diversity

MDPI

Article

Diversity and Distribution of Australian Stygobiont and Other Groundwater-Associated Amphipods (Crustacea: Malacostraca: Peracarida)

Rachael A. King [1,2,*], Steven J. B. Cooper [1,2], Benjamin Schwartz [3], Remko Leijs [1], Danielle N. Stringer [1,2], William F. Humphreys [4,5], Jake Thornhill [2] and Michelle T. Guzik [1,2]

[1] South Australian Museum, North Terrace, Adelaide, SA 5000, Australia; steve.cooper@samuseum.sa.gov.au (S.J.B.C.); remko.leijs@samuseum.sa.gov.au (R.L.); danielle.stringer@adelaide.edu.au (D.N.S.); michelle.guzik@adelaide.edu.au (M.T.G.)

[2] School of Biological Sciences and The Environment Institute, The University of Adelaide, Adelaide, SA 5005, Australia; a1211264@adelaide.edu.au

[3] Edwards Aquifer Research and Data Center, Department of Biology, Texas State University, San Marcos, TX 78666, USA; bs37@txstate.edu

[4] School of Biological Sciences, University of Western Australia, Crawley, WA 6009, Australia; billhumphreys6@gmail.com

[5] Western Australian Museum, Locked Bag 49, Welshpool DC, WA 6986, Australia

* Correspondence: rachael.king@samuseum.sa.gov.au; Tel.: +61-8-82739143

Abstract: Numerous and diverse groundwater habitats suitable for sustaining aquatic invertebrate communities exist across Australia. These habitats include enclosed subterranean aquifer systems, fractured rock, alluvial aquifers, perched aquifers, artesian springs, and spring-fed seeps and marshes. Crustaceans are a dominant member of these groundwater-associated invertebrate communities, and amphipods, both stygobiont and associated epigean species, are particularly diverse yet are still relatively poorly known. We review both the diversity and distributions of Australian amphipods associated with groundwater habitats, describing hotspots of diversity, providing notes on the unique Australian habitats, and examining the extraordinary species diversity and endemism of the Australian species. Our review highlights the significance of Australian groundwater ecosystems, their associated biodiversity, and the importance in considering these ecosystems in groundwater conservation management plans.

Keywords: amphipoda; stygobiont; conservation; groundwater; diversity; Australia

check for updates

Citation: King, R.A.; Cooper, S.J.B.; Schwartz, B.; Leijs, R.; Stringer, D.N.; Humphreys, W.F.; Thornhill, J.; Guzik, M.T. Diversity and Distribution of Australian Stygobiont and Other Groundwater-Associated Amphipods (Crustacea: Malacostraca: Peracarida). *Diversity* **2024**, *16*, 650. https://doi.org/10.3390/d16100650

Academic Editors: Simon Blanchet and Alan Myers

Received: 6 September 2024
Revised: 10 October 2024
Accepted: 15 October 2024
Published: 21 October 2024

1. Introduction

Groundwater provides the largest source of freshwater on earth, and it is exploited widely for anthropogenic activities, including irrigation, drinking, and industrial applications [1,2]. However, it is often overlooked that groundwater, in addition to directly supporting diverse terrestrial ecosystems through the provision of water and nutrients to plants, contains a huge diversity of microbial and metazoan species [3]. These species are usually unique to their specific subsurface aquatic habitats, where they provide essential ecosystem services by processing terrestrial carbon and maintaining the porosity of aquifers [4–7]. As such, groundwater ecosystems have recently been proposed as a keystone ecosystem that interacts with and supports many dependent ecosystems [8]. However, frameworks for identifying and conserving groundwater ecosystems have been limited by a lack of knowledge of the taxonomic diversity of subterranean aquatic species (stygobionts) [9].

