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Charles Chilton and the discovery of 'well-shrimps' in New Zealand: a case study of serendipity and contingency

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Abstract: the late19th century discovery in New Zealand of diverse communities of the subterranean Crustacea referred to colloquially as 'well-shrimps' represents a significant case of contingency and serendipity in speleobiology. They were discovered in 1881 and described by Charles Chilton (1860–1929), then a young Canterbury College (Christchurch) M.A. student studying crustacean taxonomy. These were the first groundwater (phreatic) fauna reported in the Southern Hemisphere. The finding significantly extended the known global range and ecological richness of aquatic subterranean ecosystems. While interest elsewhere prioritized their taxonomy and classification, Chilton spent the next fifteen years also considering their zoogeography, ecology, and evolution. He did this in his spare time balancing school teaching and research, and despite a physical disability that limited his ability to do fieldwork. He received specimens and information from others, especially William Walter Smith (1852–1942), an estate gardener and competent amateur naturalist whose employment at the time enabled him to travel and make collections and observations at various locations around South Island. Chilton's observations and perceptive insights on these (and on similar subterranean Crustacea found in Europe) were ahead of their time, potentially advancing speleobiology if heeded. But his work was underappreciated and it did not have the impact that it deserved. This is attributed to multiple factors, primarily the domination of American and French non-Darwinian thinking in this sub-science, the contemporary emphasis on classical taxonomy within biology, blinkered insular attitudes towards colonial science, and wider social factors. This case-study illustrates how scientific discovery can be shaped by the complex interplay between serendipity, individual enterprise, and a multiplicity of contingent factors.

Keywords: Amphipoda; artesian; Canterbury Plains; Darwin; evolution; groundwater; Frederick Hutton; Isopoda; natural selection; Packard; Parker; phreatic; Putnam; Racovitza; rudimentation; William Smith; George Thomson; well-shrimp.

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***In the fields of observation, chance only favours the mind which is prepared** (Louis Pasteur, 1854)*

Introduction

This paper contributes to a history of British speleobiology from a 'history of biology' perspective, the contention from the outset being that a "*more enlightening and instructive picture can be seen if the history of British and Irish speleobiology is approached from* [this] *perspective*" (Moseley, 2021 p.19). With the exception of Moseley (2022), previous articles have dealt with pre-Great War speleobiology (Moseley, 2014a, b; 2015; 2021; 2024). The present review of the work of the English-born New Zealand naturalist Charles Chilton (1860–1929) continues the study of this period.

Chilton's life and career spanned the period from Darwin to the end of the post-Great War decade. Throughout those years, speleobiology remained primarily descriptive, focussed on the collection, taxonomy, and occurrence records of those blind depigmented animals that were presumed to represent the 'true' subterranean biota: little attention was paid to entire subterranean communities (Moseley, 2007, 2022 p.40; Romero, 2009, p.146; Dumnika *et al*., 2020). Naturalists in the United States and Continental Europe were describing the biota of what are now known to be 'hot spots' of subterranean species diversity, and it was believed that specialized subterranean species were restricted to such temperate northern latitudes (Racovitza, 1907, p.458). In practice, subterranean fauna could be sampled only in caves and wells, and 'cave fauna' and 'well fauna' were looked upon and investigated as different zoological entities. The vast physical extent and ecological heterogeneity of the underground realm – and the worldwide distribution, diversity, and abundance of subterranean biota – were not yet recognized and understood.

In Britain, where caves and underground waters harbour few blind, highly adapted species, there was little interest. Investigations were severely limited in scope, consisting of opportunistic collecting and a few localized faunal surveys aimed, as elsewhere, at discovery of blind forms (Moseley, 2024).

Alongside fieldwork there was emphasis on anatomical descriptions of the degenerate visual apparatus of blind and partly blind species. This was because an understanding of the mechanism and pathways leading to partial or total loss of eyes was assumed to be the paramount need for unravelling the evolutionary history of cave animals (Packard, 1888; Poulson and White, 1969; Dumnika *et al*., 2020; Moseley, 2022, p.40). Speculative attempts to explain the mechanisms that led to regression and loss of eyes began with Darwin (1859). Wallace and other British naturalists also participated in the ensuing international debates: the only occasion that British scholarship played a crucial role in the development of speleobiology. It is important to understand that this theoretical activity was distinct from, and unrelated to, domestic investigations of British cave and well fauna (Moseley, 2021 p. 19): Darwin and others based their conjectures on examples from the American and European cave fauna.

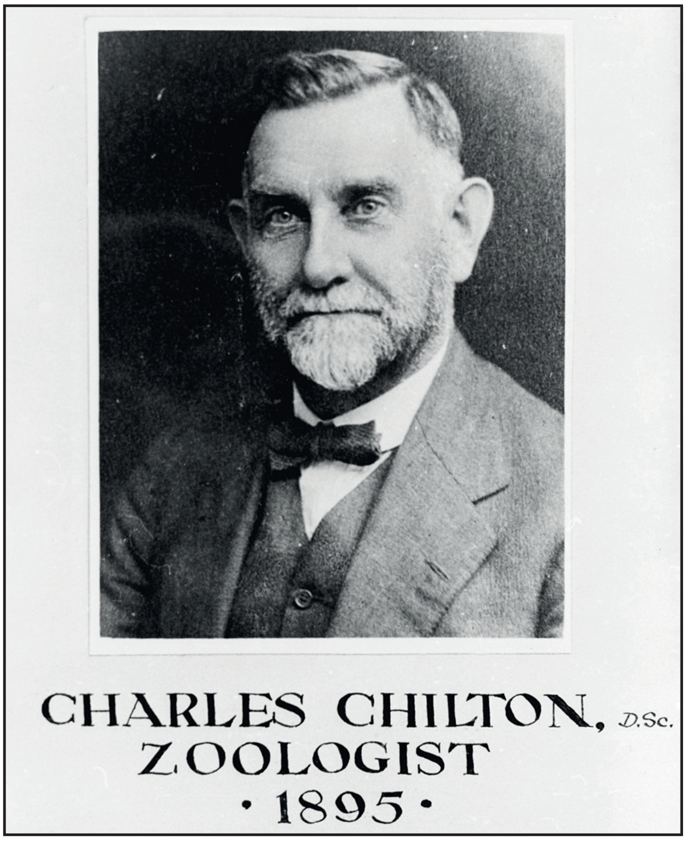

Figure 1*: Charles Chilton, M.A., D.Sc., LL.D., C.M.Z.S., Hon. Member Roy. Soc. N.S.W., F.N.Z.Inst*
[From: "Fleming, Charles (Sir): Portfolio of Royal Society members". Courtesy of the Alexander Turnbull Library, Wellington, New Zealand.]

A third element of British speleobiology has been overlooked: activities in the colonies. The historical period 1859–1914 witnessed the acme of the British Empire, which – at its peak – encompassed *circa* 24% of the land area of the globe. Throughout the period British scholars were documenting the natural history of these vast areas. The appellation 'British' in phrases such as 'British scholars' and 'British science' used always to be understood to incorporate the entirety of the Empire and its peoples. Whilst this usage might sound odd to some modern ears, it was justified, and made perfect sense at the time. There was an integrated global community of British Subjects. Many colonial scholars had been born and/or educated in Great Britain. These men worked within a British cultural milieu; their scholarly and scientific activities were a part of what they saw as the same laudable enlightenment enterprise aimed at economic prosperity and the advancement of learning; and they looked to the Royal Society and other great establishment institutions of the home islands for authority and peer recognition. Much of the mid-19th century research on the natural history of the colonies was published in British journals, principally *Annals and Magazine of Natural History* and *Journal of the Linnean Society of London.* In our present age, when traditional knowledge is becoming emphasized, it is not superfluous to point out that systematic investigation of fauna and flora throughout much of the undeveloped world awaited the arrival of British and other European explorers, collectors, and scholars.

Perusal of the contemporary literature does not evidence that British *speleobiology* prior to the Great War had this same global reach. But this is because there was so little being done. By 1914 hardly anything had been learned about cave or well fauna anywhere in the vast reaches of the world under British administration. There was little reason to expect that there was anything to be found, so no motivation to look (Howarth, 2023). In *cave* biology the one notable exception, the exploration of the Batu Caves in what was then British Malaya, produced disappointing results, which discouraged further efforts (Moseley, 2014a, b; Howarth, 2023). The current paper deals with the sole major exception for *well* fauna, the discovery of well-shrimps (subterranean aquatic amphipod and isopod Crustacea) in New Zealand. This was the first report of phreatic (groundwater) fauna in the Southern Hemisphere. The circumstances of this unexpected event are an instructive case-study of serendipity and contingency playing a beneficial role in speleobiology. The lukewarm response to what ought to have been a key advance reveals something of contemporary thinking about subterranean animals. It highlights how entrenched ideas and obsolete concepts persisted in speleobiology, even when mainstream biology had moved forward.

The report of the discovery was made early in the eighteen-eighties by Charles Chilton (1860–1929), an English-born New Zealand naturalist (Fig.1). He found them in a pump well on the Chilton family farm at East Eyreton, near Christchurch on South Island. At the time he was a 20-year-old student working on a Masters degree, and his reports and taxonomic descriptions of the finds were prominent in his first published work (Chilton, 1882d, 1883b, 1884). For the next fifteen years, while supporting himself as a schoolteacher, he continued researching well-shrimps in his spare time, gaining a Doctorate degree in 1893 and subsequently publishing two important monographic papers on this topic (Chilton, 1894, 1900). As his career advanced, he became a respected and internationally renowned invertebrate zoologist, recognized as a leading authority on the larger Crustacea, especially the aquatic forms. Despite this, his discovery and perceptive conjectures on the ecology, distribution, and origins of aquatic subterranean amphipods and isopods did not have the impact they deserved.

The present paper documents the discovery, the events that led to it, the evidence and reasons for its limited impact, and its largely unheeded potential significance is outlined. The opportunity is taken to collate and tabulate Chilton's contribution to the taxonomy of aquatic subterranean Isopoda and Amphipoda (Table 1). Finally, lessons that can be drawn from this case are outlined.

Terminology

As in previous contributions, 'speleobiology' is used in preference to the commonplace alternative 'biospeleology', to reflect a focus on the history of the sub-discipline within a history-of-biology context. Whereas it is accepted that the modern term 'subterranean biology' is more accurate and inclusive than these terms, it is not appropriate here, in view of the restricted physical and ecological concepts of the underground realm that were held in the historical period concerned. 'Groundwater fauna' and 'phreatic fauna' are used interchangeably herein. The convenient vernacular term 'well-shrimp' is used in the literature of the time. Chilton avoids it in his descriptive taxonomy but quotes it in his literature review (Chilton, 1894, p.165) and uses it when writing about the artesian water supply of the Canterbury Plains (Chilton, 1924). Use of 'Great War' for the 1914–1918 conflict reflects pre-Second World War usage.

