups (e.g. small size, long, narrow body shape) are fundamental features of nematode anatomy and physiology (Figure 23). Furthermore, the water table, which commonly separates terrestrial from stygobitic populations, is no barrier to nematodes, many of which are equally happy in damp soils. As a result, terrestrial, limnic, and even parasitic nematodes (e.g., mermithids) can turn up in groundwater samples (Eder 1986). However, only those species that have physiological characteristics enabling them to maintain populations in groundwater habitats can correctly be termed stygobites. Eder (1986) listed 33 species of stygobitic nematodes.

Adult freshwater nematodes are about 0.5–2 mm long. Most nematodes are bisexual, though parthenogenesis and a form of self-fertilising hermaphroditism are common (Traunspurger 2000). There is limited information on the life history characteristics of aquatic nematodes, and our knowledge of stygobitic and stygophilic nematodes is even more limited. Within the Nematoda, all trophic resources are utilised with generalists and food specialists represented.

Based on our limited sampling around New Zealand, it appears that nematodes are widely distributed in groundwaters throughout the country, but they are generally in low numbers. Eder (1986) noted that the availability of food resources is a key determinant of nematode distribution, and suggested that the often resource-poor nature of groundwater ecosystems constitutes an extreme environment for nematodes in relation to food supply.

Figure 23: **Nematode from a Hawke's Bay well.**

Biodiversity of New Zealand groundwaters

This review of the New Zealand groundwater invertebrate fauna indicates that 102 formally described invertebrate species can currently be classified as "stygobites" with some degree of confidence (Table 3). This number is sure to increase dramatically with further investigation because many freshwater habitats have been poorly represented in past sampling work, and several groups are currently the focus of taxonomic reviews. Of course, the true test of whether a species is an obligate groundwater species is to determine whether self-sustaining populations of the species carry out their entire life cycles within groundwaters (Gibert et al. 1994). This is clearly beyond the state of our knowledge at this point in time. However, based on morphological evidence, observations in the field, frequency of collection, and knowledge of related taxa overseas, we believe our classifications are consistent with similar reviews overseas.

***Table 3*: List of formally described stygobitic species from New Zealand groundwater habitats.**

Taxonomic group	Described species	List of species
Amphipoda	4	*Phreatogammarus fragilis, Paracrangonyx compactus, P. winterbourni, Paraleptamphopus subterraneus*
Isopoda	4	*Cruregens fontanus, Phreatoicus typicus, P. orarii, Neophreatoicus assimilis*
Syncarida	7	*Atopobathynella compagana, Hexabathynella aotearoae, Notobathynella chiltoni, N. hineoneae, N. longipes, Stygocaris townsendi , Stygocarella pleotelson*
Mollusca	10	see Table 1 for list
Coleoptera	3	*Phreatodessus hades, P. pluto, Kuschelydrus phreaticus*
Acari	71	see Table 2 for list of Hydracarina, *Lobohalacarus subterraneus*
Oligochaeta	2	*Phreodrilus subterraneus, P. beddardi*
Polychaeta	1	*Namanereis tiritiae*
Total	102	

In an attempt to address the question of how the diversity of our fauna compares with the rest of the world, we estimated global groundwater biodiversity by counting the number of freshwater stygobitic species recorded by Botosaneanu (1986). Within the groups that are covered in this review there are 3410 described species. Although out of date, this estimate indicates that New Zealand's contribution to world groundwater biodiversity is disproportionately high (i.e., on the order of 3% of the world's fauna is described from New Zealand, which makes up only 0.18% of the world's land area).

Comparing the composition of the world groundwater fauna with that of New Zealand (Figure 24) reveals two obvious points of difference. Firstly, a large proportion of our fauna (70 species) is made up of water mites (Hydracarina). This partly reflects the enormous contribution of Dave Cook, and others, to the description of our mite fauna. However, many of the species described by Cook (1991, 1992) came from only a few driven wells around Nelson (South Island), suggesting an even greater diversity of these animals awaits collection from other areas of New Zealand.

Secondly, one of the most striking omissions from our described fauna is the Copepoda. This is an important group worldwide. We know from sampling of alluvial aquifers and hyporheic zones that copepods are an important component of groundwater and hyporheic assemblages, yet we have little or no information on the taxonomy and biology of this group in subterranean habitats in New Zealand. At present most New Zealand researchers are unable to identify specimens below the level of order (i.e., Harpacticoida, Cyclopoida). This paucity of information and expertise needs to be rectified as soon as possible.