The northern hemisphere, with numerous regions rich in karst and pseudo-karst areas, dominates in terms of global exploration and the description of stygobiont and groundwater-associated species, particularly invertebrates. In recent decades, Australia has emerged as a continent with a rich diversity in groundwater-associated invertebrates, with regions of exceptional biodiversity in geologic settings such as isolated groundwater calcrete aquifers, alluvial aquifers, fractured rock systems, artesian springs, and spring-fed seeps and marshes [10,11]. Crustaceans are an important and prevalent member of Australian groundwater-associated invertebrate communities (with diverse taxa including amphipods, isopods, ostracods, copepods, syncarids, and decapods). Here, we focus on amphipods. Within Australian groundwater habitats, stygobiont and groundwater-associated epigean amphipod species are remarkably diverse, with a large contingent of species documented, but as yet undescribed.

Stygobiont amphipods live entirely aquatic lifecycles and, as members of the Peracarida, brood their young in specialized "brooding pouches" developed by mature females ventrally to their bodies. With no dispersing larval stages, juveniles emerge directly from the maternal brood pouch. Although amphipods are active swimmers, their small size combined with distributional restraints within freshwater habitats mean that freshwater amphipods have limited dispersal capabilities (i.e., restricted within creeks, springs, tributaries, or aquifers). Amphipods are keystone species within many aquatic environments, performing important functional roles in nutrient recycling, and their presence/absence is often used as a biological indicator of ecosystem health [12–14].

In the seminal reviews of global freshwater [15] and subterranean [16] amphipod biodiversity, groundwater-associated species numbers in Australia were historically considered to be important but low. Väinölä et al. [15] estimated that the entirety of the Australian freshwater amphipod species comprised approximately 6% of the global freshwater amphipod diversity, but indicated that this was likely to be an underestimate. Holsinger [16] recorded 10 Australian stygobiont species from nine genera across six families at that time, dominated by the Paramelitidae. Bradbury and Williams [17] have provided the most recent substantial revision of Australian freshwater amphipods, finding 30 species in five families from subterranean habitats and a further eight epigean species associated with groundwater (in cave pools, springs, and interstitial habitats). Subsequently, significant work has taken place incorporating molecular and morphological data that has synonymized many of these species (King et al. [18] synonymized 11 species of *Nedsia*, whereas work by Finston et al. [19] suggested a much smaller number of *Chydaekata* species in the Pilbara). Alongside this, an expansion of the exploration of groundwater systems across regions like Western Australia (WA), South Australia (SA), New South Wales (NSW), and the Northern Territory (NT) [20–23], often linked to surveys associated with resource-focused environmental impact assessment, has uncovered large numbers of new and diverse amphipod taxa and expanded ranges of others [19,24–27]. Humphreys [28] noted significant advancements and utilization of molecular "species" lineage detection methods, which accounted for an estimate of at least 140 documented but mostly undescribed Australian stygobiont amphipod species in unpublished data (across the Paramelitidae, Neoniphargidae, Chiltoniidae, "Melitidae" (now Eriopisidae), and Bogidiellidae).

2. Materials and Methods

Using nominal species, published molecular lineages from the literature, and unpublished data from our collective research efforts, we aim to provide an informed and updated comprehensive review with annotated list and summary table of amphipod taxa distributed across Australian groundwater-dependent habitats, for both stygobiont and epigean associates. We also highlight possible areas of high biodiversity for future exploration and identify specific taxon groups for future focus.

3. Results

Annotated list of Australian Groundwater-Associated Amphipod Taxa.

Superfamily Talitroidea Rafinesque, 1815 [29].

3.1. Family Chiltoniidae J.L. Barnard, 1972 [30]

The Australian Chiltoniidae were long thought to be a relictual group, consisting of a small number of epigean species widespread across southern Australia. Recent research has shown that this family has successfully colonized numerous diverse freshwater ecosystems across Australia with particular success in groundwater-associated habitats. The Australian taxa are currently comprised of 17 species in eight genera across southern Australia and Western Australia, and 14 species are associated with groundwater habitats (Table 1, Figure 1).