Charles Chilton's early life and education

Except where otherwise cited, details of Chilton's biography throughout this paper rely on Chilton (1924), Anon (1929), Thomson (1930), Hurley (1990), and Pilgrim (1996).

When he reported his discovery in a paper read before the Philosophical Institute of Canterbury (*PIC*) ***[Note 1]*** on 03 November 1881, Charles was a post-graduate student at Canterbury College in Christchurch, New Zealand, about 25km north of the East Eyreton district where the family farm was located.

[Note 1]*:* At the time the *PIC* was one of the constituent bodies of the New Zealand Institute (founded in 1867). Established in 1862, the Institute was closely modelled on the regional scholarly institutes that sprang up in Victorian Britain, and it had much the same ethos (Allen, 1978; Moseley 2024). Papers on a wide variety of topics were read at formal meetings and later published in an expensive series of printed Transactions. Even in England, as Allen (1978) observes, the self-imposed financial burden of producing expensively- printed annual Transactions contributed for example to a requirement for the levy of high membership fees, affordable only to the better-off. As in similar institutions in the home islands it was a club of "gentlemen-scholars" often many of whom were self-taught.

The Chiltons were an immigrant family, arriving among the explosive mid-century influx of newcomers attracted by assisted passage, generous land lease terms, and other incentives offered by the colonial government to encourage land settlement and agriculture in the then Colony. In the half-century 1831–1881 the immigrant population, previously a trickle, grew from perhaps a thousand to approximately half a million.

Charles Chilton was born on 27 September 1860 at Little Marstone, Herefordshire, the fifth of the nine children of Thomas Chilton (1827–1892), a farmer, and his wife, Jane (née Price) (1826–1894). He was still an infant when the family emigrated from England in 1862 and took up farming in the East Eyreton district of Canterbury Plains on New Zealand's South Island. The Chilton boys were expected to become farmers,

Name in Chilton's original combination	Name combination in current usage *(Note A)*	Current taxonomic placement	Type locality *(Note B)*	Description and Chilton types *(Note C)*
Cruregens fontanus Chilton, 1882 *[new genus and species]*	*Cruregens fontanus* Chilton, 1882	ISOPODA, Anthuridea, *Paranthuridae*	Suction pump well in gravels, *c.* 5m deep, on farm, East Eyerton.	Chilton **1882B** pp. 175–176, Pl. X, Figs. 1–12; **1883B** p. 88; **1884** p.89;**1894** (*redesc*) pp. 209–218, Pl. XIX, Figs. 1–23. **Syn**: CMNZ 2015.149.1780–1789; 2015.149.736–780. **Comment:** Wägele (1982) redescribes the ♂.
Crangonyx compactus Chilton, 1882 *[new species]*	*Paracrangonyx compactus* (Chilton, 1882)	AMPHIPODA, Gammaridea, *Paracrangonyctidae*	Suction pump well in gravels, *c.* 5m deep, on farm, East Eyerton.	Chilton **1882B** p. 177, Pl. X, Figs. 13-19; **1894** (*redesc*) pp. 218–226, Pl. XX, Figs. 1–30. **Syn**: CMNZ 2015.149.10–16; 2015.149.101–106
Calliope subterranea Chilton, 1882 *[new genus and new species]* *Calliopius subterranea* (Chilton, 1882) *['Calliope' suppressed as pre-empted]*	*Paraleptamphopus subterraneus* (Chilton,1882) (♀ only) *Ringanui koonuiroa* Fenwick, 2006 (♂ in part) *Ringanui toonuiiti* Fenwick, 2006 (♂ in part)	AMPHIPODA, Gammaridea, *Paraleptamphopidae*	Suction pump well in gravels, *c.* 5m deep, on farm, East Eyerton.	Chilton **1882B** pp. 177–179, Pl. IX, Figs. 1–10; **1884** (amends '*Calliope*' to *Calliopus*); Thomson **1889**; Chilton **1894** (*redesc*). 233–244, Pl. XXII, Figs. 1–16 (♂), Pl. XXIII, Figs. 1–9 (♂), 10–18 (♀), Fig.3 is of a ♂ *R. toonuiiti* (Fenwick, 2006) **Syn**: CMNZ 2015.149. 90–100 **Comment**: Fenwick (2001 p.351) reports possibility of inadvertently switched material in Chilton collections. Chilton's ♂ and ♀ resolved as separate genera by Fenwick (2006).
Gammarus fragilis Chilton, 1882 *[new species]*	*Phreatogammarus fragilis* (Chilton, 1882)	AMPHIPODA, Gammaridea, *Phreatogammaridae*	Suction pump well in gravels, *c.* 5m deep, on farm, East Eyerton.	Chilton **1882B** p.179, Pl. IX, Figs. 11–18; **1894** (*redesc*) pp. 226–233, Pl. XXI, Figs. 1-25. Syn: CMNZ 2015.149.26–31
Phreatoicus typicus Chilton, 1883 *[new genus and species]*	*Phreatoicus typicus* Chilton, 1883	ISOPODA, Phreatoicidea, *Phreatoicidae** ** New family (*Chilton, 1883*)*	Suction pump well in gravels, *c.* 5m deep, on farm, East Eyerton.	Chilton **1883B** pp. 89–92, Pl. IV, Figs. 1–15; Thomson & Chilton **1886**; Chilton **1894** (*redesc* ♀ only) pp. 196–200, Pl. XVIII, Figs. 1–12. **Lectotype**: CMNZ catalogue IZ 3550 (♀); 2015.149.371; **paralectotypes** CMNZ catalogue IZ 3549; 2015.149.372-373 & 2015.149.1821. 2♀ on 10 microslides reported missing.
Phreatoicus assimilis Chilton, 1894 *[new species]*	*Neophreatoicus assimilis* (Chilton, 1894)	ISOPODA, Phreatoicidea, *Phreatoicidae*	Suction pump well, Winchester, South Canterbury (*Coll: D L Inwood*).	Chilton **1884** p. 89 (tentatively assigned as *P. typicus*?); **1894*** (as *P. assimilis*) pp. 186–196, Pl. XVI, Figs. 1–10, XVII, Figs. 1–13. **Syn**: CMNZ: 1♂: 3 microslides of 16 catalogued located, 13 missing; 1♀ on microslide catalogued but missing (these microslides appear to carry those ♂ and ♀ specimens described in Chilton 1894 p. 186 *et seq.*)
Niphargus philippensis Chilton, 1921 *[new species]*	*Flagitopisa philippensis* (Chilton, 1921)	AMPHIPODA, Gammaridea, *Eriopisidae*	From a well at Los Baños, Laguna Province, Luzon Island, Philippines (*Coll: S. Lantican*).	Chilton 1921 pp. 515–523 **Syn**: CMNZ 2015.149.66–69; 2015.149.424–435. **Comment:** Redescribed by Sawiki *et al*., 2005
Phreatoicus latipes Chilton, 1922 *[new species]*	*Phreatomerus latipes* (Chilton, 1922)	ISOPODA, Phreatoicidea, *Phreatoicidae*	In artesian water from the Hergott (Marree) bore, South Australia. *(Coll: not named).*	Chilton 1922 pp.23–33 **Types**: NHM 1952.4.18. 22–24; WAM No. 10552/8 (5♂1♀) **Comment**: Redescribed by Sheppard 1927
Niphargus indicus Chilton, 1923 *[new species]*	*Indoniphargus indicus* (Chilton, 1923)	AMPHIPODA, Gammaridea, *Mesogammaridae*	Jamuria Colliery, "*300 ft. deep*", Asansol, West Bengal, India (*sent by Dr. J. Tomb, Sanitary Officer, Asanol Mines Board of Health*).	Chilton 1923 pp.195–196 **Syn**: CMNZ 2015.149.59–65; 2015.149.174–208.
Neoniphargus westralis Chilton, 1925 *[new genus and species]*	*Uroctena westralis* (Chilton, 1925)	AMPHIPODA, Gammaridea, *Paramelitidae*	Western Australia, Darling Ranges, Darlington (*Coll: Mr. L. Glauert)*. No habitat information but genus now considered groundwater-associated.	Chilton 1925 pp.82–83, Fig.1, Plates 4, 5 **Syn**: NHM 1925.3.25.9–13

Table 1*: Groundwater Crustacea described by Charles Chilton.*
Abbreviations*: CMNZ = Canterbury Museum, New Zealand; NHM = Natural History Museum, London; WAM = Western Australia Museum; Syn = Syntype; Redesc = based on detailed re-examination of the collections and new material, Chilton (1894) published comprehensive diagnoses, re-descriptions, and figures of all of his New Zealand groundwater species and higher taxa.*
Note A*: Accepted as valid in Backbone Taxonomy, Global Biodiversity Information Facility (Accessed via GBIF.org on 2024-12-24).*
Note B*: All collections were made by or directly on behalf of Chilton, except where stated otherwise.*
Note C*: CMNZ type assignments follow Shaw and Poore (2016). These authors also list other CMNZ material identified by Chilton, and disputed type assignments by other authors. Some topotypes of New Zealand species exist in the Crustacea collections of the NHM [Accession No. NHM1895.1.1–20; 1928.12.1.741–742], and in the US National Museum of Natural History.*

but this became impossible for Charles when, at an early age, his left leg had to be amputated due to a severe hip condition. The family decided on professional training as an alternative. After attending Eyreton and Papanui schools, he was sent to Christchurch West School, where he proved to be an exemplary, award-winning pupil.

From 1875 to 1878 he attended lectures at Canterbury College as one of its first students. He was allowed to do this without meeting the requirements for formal admission (matriculation), presumably because he showed real academic promise. In 1878 he gained a university junior scholarship and went on to complete his B.A. in 1880, with "*exhibition in natural science and senior scholarship in English, physics and natural sciences*". He was helped in his study of natural history by Dr Llewellyn Powell (1843–1879) ***[Note 2]***, who lectured on biology and chemistry at the College until his early death from tuberculosis.