Many of our other groups have received little attention beyond the original works in the late 19th century. For example, Beddard (1892) described an entire family of oligochaetes (Phreodrilidae) based on a specimen of *Phreodrilus beddardi* from a well in mid Canterbury. There has been no further taxonomic work on New Zealand's groundwater oligochaete fauna since. Other groups are faring somewhat better. Gaps in the taxonomy of Amphipoda, Isopoda, and Mollusca in New Zealand groundwater habitats (including springs) are currently being addressed.

Groundwaters in New Zealand constitute a huge freshwater resource that is managed primarily for human uses (e.g., provision of potable water and water for irrigation). It is hoped that this guide will provide scientists and managers with a gateway to the world to be found beneath our feet, stimulate work on the many interesting aspects of biology, systematics, and ecology that are as yet unexplored, and provide a basis for the effective management of the intrinsic values of New Zealand's groundwater resources.

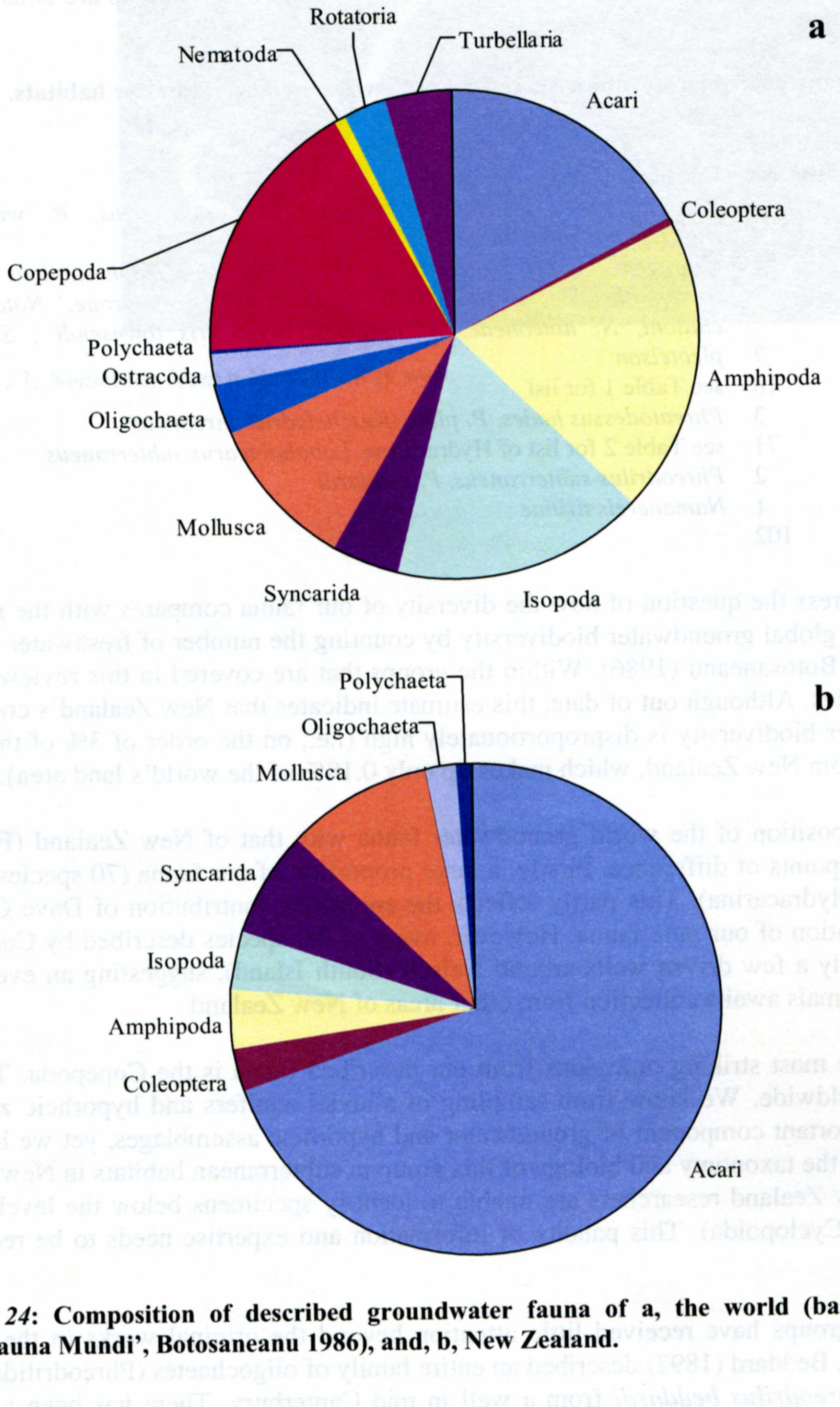

***Figure 24*: Composition of described groundwater fauna of a, the world (based on estimates from 'Stygofauna Mundi', Botosaneanu 1986), and, b, New Zealand.**

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