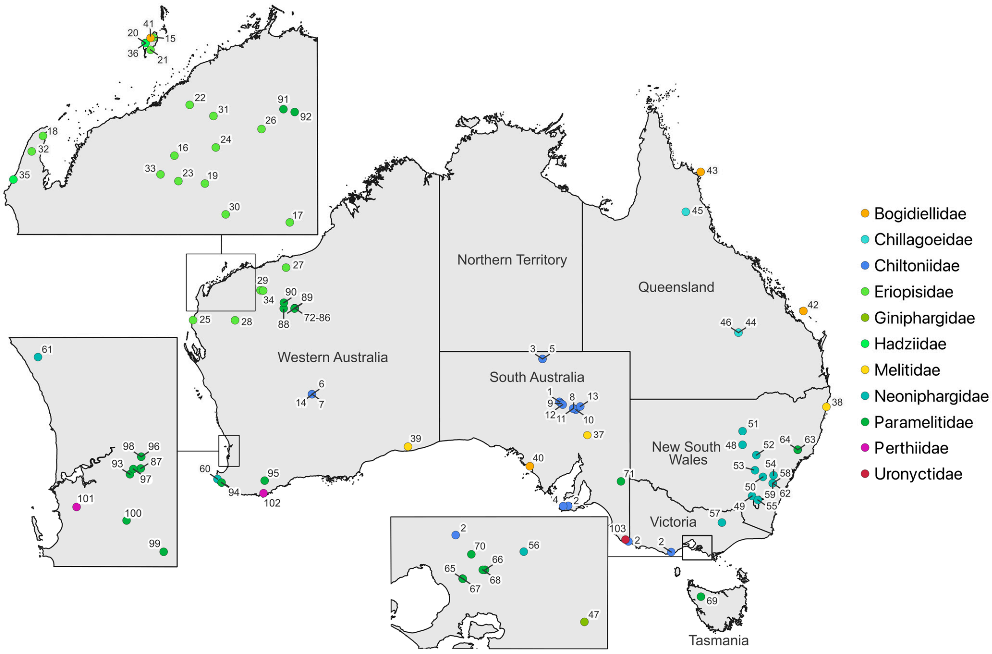

Figure 1. The distribution of described species of Australian groundwater-associated amphipods (colored by family) (the numbers are linked to species details in Table 1). The figure was created with QGIS [31] using a States and Territories digital boundary file from Australian Bureau of Statistics: Australian Statistical Geography Standard (ASGS) Edition 3.

Table 1. Australian groundwater-associated amphipod species. Locations include South Australia (SA), Victoria (VIC), Western Australia (WA), New South Wales (NSW), Queensland (QLD), and Tasmania (TAS).

Classification and Diversity	Species (Number Corresponds to Figure 1)	Stygobiont (*) or Groundwater-Associated Epigean (^)	Distribution and Habitat
Infraorder Talitrida: Parvorder Talitridira: Superfamily Talitroidea: Family Chiltoniidae 14 described species Up to 60 undescribed species	1. *Arabunnachiltonia murphyi* King, 2009 [32]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	2. *Austrochiltonia australis* (Sayce, 1901) [33]	^	SA, VIC. Spring-fed creeks.
	3. *Austrochitonia dalhousiensis* Zeidler, 1997 [34]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	4. *Kartachiltonia moodyi* King and Leys, 2014 [35]	*	SA, Kangaroo Island. Spring-fed marsh.
	5. *Phreatochiltonia anophthalma* Zeidler, 1991 [36]	*	SA, Kati Thanda–Lake Eyre. Artesian springs.
	6. *Scutachiltonia axfordi* King, 2012 [37]	*	WA, Yilgarn. Calcrete aquifer.
	7. *Stygochiltonia bradfordae* King, 2012 [37]	*	WA, Yilgarn. Calcrete aquifer.