It was at this time that he came under the influence of the recently appointed Professor of Biology, Captain Frederick Wollaston Hutton (1836–1905). Hutton, another English expatriate, was a retired army officer who had established a second career and achieved a well-deserved reputation as a zoologist, geologist, zoogeographer, and staunch Darwinist (Stenhouse, 1990). There is no doubting that Hutton was the seminal figure in Charles' career direction and early development. He must have been involved in his decision to settle on a future in natural science after finishing his B.A. When Hutton arrived in New Zealand in 1866 he had found its zoology "*practically untouched"* and vigorously set about cataloguing it (Crane, 2015a, p.63). The crustacean fauna being still poorly investigated, he steered Charles towards this potentially fruitful specialist field of study and encouraged and assisted him in his post-graduate research on local Crustacea ***[Note 3]***. Working under the supervision of Professor Hutton, Charles completed his M.A. in 1881 with First-Class Honours in zoology. His first two research reports were read that same year at meetings of the *PIC*, and published in full the following year (Chilton, 1882c, d).

Thus, by 1881 (the year before Darwin died), a long series of wholly fortuitous events had led to the presence in Christchurch of a capable young zoology student specializing in the study of Crustacea. Brought there as an infant by a pioneering farming family; the locality where they settled; diverted from farming by an unfortunate physical disability; embarking upon the alternative option of academia and teaching; and then the happenstance of the arrival of a highly knowledgeable natural historian who saw a particular need to survey the Australasian crustacean fauna. This set of proximate factors propelled Charles towards a career in natural history, and the research opportunities offered by the larger New Zealand Crustacea.

[Note 2]: Dr Powell was a Welsh immigrant practising ophthalmic surgery in Christchurch. He had a keen interest in science education and natural history, and became President of the *PIC*. In 1876 he was appointed medical officer for the Christchurch Board of Health and led a successful campaign for the installation of a municipal sewage system (Rice, 2020).

[Note 3]: At Hutton's instigation, Edward Miers, Curator of Crustacea at the British Museum (Natural History) compiled summary descriptions of known New Zealand crustacean species, from the literature and the museum's collections to serve as a starting point (Miers, 1876). The importance Hutton attached to this group is shown by the fact that he also steered Thompson in the same direction.

[Note 4]: "*The want of some closer and more frequent means of communication between our scientific men than is furnished by our excellent annual volume of Institute Transactions, has often been expressed*" (*NZJS,* Volume 1, Number 1, January 1882). By modelling itself on British regional scholarly institutes (see Note 1) the New Zealand Institute had to some extent adopted an inappropriate structure for the place and time. The first editions of *TPNZI* were criticised for the merely local interest of some content (Crane, 2015a, p.74); publication of work was slow; and they were costly to produce.

Contingency and serendipity

A serendipitous breakthrough requires both an unforeseen result or observation and fertile ground – i.e. an individual who uniquely recognizes its potential and is able and willing to pursue it. It is hard to imagine anyone more prepared for a totally unexpected crustacean find, in a position to follow it up, and willing and eager to do so, than Charles Chilton in 1881. But such an outcome was contingent upon an exceedingly scarce event: something significant, heretofore unforeseen and unrecognized had to turn up at the right time.

It is remarkable that, at the very beginning of his research career, Charles was to be gifted an unexpected and groundbreaking speleobiological discovery due to the happy accident that the Clifton family farm was one of many that by now were being worked on the Canterbury Plains. This low-lying district is underlain by thick deposits of unconsolidated alluvial gravels and sands of Pleistocene age, with – as it turned out – a biologically abundant, widespread, and diverse groundwater fauna.

It is now known that well-shrimps were common but unreported in farm water supplies in the Canterbury Plains region. Had it not been that they were turning up in his own family's well they might not have come to Chilton's attention, certainly not at the time they did. It took a prepared mind on the spot to recognize them as novel, and the will and ability to follow up his discovery and take it to publication.

Even then, Charles' personal circumstances and physical disability restricted his capacity to undertake fieldwork, which made it difficult to explore sites further afield, so he was reliant on the goodwill of others to collect for him. Remarkably, and again entirely fortuitously, there appeared on the scene a man who was particularly willing to investigate other localities around the Canterbury Plains, was able to do this just at the right time, because – temporarily – he was doing work that made it possible, and was content to pass his findings along to Chilton. This was the estate gardener, W W Smith. But this was not until half a decade after publication of the discovery itself, which must be dealt with first.

Publication

Charles Chilton began his research career conventionally enough as a classical taxonomist. Morphological taxonomy was central to 19th century zoology: such work is the bedrock of biology. The substance of his M.A. was taxonomic description of some new aquatic Crustacea from both surface and subterranean waters of New Zealand. Quite naturally these two categories were reported and published separately. His first public report was a rather inconsequential description of three new species from surface waters read before a *PIC* meeting on 13 October 1881 (Chilton, 1882C). His initial account of the Eyreton well-shrimps followed at the next meeting, held on 03 November 1881, and the full papers were published in May 1882 in *Transactions and Proceedings of the New Zealand Institute* (*TPNZI*) for 1881 (Chilton, 1882d). In the interim, abstracts had been published in the first issue of the *New Zealand Journal of Science* (*NZJS*), a short-lived monthly journal launched by G M Thomson (see below) (Chilton, 1882a, b).

Thomson had become dissatisfied with the New Zealand Institute's publications, and the new periodical was intended as a less ponderous alternative to *TPNZI*. Recognizing that most natural history exploration and research was being done in isolation by amateurs, it sought to be a more nimble forum for discussion, sharing of knowledge, and what would today be termed networking. It offered up-to-the-moment news, quick publication of short original articles, and "*short and concise*" abstracts of papers read at *TPNZI* meetings (Speirs, 1993; Senadhira, 1995; Crane, 2015a, p.73; Roche, 2017a, p.91) ***[Note 4]***.

The first collections of well-shrimps were pumped from a depth of about 5m below ground by a suction-pump well raising water from alluvial gravels. There were several species. All were taken at various times during 1881 (Chilton, 1882d, p.175; 1883b, p.92). From this material Chilton distinguished and described three new blind amphipods (*Crangonyx compactus* [Fig.2], *Calliope* [later amended to *Calliopius*] *subterranea*, and *Gammarus fragilis*) representing three different families, and a new blind isopod (*Cruregens fontanus*) **(**Fig.3**)** (Chilton, 1882b, d; Table 1 herein).

Although not announced as such, in essence both papers were progress reports, presumably intended to bring Chilton and his work to the notice of the domestic scholarly community as quickly as possible. They were followed by a much-expanded taxonomic work on surface species (Chilton, 1883a) and a supplement on the well-shrimps. The latter was read at a *PIC* meeting on 05 October 1882 and duly published in *TPNZI* for that year (Chilton, 1883b). It provided more information about the four previously reported species and their occurrence, and also described a second new blind isopod collected from the same well in September 1882 (*Phreatoicus typicus*) (Fig.4).

Dissemination and popular and professional reception

The local response in New Zealand serves to underline the point made above, that these well-shrimps would almost certainly have continued to be overlooked had it not been for the chance fact that they occurred in the Chiltons' own well. The response is best described as 'muted interest'. Local press at the time reported only the titles of papers read at New Zealand Institute meetings (e.g. Anon, 1881a; b). Despite being widespread in the Canterbury Plains district, the next decade after announcement of their discovery saw only a handful of reports trickle in. Most were opportunistic finds. This is understandable and readily explained. Tiny shrimps in the wells of hard-working local farmers were to them a trivial matter. Even those individuals interested in local or regional natural history were most unlikely to have heard anything of the meagre knowledge of blind fauna elsewhere in the world. It is safe to assume that well-shrimps were nothing more than another natural curiosity in a country abounding with, what seemed to European settlers, very strange endemic animals and plants. However, from time to time, someone who had heard of Chilton's interest in them gave him specimens that had turned up in their local wells.

In late 1883 the proprietor of a flour mill in Winchester, Mr D L Inwood, wrote that he had seen similar crustaceans coming from a pump in the vicinity. Requested specimens revealed a community similar to that at Eyreton: *C. fontanus*, *C. subterranea*, *G. fragilis*, and a *Phreatoicus* tentatively identified as *typicus*. This new locality, at a considerable distance (*circa* 140km) from the original, was reported quickly as a note in *NZJS* (Chilton, 1884). The *Phreatoicus* was later placed as another new species, *P. assimilis* (Chilton, 1894).

It was to be five years before anything more was heard, this time from Ashburton, *circa* 80km from Christchurch, where G M Thomson, science master at Otago High School, reported the occurrence of *C. subterraneus* (Thomson, 1889). George Malcolm Thomson (1848–1933) was a colleague of Chilton and had also been encouraged to study the Crustacea by Hutton. He was an example of the self-taught 'amateur' scholar who achieved international respect as an authority in his field, despite not having a university degree or other formal academic qualifications. Born in Calcutta, he grew up in Scotland, and immigrated to New Zealand at age 20. During his life he had many notable achievements, including as a successful colonial politician and election as a Fellow of the Linnean Society (Speirs, 1993). However, the credit for this discovery really belongs to the unassuming W W Smith, who was working in

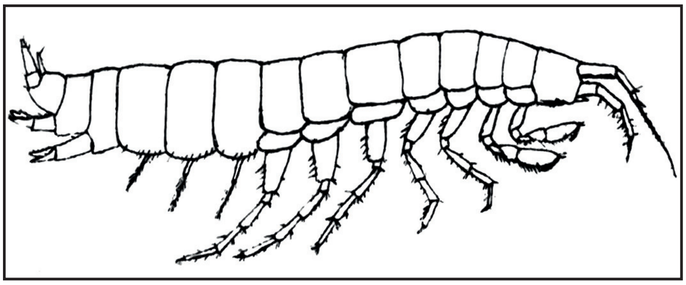

Figure 2*:* Crangonyx compactus *(Amphipoda) habitus. After Chilton 1894, Plate XX, Fig.1.*

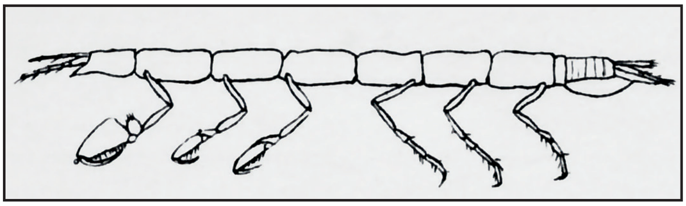

Figure 3*:* Cruregens fontanus *(Isopoda) habitus. After Chilton, 1882d, Plate X, Fig.1. Note the presence of only six leg-bearing segments, with what appears to be a vestigial 7th leg-bearing segment (see text for explanation and significance).*

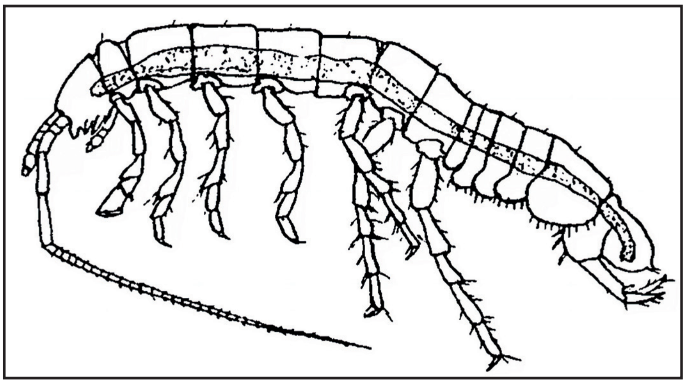

Figure 4*:* Phreatoicus typicus *(Isopoda) habitus. After Chilton 1883b, Plate IV, Fig.1. This isopod has some amphipod-like morphological characters, especially obvious being lateral flattening of the body (typical isopods are flattened dorso-ventrally). Chilton recognized it to be an evolutionary ancient isopod, now placed in a new Suborder Phreatoicidea.*

Ashburton and had given specimens from a nearby well to Thomson for investigation (Thomson, 1889). Over the next few years Chilton (1894) reported receiving *C. fontanus, C. subterranean, G. fragilis*, and *P. typicus* from various wells in the vicinity, collected by Smith and Mr J B Mayne, Headmaster of Ashburton Public School (Chilton, 1894, pp. 181, 185).

Between 1891 and 1894 Mr R M Laing, of the Christchurch Boys' High School, sent specimens of *C. fontanus*, *C. compactus*, and *G. fragilis* from wells at Leeston. In 1892 Mr E Wilkinson, of the Lincoln School of Agriculture, sent examples of *C. subterraneus* from wells at Lincoln. There were also sight reports of well-shrimps at various other places, one as far away as Leithfield, *circa* 42km to the north, and another farther inland, close to the Southern Alps at Alford Forest (Chilton, 1894, pp. 181, 185).

Internationally, the discovery, published in little-read journals from what was then still a part of the world remote from European and North American centres of learning, received little notice. Judging by the rarity of surviving copies in libraries, *NZJS* was unread elsewhere. Despite wide dissemination via exchanges with other scholarly societies around the world, *TPNZI* was far from what would today be considered a high-impact journal. Many articles were of only local interest, reporting small-scale and parochial research (Crane, 2015a, p.74). The work did receive mention in publications in the major scientific languages (English, French, and German) but was generally buried within a specialist taxonomic study.

As far as the current author is aware, there were only two early notices. The first *TPNZI* paper (Chilton, 1882d) was abstracted in the *Biological Notes* news section of the prestigious London-based weekly magazine *Nature* (Anon, 1882) and the Swiss zoologist Aloïs Humbert ***[Note 5]*** reviewed it briefly in French (Humbert, 1882). But, for the next decade, the new species appeared in monographic works likely to be read only by specialists. Two were taxonomic works restricted to the amphipods, the most important being the exhaustive *Bibliographic Introduction to the Amphipoda* by the Reverand T R R Stebbing (1835–1926), prefacing his report on the *Challenger* expedition amphipods (Stebbing, 1888). Wrześniowski (1890) included them in a comprehensive German-language taxonomy of subterranean Amphipoda (an updated version translated from an earlier publication in Polish [Wrześniowski, 1888, pp. 307, 310]). Moniez (1889) referred to them when reporting fauna discovered in groundwaters in Northern France. There was scant interest in the United States, where it was the renowned cavernicolous fauna, especially cave fishes, that was attracting the attention of naturalists: in a classic review of cave fauna, the American zoologist Packard (1888 p.149) cites Chilton (1882d, 1883b) in his Bibliography but there is no mention in the text. With so little attention paid to discovery of well-shrimps in the Southern Hemisphere, it is unsurprising that there was even less note of Chilton's evolutionary and other speculations.

Except for Packard (1888), only the first paper (1882d) appears in the above-listed sources. To all intents and purposes, the later articles (Chilton, 1883b; 1884) were unread beyond New Zealand. The isopod *Phreatoicus* became noticed later, but as an outstanding taxonomic, phylogenetic, and zoogeographical discovery rather than for its speleobiological significance.

Historical outline of well-shrimp research up to 1881

In 1881, the year that Chilton made his discovery, knowledge about well-shrimps was in its infancy. Such facts as were known were based mostly upon sporadic opportunistic *ad hoc* collections and emphasized occurrence records and taxonomy. Almost nothing was known about their true habitat, abundance, or geographical distribution. The presence of groundwater species in *caves* had hardly yet been recognized; recording of aquatic subterranean species was confined primarily to collections from wells and other potable water sources (many, at least in Britain, made by individuals motivated by drinking-water hygiene concerns) (Moseley, 2024).

Fewer than ten species – most of them amphipods – had been described definitively, all from Northern Temperate latitudes. The first undoubted subterranean amphipod had been described in 1836 from a well in Germany, whereas four additional species had been described from various wells around southern England (in 1855–1862) and Dublin, Ireland (in 1859) (Moseley, 2024, Table 1). These early, internationally important, British discoveries of well-shrimps had not triggered lasting interest. In the meantime, there were a few reports, varying in details and reliability, from wells in mainland Europe (including Germany and Belgium), but almost nothing more at all from the British Isles after 1862. Syntopic ***[Note 6]*** populations had been observed in wells at two localities: one in England (3 species) and one in Germany (5 species).

A cave-dwelling amphipod was collected in 1851 from the Carniolan (present-day Slovenia) caves, and cavernicolous species were also known from American caves and – published the following year – from one well (Hay, 1882), but they were poorly described. One blind Isopod species was known from the caves of mainland Europe, and one from US caves. Despite these clues, the physical and ecological continuity between wells, underground waters, and caves remained only dimly perceived and in practice these subterranean habitats and their biota were still viewed and investigated independently (Moseley, 2024, p.14). In contrast, when populations of blind amphipods had been found in deep Swiss lakes (in 1869 and 1873) it had already been surmised that they had likely arisen from adjacent, hydrologically contiguous, underground waters (Forel, 1885).

Charles Chilton in 1881 to 1895: education and employment

After completing his M.A., Chilton made a living for the next five years as a teacher in Christchurch. In 1886 he relocated, taking up an appointment as tutor at Dunedin Training College. He also registered in the newly instituted science degree programme at the then Otago College, University of New Zealand (*UNZ*). After graduating in 1888 as the first recipient of the *UNZ* BSc he took up the post of Rector of Port Chalmers District High School. That same year he married Scottish-born Elizabeth Jack. This new position at a small primary school with an enrolment of just a few hundred pupils, situated on the north side of Otago Harbour, made it possible to devote much of his free time to continuing his studies of the marine Crustacea of the harbour and the well-shrimps of the Canterbury Plains.

Results of his work on well-shrimps became his doctoral thesis and led to the award of a DSc in 1893. His Examiner was Dr George Bond Howes (1853–1905), who was then a Professor of Zoology at the Royal College of Science (South Kensington, London). Being the first science doctoral degree in the Colony, Chilton's doctorate was announced prominently in the local New Zealand press (Anon, 1893). It was published in England the following year by the Linnean Society (Chilton, 1894). Howes had been appointed to the Royal College post by no less a figure than "*Darwin's Bulldog*" Thomas Henry Huxley (1825–1895). He was a close friend of the then Zoology Professor at Otago, T J Parker (see below). Parker's family had a close connection with Huxley, and for the eight years from 1872 until his move to New Zealand, he was demonstrator in biology at the Royal School of Mines (South Kensington, London) where Huxley held the position of Professor of Natural History (Crane, 2015a).

However, elementary school teaching offered little financial reward or opportunity to advance a career in science, and he made the difficult decision to abandon natural history and retrain in medicine. In 1895 he resigned his position and, despite the great financial hardship involved, the couple moved to Scotland, where Charles entered medical school at the University of Edinburgh (at that time considered to be the best medical school in the English-speaking world).

Influences and well-shrimp research: Otago College 1886 to 1894

Throughout these years, Chilton had continued his studies of well-shrimps and other New Zealand Crustacea. The Zoology Professor at Otago from 1880 until his untimely death was another Englishman, the eminent and influential zoologist Thomas Jeffery Parker (1850–1897). Parker, who later became a Fellow of the Royal Society (elected 1888), was the first trained biologist in the Colony (Crane, 2015a, 2017). He had a particular interest in vertebrate anatomy, morphology, and embryology; and the remarkable endemic avian fauna including the extinct moa, writing extensively on these and other New Zealand fauna, including the marine crustacean family Palinuridae (spiny lobsters).

[Note 5]: The Swiss zoologist and palaeontologist Aloïs Humbert (1829–1887) was the son of a prosperous notary, who despite having inherited a considerable fortune devoted his life to exploration and science. In 1852 he became a curator at the Muséum d'Histoire Naturelle de la Ville de Genève. By the time of his death he was among the most renowned Swiss scientists. His only publication related to well-shrimps was a description of *Niphargus puteanus* from Lake Leman first published in French: an English translation followed (Humbert, 1877A, B).

[Note 6]: Syntopic = the joint occurrence of two or more related species in the same habitat at the same time. It is a special case of sympatry i.e. the occurrence of two or more related species in the same geographical area.

Parker's interest in these Crustacea can perhaps be traced back to Huxley's work on the European freshwater crayfish *Astacus* as a zoological type (Huxley, 1880), and it is possible that he became closely involved – perhaps in a supervisory capacity – in Chilton's research (Crane*, pers. comm*.).

In 1898 Parker co-authored, with William Haswell, a highly successful introductory biology textbook that went into eight revised editions: the present author recalls using 'Parker and Haswell' as a student during the early nineteen sixties (Parker and Haswell, 1897; Don, 1993; Crane, 2015b, 2017). He was an ardent supporter and advocate for Darwinism, and a self-declared Huxleyite (Parker, 1895). His work on kiwi (*Apteryx*) embryology was an attempt to understand its evolutionary placement (Parker, 1891) ***[Note 7]***. There can be little doubt that he influenced Chilton's thinking about evolution.

With new collections of well-shrimps to hand from multiple localities, and his increasing confidence and expertise in crustacean systematics, Chilton set about a monographical revision and re-figuring of the descriptions and diagnoses of all the New Zealand taxa. Evidently, he grasped the potential evolutionary, zoogeographical, and ecological significance of these animals and so, in addition to the foundational cataloguing process, embarked on a pioneering investigation of these wider issues. This approach was not entirely unique in New Zealand at the time. According to Crane (2015a, p.64) descriptive taxonomy was seen as preliminary: the origins of the unique endemic biota of the new nation demanded explanation, and this motivated Hutton for example. But the important point is that nothing similar had happened in England following the discoveries of well-shrimps in the middle years of the 19th century (Moseley, 2014).