Table 1. *Cont.*

Classification and Diversity	Species (Number Corresponds to Figure 1)	Stygobiont (*) or Groundwater-Associated Epigean (^)	Distribution and Habitat
Infraorder Talitrida: Parvorder Talitridira: Superfamily Talitroidea: Family Chiltoniidae 14 described species Up to 60 undescribed species	8. *Wangiannachiltonia ghania* Murphy and King, 2015 [38]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	9. *Wangiannachiltonia gotchi* Murphy and King, 2015 [38]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	10. *Wangiannachiltonia guzikae* King, 2009 [32]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	11. *Wangiannachiltonia olympicdamia* Murphy and King, 2015 [38]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	12. *Wangiannachiltonia stuarti* Murphy and King, 2015 [38]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	13. *Wangiannachiltonia wabmakabarbu* Murphy and King, 2015 [38]	^	SA, Kati Thanda–Lake Eyre. Artesian springs.
	14. *Yilgarniella sturtensis* King, 2012 [37]	*	WA, Yilgarn. Calcrete aquifer.
Infraorder Hadziida: Parvorder Hadziidira: Superfamily Hadzioidea: Family Eriopisidae 20 described species Up to 10 undescribed species	15. *Aenigmata megabranchia* Stringer and King, 2024 [39]	*	WA, Barrow Island. Alluvial aquifer.
	16. *Nedsia canensis* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	17. *Nedsia cheela* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	18. *Nedsia douglasi* Barnard and Williams, 1995 [40]	*	WA, Pilbara. Alluvial aquifer.
	19. *Nedsia erinnae* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	20. *Nedsia hurlberti* Bradbury and Williams, 1996 [41]	*	WA, Barrow Island. Alluvial aquifer.
	21. *Nedsia macrosculptilis* Bradbury and Williams, 1996 [41]	*	WA, Barrow Island. Alluvial aquifer.
	22. *Nedsia mcraeae* King and Cooper, 2022 [18]	*	WA, Barrow Island and Pilbara. Alluvial aquifer.
	23. *Nedsia nanutarra* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	24. *Nedsia pannawonica* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	25. *Nedsia quobba* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	26. *Nedsia robensis* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	27. *Nedsia shawensis* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	28. *Nedsia wanna* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	29. *Nedsia weelumurra* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	30. *Nedsia wyloo* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	31. *Nedsia yarraloola* King and Cooper, 2022 [18]	*	WA, Pilbara. Alluvial aquifer.
	32. *Norcapensis mandibulis* Bradbury and Williams, 1997 [42]	*	WA, Cape Range. Cave pool.
	33. *Pilbarana grandis* Stringer and King, 2022 [43]	*	WA, Pilbara. Alluvial aquifer.
	34. *Pilbarana lowryi* Stringer and King, 2022 [43]	*	WA, Pilbara. Alluvial aquifer.