As mentioned above, Chilton's physical disability and personal work responsibilities restricted his fieldwork. It appears (from the information he gives in the 1894 Linnean Society paper) that the only shrimps he collected himself were those from the family farm and immediate vicinity: all other material was generously provided by others. There was also the problem of acquiring literature: he thanks Thomson for access to his personal library (presumably shipped from England) and exchanged correspondence with individuals in other countries including – in America – the entomologist and cave biologist Alpheus Packard (1839–1905), and the zoologist Oliver Perry Hay (1846–1930). Given this background, he was indebted to W W Smith, without whose unstinting help less could have been achieved.

William Walter Smith (1852–1942)

Smith was a young Scottish immigrant estate gardener who was working in the district at the time. Apprenticed to the trade at age 13, Smith, who arrived in New Zealand in 1875, was one of those 19th century working-class men who, despite their 'amateur' status, little formal education, limited free-time, and relatively impoverished circumstances, achieved recognition and respect for notable contributions to natural history or some other scholarly field.

After working for several years as gardener for a large local estate, he took on several temporary positions as estate gardener on other properties. This gave him some freedom, as time permitted, to travel widely in the Canterbury Plains and foothills of the Southern Alps. It was during this period that he became recognized as a highly competent naturalist, observing and collecting native plants, animals, moa bones and archaeological artefacts. Additionally, he made field observations of the hydrology of the area (which he passed on to Chilton), corresponded with local and overseas authorities, and published notes in scientific journals. But he was a field naturalist not a taxonomist, so he routinely sent his specimens to recognized authorities for expert identification, and formal description when warranted (Galbreath, 1996; Roche, 2017a, b). It was a propitious time for Chilton: exactly the right time for his well-shrimp studies. He pays tribute to Smith's help during this period as follows: "*Mr. Smith, of Ashburton, has been particularly zealous and unwearying in his efforts to obtain specimens for me, and I am much indebted to him for additional knowledge on their distribution and on the general question of the underground waters of the plains"* (Chilton, 1894, pp.164–165; Galbreath, 1996; Roche, 2017a, b).

In 1894 Smith's unpaid efforts were rewarded with a position as a museum curator, and he went on to become one of New Zealand's most prominent naturalists and conservationists. Roche (2017a) portrayed him as "*Second to none in the Dominion as a field naturalist*".

Publication

In 1894 Chilton published what is essentially a compendium of work he had accomplished up to the time that the project had to be terminated because of his move to Scotland, and this is the first publication of his work in a widely read, prestigious, British journal. It is a key work, which provides an overview of what was known at the time about subterranean fauna, covering much the same ground as Packard (1888), but, unlike that work, it is written within a neo-Darwinian framework. Chilton makes several perceptive points, and is prescient in touching upon issues that are still important in modern speleobiology. He (a) reviews the published literature, (b) redescribes and re-figures all New Zealand well-shrimps, (c) describes and discusses what was known about their occurrence and distribution, and (d) discusses morphological and other characteristics of subterranean fauna in general. Much of this is only of historical and taxonomic interest, although it is worth pointing out that his taxonomy for the most part remains valid more than a century later, a testament to his accurate and meticulous work (Table 1). In the present context (i.e. the history of speleobiology), the most significant part of Chilton's (1894) paper is a discussion about the origins and evolution of subterranean fauna.

Origins and evolution of subterranean fauna

Backdrop

To understand the significance of Chilton's views on evolution of blind subterranean animals, it is necessary to understand contemporary thinking about evolution in general and the evolutionary origins of cave animals in particular.

By the final decade of the 19th century – the time that Chilton was writing his paper – overwhelming evidence for the fact of organic evolution had consigned creationist myth to the fringes of reputable biology, but Darwinian natural selection had not yet triumphed as the accepted process. There was a broad consensus that *evolution* (i.e. descent with modification) had happened, but what about the mechanism? All that Darwin (and Wallace) had done was to propose a plausible but unproven mechanism or driving force: natural selection. In the absence of an understanding of genetics and inheritance, this remained a conjectural hypothesis. It explained many observations and facts, but many biologists harboured grave doubts that the – seemingly – agonisingly slow step-by-step process of natural selection, acting on tiny, fortuitous, variations, could account for the origin of new species, and even less so, higher categories. Various competing and/or auxiliary explanations were proposed. Neo-Lamarckian theories of inheritance, saltationist ideas (discontinuous evolution), and versions of teleological change and orthogenesis, persisted well into the next century (Amundson, 1996, pp. 32–33; Junker and Hoßfeld, 2001). The blind cave animals that had by this time been discovered in some numbers in America and mainland Europe had been

[Note 7]: Among naturalists there was widespread belief in the Recapitulation Theory: "*Ontogeny recapitulates phylogeny*."

cited as supposedly supportive examples by proponents of several theories (even including special creation by Biblical literalists). It was Darwin himself who was the first to refer to them in the context of natural selection although, as is shown below, a critical reading of the relevant passage in *The Origin* ... reveals that he was using them only as one, albeit an excellent, *example* of the widespread natural phenomenon of rudimentation (atrophy) (Darwin, 1859, p.137: and all subsequent editions). The fact that rudimentation is ubiquitous in nature is a non-trivial issue, which continues to be overlooked by speleobiologists (Dobzhansky, 1970; Romero, 2009, pp. 54–55).The present author has pointed out (2022, p.40) that whenever a phrase such as 'the evolution of cave fauna' appears in the speleobiological literature, almost without exception it is restricted to, and indeed is virtually synonymous with, the evolution of troglobitic rudimentation, i.e. eyelessness and depigmentation. Debates about the evolution of obligate subterranean biota came to revolve around eye loss, which conflated and became almost synonymous with biological degeneration of the whole organism (Moseley, 2022, p.41).This was particularly true of those naturalists whose focus was on the evolutionary origins of cave animals rather than upon evolution in general, that is those in America and Europe who had direct access to and were investigating 'hotspots' of subterranean fauna. Romero (2009, Chapter 1) provides an account of their views, which therefore do not need to be discussed here in detail. Suffice it to say that (a) in America, exemplified by Alpheus Spring Packard (1839–1905) and his close colleague Frederic Ward Putnam (1839–1915), the involvement of natural selection in troglobitic rudimentation was rejected in favour of neo-Lamarckian explanations, whereas (b) European, primarily French, explanations likewise rejected neo-Darwinism, usually in this case in favour of orthogenesis and teleological processes. The latter, which survived in speleobiological circles until the 1960s (Moseley, 2022), was not mentioned by Chilton and need not be discussed further herein ***[Note 8]***. Chilton discusses subterranean fauna from the perspective of neo-Lamarckian versus neo-Darwinian theory. And here, by advocating natural selection he was an outlier. Neo-Lamarckians and the French orthogeneticists had taken a firm hold of speleobiology. It was not until the early-1960s, well after the Modern Evolutionary Synthesis had become established in mainstream biology, that other speleobiologists, first in the USA, started to approach the subject from a neo-Darwinian perspective (Kane and Richardson, 1985; Romero, 2009; Culver and Pipan, 2015).

Romero (2009, p.21 *et seq*.) makes a plausible case that Charles Darwin himself was a major influence behind support for neo-Lamarckian explanations of blindness in cave-dwelling animals ***[Note 9]***. In formulating his theory of natural selection, Darwin encountered difficulty in explaining how this evolutionary mechanism might account for *some* cases of rudimentation. There was no need to invoke inheritance of acquired characteristics or any mechanism other than natural selection to explain the regression of traits that, through changing conditions, had become disadvantageous. He gave loss of wings in insects of isolated windswept islands as an example (Darwin, 1859, Chapter V).

[Note 8]: For reviews of these ideas in the context of speleobiology, see Romero (2009) and Moseley (2022).

[Note 9]: Considerable weight is given to this notion by a passage in Packard (1888), who was able to use it to co-opt Darwin into the neo-Lamarckian cause. On page 143 of this influential book he writes, referring to Darwin, the following: "*The inheritance of functionally produced modifications* [which] *would seem to have been at one time denied, but which, as we have seen, was always to some extent recognized, came to be recognized more and more, and deliberately included as a factor of importance*."

The puzzle for Darwin was how to explain evolutionary regression where the characteristic in question appeared to confer neither advantage nor harm. By definition, the mechanism of natural selection acts on *advantageous* and *disadvantageous* traits. For Darwin, eyes seemed to be neither of these for an animal living in total darkness: absence of vision and superficial pigmentation are hardly the most important features *enabling* an organism to survive in the lightless subterranean. Unable to see a 'Darwinian' selectionist explanation, and without the benefit of modern knowledge of the genetic mechanism of inheritance, he had no alternative mechanism to propose and did not totally dismiss the possibility – *in particular cases such as this* – of non-selectionist causes. In the examples of (apparently) inexplicable rudimentation, he resorted to the vague concept of "*disuse*" (Darwin, 1859, p.137; and all subsequent editions). This issue impacted speleobiology because in a famous passage he pointed to loss of eyes in cave animals as an outstanding example: "*As it is difficult to imagine that eyes, though useless, could be in any way injurious to animals living in darkness, I attribute their loss wholly to disuse*" (Darwin, 1859, p.137). Still frequently cited, usually out of context, this statement implies that Darwin's *central* purpose was to explain the evolution of blind cave animals. A more nuanced reading is that cave animals provided him a good example, among many, of inexplicable rudimentation. There is some debate whether Darwin really implied by '*disuse*' inheritance of acquired characteristics, or it was merely a form of words. This doesn't matter here – contemporaries took it to mean what it said. The issue was revisited, revised and discussed in all editions of *The Origin* … with no change in his fundamental view. In fact, he became more convinced: by the sixth (final) edition he is placing *more* weight on disuse: "*It appears probable that disuse has been the main agent in rendering organs rudimentary*" (Darwin, 1872). He was to cling to this view until he died in 1882.

It was only after Darwin's death that plausible mechanisms explaining troglomorphic atrophy were suggested. Between 1882 and 1894, the years that Chilton was working on well-shrimps, several important and relevant papers were published. Plausible explanations of atrophy in cave animals consistent with natural selection and not requiring inheritance of acquired characteristics were proposed byWeismann (1885, 1891) ***[Note 10]*** and Wallace (1889) ***[Note 11]***. The modern debate revolves around the relative contribution of natural selection and genetic drift. Meanwhile in America, Packard and Putnam were building a case that blind cave biota, especially cavefishes, are superbly useful as subjects for investigation of evolution (Packard, 1888). Both men remained committed to neo-Lamarckian explanations and – bolstered by Darwin's view on this topic – were to be instrumental in the ensuing domination of non-Darwinian concepts in speleobiology (Romero, 2009, p.33 *et seq*.).

[Note 10]: Weismann solves this problem by invoking the power of conservation exerted by natural selection. As long as an organ is under selection pressure, only those individuals that have the best organs survive. However, once the selection pressure is relaxed (for example, when the presence of sharp eyes is no longer crucial to the survival of an organism, as in the case of cave dwellers), perfection of that organ is no longer maintained (conserved) by natural selection. Coupled with competition for tissue substrate for other essential organs, he argued that, this can lead to degeneration of organs. Thus, Weismann was able to provide a satisfactory solution to the problem that was consistent natural selection (Weismann, 1885; 1891).

[Note 11] "*The complete loss of eyes in some cave animals may, perhaps, be explained in a somewhat similar way. Whenever, owing to the total darkness, they became useless, they might also become injurious, on account of their delicacy of organisation and liability to accidents and disease ; in which case natural selection would begin to act to reduce, and finally abort them ; and this explains why, in some cases, the rudimentary eye remains, although completely covered by a protective outer skin*" (Wallace, 1889 p.416).

Chilton on the origin and evolution of subterranean animals

Chilton (1894) considers the phylogenetic origins of New Zealand well-shrimps, touches upon the role of isolation in their evolution, and argues in favour of neo-Darwinian versus neo-Lamarckian explanations of atrophy of eyes.

In a section entitled "*The Bearings of the Phenomena of Subterranean Life on the Theory of Descent*" (1894, pp. 267–272) he posits that the subterranean realm and its fauna offer special advantages for investigating evolution (which he calls the Theory of Descent ***[Note 12]***): "*Here the conditions of life are so peculiar, so abnormal, the fauna so scanty, and its environment so simple and so restricted that we may naturally expect to find the problems that are to be solved presented to us in their simplest forms*." This is the first explicit formulation of an idea implicit in Packard (1888, pp. 116–117) in reference to evolution. It entered the speleobiological mainstream when it was formalized in a prestigious *Science* article by Poulson and White (1969), who expanded the concept to include ecological studies ***[Note 13]***. These authors expressed it in quite similar language to that used by Chilton: "*Cave ecosystems have been considered natural ecological and evolutionary laboratories because of the relative simplicity of their communities and the temporal and spatial isolation of their biota*." However, a retrospective review by Poulson and White (Mammola, 2019) overlooked the early references, citing nothing before Racovitza (1907). ***[Note 14]***.

Chilton goes on to address two of the questions: (a) the role of isolation in speciation (current author's word) of subterranean animals, and (b) the mechanism(s) driving eye-loss. He mentions the former briefly, hypothesizing that the spatial isolation of well-shrimp habitat supports the view put forward by Packard (1888, pp.140–141) that, once a species is fully adapted to the subterranean environment isolation, absence of competition, and the stability of conditions, will ensure stability and evolution will cease. Chilton did not expand on his, admittedly very brief but nevertheless pioneering, endorsement. It has been overlooked in the subsequent literature. For example, Mammola (2019) states: "*It had generally been viewed that subterranean species had reduced phenotypic and genetic diversity because of population bottlenecks resulting from their isolation in cave habitats and adaptation to a stable environment, a hypothesis attributed to Poulson and White (1969). This hypothesis suggested that there would be a limited capacity for subterranean species to undergo adaptive evolution and formation of new species"*. The belief that highly adapted blind subterranean animals are thus 'evolutionary dead-ends' was accepted widely, but recent molecular genetic studies (e.g. Wessel *et al*., 2013; Stern *et al*., 2017) have challenged it.

Turning to the question of atrophy of eyes in subterranean animals, this topic is prefaced with a revealing disclaimer that it "*would be utter presumption on the part of the writer*" to approach the controversy between the neo-Darwinians and neo-Lamarckians. He intends, he goes on to say, to confine himself to reviewing the opinions of other writers as it relates to subterranean fauna. This is a little disingenuous, because he takes a critical approach and offers his personal stance, which – on careful reading – is hardly supportive of the latter (Chilton, 1894, pp. 267–272).

Use of the word presumption in this academic setting might be significant. It seems to imply more than that the topic lay outside his area of competence, rather a wish to avoid confrontation. He quite likely had Darwin in mind – after all a selectionist explanation of atrophy in this particular case is a direct challenge to the authority of the great man, who had not accepted the action of the struggle for existence and downplayed natural selection in caves.

It is notable that, many years later, when asked his opinion directly on whether "*disuse, environment, or heredity*" led to eyelessness, it was reported that Chilton "*declined to deliver a dictum as to whether acquired characteristics were transmitted or not*" (Anon, 1914). Nevertheless, despite his prudence, he proceeds to make a case that natural selection is a major driving force in the evolution of cave animals, not only in the enhancement of non-visual sense organs, which is uncontroversial, but also in the process of atrophy of the eyes.

He challenges directly the opinion of Packard, who was the pre-eminent authority at the time, that there is little room for natural selection, by pointing out, for instance, that cave animals *are* subject to "*the struggle for existence*" ***[Note 15]***. In order to drive this home, it is emphasized in the Conclusions (p.273): "*But one fact that has been impressed upon me more than any other by the existence of subterranean life is the keenness of the struggle for existence that goes on in the world of animals and plants*". He endorses Wallace (1889) and Weismann (1885, 1891), whereas the nearest he comes to endorsing a use–disuse explanation is " *if we accept* [Weismann's] *dogma of the non-heredity of acquired characters, that at once excludes the effects of disuse as an explanation of the blindness of cave animals; but even without going to this length ...*" (p. 270). To the present author, this seems to be a case of 'damning with faint praise.'

Admittedly, with some exceptions, Chilton's arguments are merely informed speculation, so he is on rather shaky ground, but the same is true of everyone else at the time, including of course Darwin himself. Deeply held religious, spiritual, and metaphysical worldviews lay behind the thinking of the neo-Lamarckians and orthogeneticists (see e.g. Moseley, 2021, p.28, and references therein). There can be little doubt that Chilton's support of natural selection is, at least in part, also an *à priori* conviction.

It is not difficult to see the influence of his teachers, mentors, and scientific colleagues on his acceptance of natural selection. The late 19th century scientific elite of the Colony were a small close-knit community, almost exclusively British in origin, who had come of age and learned their biology in the decades following publication of *The Origin of Species* (1859). So far as the present author is aware, they shared core beliefs in Darwinian evolution and appear not to have been troubled by those doubts that had arisen elsewhere, which have famously been referred to as "*the eclipse of Darwin*" (Bowler, 1992).

As previously mentioned, the first trained biologist in the Colony, T J Parker, had worked in London for eight years as demonstrator for the prominent evolutionist T H Huxley. He arrived in New Zealand in 1880 to take up the position of Professor of Biology and curator of the Museum of Otago University (Crane, 2015, 2022).

[Note 12]: Darwin first used the word 'evolution' in the last (1872) edition of *The Origin*. It is unclear why Chilton stayed with a contraction of 'descent with modification'.

[Note 13]: Although the word 'ecology' was coined in 1866, ecology as a science was in its infancy in the late 19th-century, and it is hardly unexpected that a naturalist working in New Zealand did not recognise this possibility.

[Note 14]: This reflects the extent to which Chilton had been overlooked in the past, and is not to be read as a criticism of any modern author in this regard.

[Note 15]: Packard refers to cavernicolous crustaceans as living "*in a sphere where there is little, if any, occasion for struggling for existence between these organisms*" [1888, p.110].

Arrested development

Chilton consistently viewed subterranean Crustacea through the lens of evolution or, as he called it, "*the theory of descent*". The earliest published work of the young student already suggests a sound grasp of broad principles as understood at the time (Chilton, 1882, 1894). This is revealed in his interpretations of unusual morphological characteristics possessed by the newly described isopod genera *Cruregens* and *Phreatoicus*. *Cruregens* possesses only six leg-bearing thoracic segments instead of the usual seven (Fig.3). This is a defining characteristic of the post-larval juvenile '*manca*' stage of related genera, which closely resembles the adult form but for the absence of the last pair of legs. Because *all* of his specimens had only six legs, Chilton deduced correctly that they were mature adults not juveniles and surmised that this trait is a recent result of "arrested development" (associated, he hints, with a subterranean habitat) not a 'primitive' trait surviving from early phylogenetic history. This interpretation is supported in all its essentials by Wägele (1982, pp. 52, 57) who states unambiguously that this isopod "*reaches sexual maturity in the manca stage*", and goes on to say: "*As far as our present knowledge goes* [Cruregens] *must be placed within a young, specialized group of the Paranthuridae*." ***[Note 16]***.

Phylogeny of New Zealand well-shrimps.

When a second new isopod, *P. typicus,* (Fig.4) was discovered in the Eyreton well, Chilton was at first unsure how to classify it. Thomson initially believed it to be an amphipod (Thomson and Chilton, 1886). It was highly unusual in having a superficially amphipod-like body shape and combining the morphological characters of several isopod families ***[Note 17]***. Leaving the question of taxonomic placement unresolved for the time being, Chilton stated that "*One thing is made clear ... that Phreatoicus, possessing as it does affinities to several distinct groups, must be of considerable antiquity*" (Chilton, 1883, p.92). It was the first representative of what was to be recognized as a very ancient basal group of the Isopoda, now classified as a separate suborder.

Noting that the nearest allies of this isopod and of *C. fontanus* were all marine species, and that *C. subterranea* had no known closely allied freshwater species in New Zealand, he conjectures initially that New Zealand well-shrimps evolved from marine ancestors (Chilton, 1883b, p.88). However, consideration of further evidence led him quickly to abandon this view and, whilst acknowledging that evidence was still rather thin, committed himself to the following: "*It will thus be seen that there is no difficulty in supposing that the subterranean fauna of New Zealand has been derived directly from a freshwater fauna, and when we consider the affinities of the general fauna of the North-American caves as given by Packard, or of the various European caves, there can no longer be any doubt that the cave and well-fauna has been derived from the surface-fauna of the neighbourhood*" (Chilton, 1894, p.256). He went on to point out that this should not be taken to imply descent from species still living in New Zealand, but rather that these subterranean species are ancient forms descended from now-extinct freshwater ancestors.

[Note 16]: The evolutionary loss or reduction of a structure often results from the early termination of its developmental trajectory (Lande, 1978). Wägele (1982) refers to it as "*a process of fetalization*". The loss or reduction of eyes in cavefishes and salamanders has been attributed to this phenomenon (Stynoski *et al*, 2021). The paedomorphism exhibited by the European Cave Salamander *Proteus* is an excellent example.