Table 1. *Cont.*

Classification and Diversity	Species (Number Corresponds to Figure 1)	Stygobiont (*) or Groundwater-Associated Epigean (^)	Distribution and Habitat
Family Hadziidae 2 described species	35. *Hadzia branchialis* Bradbury and Williams, 1996 [41]	*	WA, Cape Range. Anchialine cave.
	36. *Hadzia subthalassicus* Bradbury and Williams, 1996 [41]	*	WA, Barrow Island. Anchialine cave.
Family Melitidae 3 described species Up to 10 undescribed species	37. *Brachina invasa* Barnard and Williams, 1995 [40]	*	SA, Flinders Ranges. Interstitial water.
	38. *Josephosella plumulosa* Zeidler, 1989 [44]	^	NSW, north-east coast. Groundwater-fed lake.
	39. *Nurina poulteri* Bradbury and Eberhard, 2000 [45]	*	WA, Nullarbor Plain. Cave pool.
Infraorder Bogidiellida: Parvorder Bogidiellidira: Superfamily Bogidielloidea: Family Bogidiellidae 4 described species	40. *Bogidiella veneris* Leijs et al., 2011 [46]	*	SA, west coast. Coastal aquifer.
	41. *Bogidomma australis* Bradbury and Williams, 1996 [41]	^	WA, Barrow Island. Cave pool.
	42. *Xystriogidiella capricornea* Stock, 1984 [47]	*	QLD, Great Barrier Reef. Marine interstitial habitat.
	43. *Xystriogidiella juliani* Coleman, 2009 [48]	*	QLD, Great Barrier Reef. Marine interstitial habitat.
Infraorder Gammarida: Parvorder Crangonyctidira: Superfamily Crangonyctoidea: Family Chillagoeidae 3 described species	44. *Carnarvonis katjae* King, Stringer and Leijs, 2023 [49]	*	QLD, north-east. Artesian spring.
	45. *Chillagoe thea* Barnard and Williams, 1995 [40]	*	QLD, north-east. Cave pool.
	46. *Warregoensis lowryi* King, Stringer and Leijs, 2023 [49]	*	QLD, north-east. Artesian spring.
Family Giniphargidae 1 described species	47. *Giniphargus pulchellus* Sayce, 1899 [50]	*	VIC, Gippsland. Spring-fed creek.
Family Neoniphargidae 15 described species Up to 20 undescribed species	48. *Jasptorus solepti* Bradbury and Williams, 1997 [42]	*	NSW, south-east. Cave pool.
	49. *Neocrypta annae* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	50. *Neocrypta georginae* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	51. *Neocrypta moniae* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	52. *Neocrypta primaris* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	53. *Neocrypta robinae* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	54. *Neocrypta simoni* Bradbury and Williams, 1997 [42]	*	NSW, central. Cave pool.
	55. *Neoniphargus coolemanensis* Bradbury and Williams, 1997 [42]	^	NSW, Mt Kosciuszko. Cave pool.
	56. *Neoniphargus fultoni* Sayce, 1902 [51]	^	VIC, Warburton. Spring.
	57. *Neoniphargus obrieni* Nicholls, 1926 [52]	^	VIC, Mt Buffalo. Beneath bog mass.
	58. *Neoniphargus richardi* Bradbury and Williams, 1997 [42]	*	NSW, Wombeyan. Cave pool.
	59. *Neoniphargus secus* Bradbury and Williams, 1997 [42]	*	NSW, Wombeyan. Cave pool.
	60. *Wesniphargus nichollsi* Straškraba, 1964 [53]	^	WA, south-west. Cave outflow.
	61. *Wesniphargus yanchepensis* Bradbury and Williams, 1997 [42]	*	WA, Yanchep. Cave pool.
	62. *Wombeyanus botulosus* Bradbury and Williams, 1997 [42]	*	NSW, Wombeyan. Cave pool.

Table 1. *Cont.*

Classification and Diversity	Species (Number Corresponds to Figure 1)	Stygobiont (*) or Groundwater-Associated Epigean (^)	Distribution and Habitat
	63. *Austrocrangonyx barringtonensis* Chilton, 1917 [54]	^	NSW, Barrington Tops. Spring-fed creeks.
	64. *Austrocrangonyx hynesi* Williams and Barnard, 1988 [55]	^	NSW, Barrington Tops. Spring-fed creeks.
	65. *Austrogammarus australis* Sayce, 1901 [33]	^	VIC, Bayswater. Spring-fed creeks.
	66. *Austrogammarus haasei* Sayce, 1902 [51]	^	VIC, Monbulk. Spring-fed creeks.
	67. *Austrogammarus multispinosus* Williams and Barnard, 1988 [55]	^	VIC. Spring-fed creeks.
	68. *Austrogammarus saycei* Williams and Barnard, 1988 [55]	^	VIC, Sassafras. Spring-fed creeks.
	69. *Austrogammarus smithi* Williams and Barnard, 1988 [55]	^	TAS, north-west. Spring-fed creeks.
	70. *Austrogammarus spinatus* Williams and Barnard, 1988 [55]	*	VIC, Croydon. Spring-fed creek.
	71. *Austrogammarus telsosetosus* Barnard and Williams, 1995 [40]	*	SA, south-east. Spring-fed creek.
Family Paramelitidae 38 described species Up to 60 undescribed species	*Chydaekata* species complex: 15 species. 72.*Chydaekata acuminata* Bradbury, 2000 [56] 73. *Chydaekata anophelma* Bradbury, 2000 [56] 74. *Chydaekata brachybasis* Bradbury, 2000 [56] 75. *Chydaekata carscutica* Bradbury, 2000 [56] 76. *Chydaekata diagonalis* Bradbury, 2000 [56] 77. *Chydaekata dolichodactylus* Bradbury, 2000 [56] 78. *Chydaekata gyraspis* Bradbury, 2000 [56] 79. *Chydaekata nudulum* Bradbury, 2000 [56] 80. *Chydaekata ovatosetosa* Bradbury, 2000 [56] 81. *Chydaekata scopula* Bradbury, 2000 [56] 82. *Chydaekata scuticari* Bradbury, 2000 [56] 83. *Chydaekata simulata* Bradbury, 2000 [56] 84. *Chydaekata tetraspis* Bradbury, 2000 [56] 85. *Chydaekata transversi* Bradbury, 2000 [56] 86. *Chydaekata unispinulata* Bradbury, 2000 [56]	*	WA, Pilbara. Alluvial aquifers.
	87. *Hurleya kalamundae* Straškraba, 1966 [57]	*	WA, south-west.
	88. *Kruptus linnaei* Finston, Johnson and Knott, 2008 [58]	*	WA, Pilbara. Confined aquifer.
	89. *Maarrka etheli* Finston et al., 2011 [24]	*	WA, Pilbara. Confined aquifer.
	90. *Maarrka weeliwollii* Finston et al., 2011 [24]	*	WA, Pilbara. Confined aquifer.
	91. *Molina pleobranchos* Bradbury, 2000 [45]	*	WA, Pilbara. Alluvial aquifer.