[Note 17]: *Phreatoicus* resembles the isopods *Idotea* (Idoteidae); *Anthura* and *Pananthura* (Anthuridae) and also has affinities with the Tanaeidae.

Reception and impact

Publication in a prestige British scientific journal ensured that the paper was read more widely than his earlier works had been. Google Scholar (Accessed 09 March 2025) lists 59 citations of this paper. Nevertheless, initially it had little impact. It is particularly unfortunate that his words in defence of the role of selectionist mechanisms in the evolution of cave animals fell on stony ground. Apart from Racovitza (1907), all early citations are in relation to inconsequential remarks (Lendenfeld, 1896; Ward, 1898; Eigenmann, 1899; Banta, 1910) or to taxonomic works. The rest of the citations are within modern articles related to groundwater ecology and conservation.

Racovitza's (1907) citation is the most germane in the present context. Considered to be a key biospeleological foundation text and a milestone in the historical development of the science, it carried considerable weight. Whereas it is entitled an '*essay'*, it is far more than that, having been portrayed as a speleobiological manifesto. The author provides a critical and clear-sighted review of prior literature on the physical nature and biology of the subterranean milieu. His conclusion is that biospeleology lacked a foundation of factual detail, relying instead upon wholly inadequate and commonly unreliable observations. Accordingly, he says, it had become pervaded by contradictory and conflicting opinions, premature generalizations, and unjustified speculation. Considerably more data and observations would be needed before there could be any possibility of placing it on a firm footing. His prescription was to begin with a systematic, broad-based, international survey of caves and cave fauna, supplemented by experimental investigations of the behaviour, physiology, and other characteristics of cavernicolous biota. These conclusions and recommendations have never been seriously disputed.

Chilton (1894) is cited several times: p.374 (struggle for life in caves); p.387 (existence of phreatic fauna in unconsolidated sediments); p.417 (low temperature assists survival in low food conditions); p.150 (flattening and lengthening as adaptation to narrow cracks); p.455 (natural selection versus non-use); p.467 (age of the fauna). For all that, there is nothing here to distinguish the worth of Chilton's views from those of other authors, thus leaving the reader with the impression that he shares responsibility for the confusing state of the science. For example, on page 374: "*La lutte pour l'existence est nulle dans les grottes (Darwin, Packard); elle est très violente (Chilton, Verhoeff, etc.)*". (There is no 'struggle for existence' in caves [Darwin, Packard]; it is very fierce [Chilton, Verhoeff, etc.] [current author's translation]). In this specific example, Racovitza agrees with the latter elsewhere in his paper, but without naming Chilton (pp. 426–427). Regarding Chilton's views on the evolution of cavernicoles, Racovitza states (p.455): "*Tout en admettant l'importance de l'influence du milieu, et celle de l'usage et du non-usage, il croit à l'existence de la sélection naturelle*". (While admitting that the influence of the environment and use and non-use are important he [also] believes in the existence of natural selection [current author's translation]). This sentence in no way endorses Chilton's acceptance of the *fundamental* role of natural selection, and it *overstates* his stance on the role played by disuse.

It must be concluded that this widely read foundation publication did nothing to draw attention to the potential merit of Chilton's work, and especially to his endorsement of a selectionist interpretation. Chilton was not alone: Weismann (1885, 1891) and Wallace (1889) are both overlooked and, similarly, had little positive impact on contemporary speleobiology. However, ***they*** were not specialists: Chilton was addressing the question of the evolution of cave fauna explicitly.

Taxonomic placement	Species	Collector	References
Platyhelminthes: Prorhynchidae	*Prorhynchus putealis* Haswell, 1898	Chilton	Haswell 1892, 1898; Chilton, 1894
Oligochaeta: Haplotaxidae	*Phreoryctes* (now *Haplotaxis*) *smithii* Beddard, 1888	Chilton	Beddard 1888; Chilton, 1894;
Oligochaeta: Phreodrilidae	*Phreodrilus subterraneus* (Beddard 1891)	William Smith	Beddard, 1891; Chilton, 1894; Smith, 1901.
Gasteropoda: Tateidae	*Potamopyrgus antipodarum* (J. E. Grey 1843) ***(Note A)***	William Smith	Chilton, 1894; Smith, 1901.
Copepoda: Cyclopidae	*Cyclops novaezealandiae* Thomson G. M. 1879 ***(Note B)***	William Smith	Chilton, 1894; Smith, 1901.

Table 2*: New Zealand groundwater invertebrates other than Amphipoda and Isopoda known and identified up to 1914.*
Note A*:* P. antipodarum *is an ecologically catholic, wide-ranging New Zealand endemic (now a globally common invasive) with a propensity to utilize shallow caves. It occurred in subterranean waters (wells) at many places in the Canterbury Plains, and Smith reported seeing it in caves at Collingwood (Smith, 1901). Noting that live specimens from a well lacked pigment, Chilton (1894) concluded that they represented permanent subterranean populations, and reported it as a variety* subterraneus*).*
Note B*: because it was a surface species with no apparent troglomorphic features, Chilton (1894, p.247) assumed that* Cyclops *was merely accidental in this habitat: "...had no doubt got in to the well by accident...". This was a commonplace misconception at the time. It persists nowadays to some extent in that, whereas it is known that subterranean habitats support many organisms that are also found on the surface, they are widely overlooked as being uninteresting speleobiologically.*

Nature of the New Zealand phreas and its fauna

Racovitza (p.387) does credit Chilton with the key insight that sub-surface waters are inhabited and extensive. This is important because, as mentioned above, this had hitherto been only dimly perceived. Chilton deduced it from Canterbury Plains distribution data and an understanding that the voluminous artesian waters of this relatively low-rainfall South Island area were fed by sources far inland to the west. The hypothesis was reinforced by published evidence from continental Europe, the British Isles, and the United States: "*The widespread distribution of the genus* Niphargus *in Europe, and of the closely allied genus* Crangonyx *in North America and elsewhere, remind us of what might otherwise be overlooked viz. the universality and great extent of underground waters*" (Chilton, 1894, p.251) [current author's underline]. He was also aware that well-shrimps are members of viable subterranean biological communities, citing findings of taxonomically diverse groundwater communities in Northern France (Moniez, 1889), and the cave work of Packard (1872) in America, and Joseph (1882) in Europe. It was also evident in New Zealand, where various other invertebrates were sometimes pumped up alongside the well-shrimps (Table 2).

Charles Chilton: 1895 to 1901

Chilton attended medical school in Edinburgh from 1895 to 1898, successfully attaining his M.D.C.M., with Honours. Having opted to specialize in diseases of the eye, he spent a year as House Surgeon in the Ophthalmic Ward, Edinburgh Royal Infirmary. For most of 1900 he moved around Europe, furthering his study of ophthalmology in Germany (Heidelberg), Austria (Vienna), and England (London), before returning to New Zealand at the end of that year. Sometime during these years, he found the time to publish a review of the British and Irish well-shrimps (Chilton, 1900).

Chilton's review of the well-shrimps of the British Isles

The review was published by the Linnean Society (Chilton, 1900). In his earlier monographic work, focussed on New Zealand's well-shrimps, Chilton had commented that, although extant occurrence records suggested that they would be found to be more widespread and abundant in the British Isles than had so far been realized, it was puzzling that no more had been done on them in three decades since Spence Bate and Westwood (1862) (Chilton, 1894, p.169).

Comparison of the two papers highlights a stark contrast between what little had been accomplished in Britain by 1900, and what Chilton had achieved almost singlehandedly in New Zealand. In the former, there were approximately two dozen occurrence records of the four described species, but little else (see Moseley, 2024). This contrasts unfavourably with Chilton's accomplishments, in New Zealand, described in the present paper.

Chilton says his intention in this new contribution is to shed fresh light on the distribution and abundance of the British species, and also that – by drawing attention to them – it might stimulate further work. In the event, he was unable to add much to the scanty knowledge of British well-shrimps. He had little to go on: only the previously published records and a few specimens given to him for dissection and description by colleagues. No new material was available. Echoing Stebbing (1888), he attributes the absence of new collections to two factors: "*... they are either altogether overlooked by the ordinary householder, or, if they are seen, their presence is, as Mr. Stebbing has pointed out, kept a secret for fear that the well may otherwise be closed by the sanitary authorities*" (Chilton, 1900, p.140). ***[Note 18]***. All that could be done was to review the literature, reprise what was already recorded about British occurrences, amend and re-figure them using specimens acquired from others, and revise the higher nomenclature. He observes that well-shrimps had not been found in Scotland although searched for, adds to the taxonomic descriptions by comparing English and Irish specimens with examples from the continent, and by providing exhaustive synonymies. The meticulousness of his descriptions cannot be faulted. It is illustrated by his observation of subtle morphological differences between English and Irish "*Niphargus kochianus*". Their significance had to await the development of modern genetic techniques, which proved them to be two distinct species. The only important mistake – an error of judgment not of observation – lay in assigning *Niphargus aquilex* as a junior synonym of the *subterraneus* of Leach (1814): this synonymy is no longer accepted.

His stated hope of stimulating British interest in these unusual animals was not realized: Google Scholar gives only five citations of his paper (Accessed 09 March 2025). The reasons have been discussed elsewhere. It was not until mid-century that interest was revived by British Speleological Association caver-biologists (Proudlove *et al*., 2003; Moseley, 2024). ***[Note 19]***

[Note 18]: Cholera and typhoid outbreaks in Victorian Britain had caused justified concerns about contaminated water supplies. But there were also social factors within the scholarly community, which might further account for indifferent interest in these animals (Moseley, 2024, pp. 7–8, 12 *et seq.*)

[Note 19]: New records, unknown to Chilton, were in fact accumulating. By 1914, when natural history activity ceased for the duration of hostilities, there were enough to have added considerable weight to his perceptive conjectures that well-shrimps are widespread and not at all rare in the south of England and Ireland, and absent from Scotland. However they were almost all unpublished sporadic *ad hoc* finds preserved in museum collections. When active studies of well-shrimps finally resumed in the mid 20th-century those involved also remained unaware of the existence of this resource, and much else of the knowledge gained pre-war. The extent and (by this time obsolete) putative value of the earlier work did not become apparent until these forgotten collections, and certain directly relevant but hitherto overlooked publications, were brought to light, collated, tabulated, and published recently (Moseley, 2024 p.15, Table 1).

***Figure 5**: Photograph of Dr Charles Chilton (back), and eight women students from Canterbury College, at Cass Biological Station, taken* circa *1920 by an unidentified photographer. The woman second from right is possibly Chilton's wife Elizabeth. [Source of description: notes on back of photograph.]*

Reference: PAColl-8856. Alexander Turnbull Library, Wellington, New Zealand, /records/22917956.