Table 1. *Cont.*

Classification and Diversity	Species (Number Corresponds to Figure 1)	Stygobiont (*) or Groundwater-Associated Epigean (^)	Distribution and Habitat
Family Paramelitidae 38 described species Up to 60 undescribed species	92. *Pilbarus millsi* Bradbury and Williams, 1997 [42]	*	WA, Pilbara. Springs.
	93. *Protocrangonyx fontinalis* Nicholls, 1926 [52]	*	WA, south-west.
	94. *Totgammarus eximius* Bradbury and Williams, 1995 [59]	*	WA, south-west. Spring-fed creek.
	95. *Toulrabia willsi* Barnard and Williams, 1995 [40]	*	WA. Spring-fed creek.
	96. *Uroctena affinis* Nicholls, 1926 [52]	^	WA, south-west. Spring-fed creek.
	97. *Uroctena setosa* Nicholls, 1926 [52]	*	WA, south-west. Spring-fed creek.
	98. *Uroctena westralis* Chilton, 1925 [60]	*	WA, south-west. Spring-fed creek.
	99. *Uroctena whadjukia* Barnard and Wiliams, 1995 [40]	*	WA, south-west. Spring-fed creek.
	100. *Uroctena yellandi* Nicholls, 1926 [52]	^	WA, south-west. Spring-fed creek.
Family Perthiidae 2 described species Up to 10 undescribed species	101. *Perthia acutitelson* Straškraba, 1964 [53]	^	WA, south-west. Groundwater-fed lake, creeks.
	102. *Perthia branchialis* Nicholls, 1924 [61]	^	WA, Perth and south-west region. Spring-fed creeks
Family Uronyctidae 1 described species	103. *Uronyctus longicaudus* Stock and Ilife, 1990 [62]	*	SA, Mount Gambier. Cave pool/aquifer.