[https://commons.wikimedia.org/wiki/File:Charles_Chilton,_1920.jpg]

Marked as public domain... more details on Wikimedia Commons: [https://commons.wikimedia.org/wiki/Template:PD-New Zealand]

Career 1901 to 1929

Early in 1901 Chilton set up a practice in Christchurch, as an ophthalmic surgeon. Ironically, just the following year, and after all the effort and financial hardship pursuing a medical career, he gave it up when an unexpected opportunity arose to return to working in the field he had always wanted – natural history. When Professor Arthur Dendy, Chair of Biology at Canterbury College, took leave of absence in 1902, Chilton was offered and accepted a position as *locum tenans*, presumably planning to resume his medical practice after Dendy returned. However Dendy resigned unexpectedly, and Chilton was appointed to a permanent position as Chair of Biology and Palaeontology (later renamed the Chair of Biology), a position he occupied for twenty-five years. He retired for health reasons in 1928. By the time of his death the following year at age 69, he had authored 130 works and had established a well-deserved international standing as a zoologist, zoogeographer, and educator. His expertise on the larger Crustacea, especially the Amphipoda and Isopoda, was widely recognized. He described four new aquatic subterranean forms from Australia, India, and the Philippines sent to him by correspondents (Table 1) (Chilton, 1921, 1922, 1923, 1925), and a terrestrial isopod from Batu Caves in Malaya (Chilton, 1929). During his term of office, he was also acting curator of the Canterbury Museum (1905–1906), took part in scientific expeditions to the sub-Antarctic islands (1907), played a leading role in the establishment of the Cass Mountain Biological Station (Fig.5) – constructed in 1912; first used in 1914 – and accompanied the Mortensen Pacific Expedition (1914–1915).

Although now in a position to devote much of his time to his studies of crustaceans, Chilton attempted no further direct research on the well-shrimps or other New Zealand subterranean fauna during those years ***[Note 20]***. Conceivably, in view of the lacklustre response he had experienced, he knew that there was little to be gained by pursuing the topic. Or, perhaps, shifting priorities engaged him more. However, he did maintain a strong personal interest in the subject. In 1904 he gave a short presentation outlining new information at an Australasian Association for the Advancement of Science congress, which was held in Dunedin that year, but there was little to report since the 1894 Linnean Society paper. Two isopod species had been collected from an artesian well at St Albans, the first records from Christchurch. One was a *Phreatoicus*, the other he does not name but presumably it was the only other possible isopod, i.e. *Cruregens*. Elsewhere, abundant "*Paraleptamphopus subterraneus*" (Amphipoda) had been discovered living in surface waters at an altitude of *c*. 2000ft [*c*. 600m] at Castle Hill in central eastern South Island (Chilton, 1905). This is a limestone karst area with caves and underground streams. Most tellingly, a decade later he chose the topic of "*Animal Life in Caves*" for his 1914 ex-Presidential Address to the *PIC*. Informative summaries of this presentation were published by local newspapers (e.g. Anon, 1914).

Previous acquaintance with well-shrimps must have stimulated his continuing interest in all aspects of artesian waters, whose value to Christchurch he promoted through lectures (e.g. Anon, 1916), and a book devoted to this subject (Chilton, 1924). In that book he wrote: "*The waters that feed the reservoirs under the city, tapped by the artesians, come from much farther afield. To understand the problems connected with the artesian system, it is therefore necessary to know something about the Canterbury Plains, their extent, origin and structure, and particularly of the underground waters of the plains and the subterranean animals or 'well shrimps' that are found in some of them.*" Apparently, he was sometimes quite forceful, even confrontational: "*… 'I consider that I know more about the question of underground waters than the Christchurch City Council or their engineers, as I have gone into the matter very fully, and corresponded on the question with people all over the world' said Dr. Chas. Chilton…*" (Anon,1924).

At the time of his death from pneumonia in 1929, he had made arrangements to work at the recently established (1924) Cawthron Institute in Nelson, South Island, where he intended to write a comprehensive work on Crustacea (Thomson, 1929). Perhaps this would have included an update on well-shrimps, which might have re-invigorated interest, though it must be noted that biological research was at a low ebb because of the loss of many young men of promise in the war. In the event, the subterranean Crustacea of New Zealand were to be neglected for many years.

[Note 20]: There were a few incidental new records. Hurley (1954) illustrates a *P. fragilis* collected in May 1921. *C. fontanus* was collected by a R. Dean from a well at Waddington (Canterbury) in 1922 (Shaw and Poore, 2016, p.40).

Assessing Charles Chilton's contribution to speleobiology

From a speleobiological perspective Chilton's research was leading-edge. His report of a Southern Hemisphere groundwater fauna was a major zoogeographical advance, equivalent to the later recognition of the existence of terrestrial troglobionts in the tropics and sub-tropics ***[Note 21]***. Then, by pursuing this unexpected discovery, he was able to confirm that sub-surface waters are extensive and inhabited. Further, the taxonomic diversity (Amphipoda, Isopoda, Copepoda, Turbellaria, Oligochaeta, and Gastropoda) and species diversity, including syntopic populations of well-shrimps, pointed to the zoological richness of groundwater communities. Much more parochially, but relevant in the context of the present paper, he predicted correctly by extrapolation that British well-shrimps would be found to be more common and widespread than realized. On the theoretical side, his advocacy for neo-Darwinian natural selection over neo-Lamarckian and orthogenetic explanations challenged prevailing views: his belief in the existence of competition and natural selection in the cave environment was the most perceptive assessment available at the time. But most of this fell on stony ground. Other than its taxonomic aspects, his work was virtually comprehensively overlooked. It was many years – decades in the case of his stance on evolution in caves – before he was vindicated by the glacial advance of speleobiology. This raises two questions: how was Chilton able to see what experienced speleobiologists elsewhere had not understood, and why then did the latter fail to recognize its value, or even debate it?

When he made his discovery, Chilton was a young man at the beginning of his zoological career, and largely unburdened by established pre-conceived notions. That has often been the genesis of innovative thinking. And he was also an outsider, geographically far removed from zoological establishments in Great Britain, Europe and the United States. In explaining the roots of his own imaginative ideas, the prolific science-fiction writer Robert A Heinlein said that "*You can see more from the edge*". The present writer has noted previously that within Britain it was provincial naturalists, not the metropolitan elite, who engaged actively in field collecting and recording in caves and water sources (Moseley, 2021, p.25; 2024, p.9). Chilton was also working in the supportive environment provided by a network of talented – and mainly amateur – naturalists living in what must have been a more open egalitarian society than that of the home nations. Further, no other speleologist was working in a region with such unique endemic biota as was Chilton. His interest in the evolution of well-shrimps must have stemmed from his mentor Parker's efforts to explain the origins of Australasian animals.

Looking at the second question, it must be said that Chilton himself bears some of the responsibility. Nowhere does he draw attention to the global zoogeographical significance of the discovery of well-shrimps in the Southern Hemisphere. His public ambivalence on the question of natural selection in caves was especially unfortunate. By failing to take a firm stance in opposition to the neo-Lamarckians, he left them with no case to answer.

Nevertheless, he would still have faced a very steep hill to climb were he to have contested the preconceptions of the specialists in the United States and Europe. Self-referenced, and mutually-reinforcing, these men were wedded to non-Darwinian explanations of the evolution of blind cave animals. Intellectually blinded by such conceptual dead-ends, they were dismissive of Chilton's hesitant neo-Darwinian interpretation and had no interest in it. Support from within the wider biological community could not have been counted upon either: this was the era of widespread scepticism regarding natural selection – the "*eclipse of Darwin*" (Bowler, 1992). Challenges emanating from the intellectual periphery that was New Zealand science could readily be ignored.

The Great War dealt the final blow. Speleobiological investigations ended for the duration of hostilities, remained at low ebb in the aftermath and, as in Great Britain, knowledge gained pre-war was largely forgotten. By the time it was recovered – decades later – the science had moved on, and pre-war findings had become of only historical interest in both nations (Moseley, 2024, p.15).

[Note 21]: Howarth (2023) reviews and discusses the early history of discoveries of troglobionts in the tropics and sub-tropics.

Concluding comments

The genesis of this case study was something noticed during previous work on pre-Great War groundwater fauna discoveries in Britain (Moseley, 2024). It had become apparent that significant finds had not been followed-up by British naturalists, so it was intriguing to learn that an obscure – in this context – naturalist from 'down under' had noted this at the time, questioned why it was, and perceptively predicted that well-shrimps would be found to be widespread and common if searched for. When investigated, the previously overlooked place of Charles Chilton in the history of speleobiology was revealed. It turned out that this seemingly minor figure had done much more than comment on British well-shrimps. Not only had he made the very first collections of phreatic fauna from the Southern Hemisphere, but he was also prescient in his writings about their ecology and evolution.

When the serendipitous discovery of New Zealand well-shrimps fell into his lap, Charles took full advantage of the opportunity, and almost immediately began speculating about their distribution and origins. He was to go on to investigate and hypothesize about these and other aspects of their biology. His papers on these Crustacea went well beyond taxonomic descriptions, to include perceptive insights into their origins, evolution, zoogeography, occurrence, and ecology. His observations and insightful writings on these (and similar subterranean Crustacea found in Europe) were ahead of their time, potentially advancing speleobiology if heeded. But his work was underappreciated, did not have the impact that it deserved, and was largely forgotten. It was not until a short paper by a local New Zealand zoologist, the late Desmond Hurley, that he was recognized by anyone as a "*phreatic pioneer*": an observation that, in its turn, has been missed by speleobiologists (Hurley, 1990).

The obvious question to ask was "Why?" The story that unfolded underscores how scientific discovery can be shaped and driven forward by the complex interplay between serendipity, personal circumstances, a multiplicity of other contingent factors, and the key roles of individual insight and enterprise. It also illustrates how progress can be hindered – or even thwarted – by the intellectual environment, entrenched preconceived notions, undue deference to authority, and restricted disciplinary focus.

Finally, a few words about Charles Chilton himself might be appropriate. He was a man of his time. The Edwardians and late Victorians expected to be hard-working, self-reliant, and uncomplaining to the point of stoicism. Chilton overcame physical disability, financial hardships, and personal tragedy when his only son (and only child) was killed at Gallipoli, to achieve considerable personal success. On the other hand, the more egalitarian colonial social environment gave him opportunities that he seized. Although there were exceptions back home in Britain, it would have been far more difficult for a boy from a not very well-off farming family in rural England to craft a career in science at that time. He left a recognized legacy in crustaceology: hopefully the present paper will serve to contribute some degree of delayed recognition of his speleobiological legacy too.

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