The vast majority of the chiltoniid radiation is associated with the Great Artesian Basin (GAB), where the chiltoniids have become established as dominant and critical taxa within spring invertebrate communities in surface pools, seeps, and springs. Four genera *Arabunnachiltonia*, *Austrochiltonia*, *Phreatochiltonia*, and *Wangiannachiltonia* are described from artesian springs within the Kati Thanda–Lake Eyre region of the GAB [32,34,36,38], with an additional speciose genus documented from northern Kati Thanda–Lake Eyre [26] (King unpublished data) and numerous documented but undescribed genera and species known from across GAB artesian springs in Queensland (QLD), NSW, as well as WA (Atlas of Living Australia at https://doi.org/10.26197/5d7f2348165a0 accessed on 4 September 2024) [63]. *Austrochiltonia* has been recorded as the most widespread of the Australian chiltoniid genera; however, molecular data indicate more discrete generic taxa, leaving *Austrochiltonia* (five epigean species in Victoria (VIC), SA, and Tasmania (TAS)), as it is currently known, as likely paraphyletic [32,64]. *Arabunnachiltonia* is a monotypic epigean genus existing within the Kati Thanda–Lake Eyre springs. The *Wangiannachiltonia* complex of six species are also distributed within the Kati Thanda–Lake Eyre region and remain morphologically cryptic despite significant isolation within springs [38]. Whilst most of the GAB species are considered epigean and have eyes, two documented species are considered true stygobionts: *Phreatochiltonia anophthalma* was described from the Witjira-Dalhousie springs and remains monotypic, and unpublished data (Stringer et al.) have revealed an additional stygobiont species of *Arabunnachiltonia*.

The calcrete aquifers of the Yilgarn region of WA are another habitat dominated by chiltoniid and paramelitid amphipods [25]. Three described chiltoniid genera, including *Scutachiltonia*, *Yilgarniella*, and *Stygochiltonia* and their associated type species, are all distributed in a single calcrete aquifer (Sturt Meadows) in the Yilgarn from three demonstrated separate colonization events dating back to the Miocene [37,65,66]. In addition to these three species, six chiltoniid evolutionary lineages have previously been identified, based on mitochondrial DNA sequence analyses, and are likely to represent distinct species [25].

Each are restricted in their distribution to single calcrete aquifers with multiple species sometimes occurring in discrete calcretes [25,37].

The monotypic *Kartachiltonia* is not a true stygobiont but was collected from interstitial habitats and pools in spring-fed marsh areas on Kangaroo Island in SA [35]. Significant bushfires in 2020 on the island removed previously thick vegetation and allowed for more comprehensive sampling to take place, indicating additional species of *Kartachiltonia* exist from newly sampled spring sites (Leijs, unpublished data).

Unpublished data (Leijs and King) indicate that as many as 40 documented, but yet to be described, chiltoniid species exist in radiations across the Yilgarn (WA), Amadeus basin (NT), Great Artesian Basin (SA, NSW, and QLD), Flinders Ranges (SA), the Eyre Peninsula (SA), the SE Australian mainland including the Murray Darling basin (SA and VIC), and TAS. Additionally, at least seven undescribed epigean species have been found associated with rivers and streams in the south-west of WA (Leijs, unpublished data). Given that individual calcrete aquifers are likely to contain unique communities of species, and around 210 major calcrete bodies and numerous small calcretes exist in the Yilgarn region of central WA [67] with many yet to be surveyed, there is likely to be a huge diversity of chiltoniid amphipod genera and species in that region (King, unpublished data). It is also likely that further exploration of spring vents across GAB spring complexes will uncover more stygobiont species.

Superfamily Hadzioidea S. Karaman, 1943 (Bousfield, 1983) [68].

3.2. Eriopisidae Lowry and Myers, 2013 [69]

The Eriopisidae is a cosmopolitan family comprised of marine, freshwater, epigean, and hypogean species [69]. There are four genera and 20 species of groundwater-associated eriopisids that have been described in Australia (Table 1, Figure 1), which were historically identified as Melitidae until revised by Lowry and Myers [69]. All are stygobiont and largely occur in unconfined alluvial aquifer systems in WA.

The monotypic *Norcapensis* (for *Norcapensis mandibulis*) is found in pools in deep limestone caves of Cape Range (North West Cape) in WA.

Nedsia is largely a morphologically cryptic species complex of 16 species, distributed through unconfined alluvial aquifer systems across the Pilbara, Barrow Island, and Cape Range (North West Cape) [18]. Barrow Island is an anticline of Miocene limestone, similar to Cape Range (North West Cape), but there are alluvial deposits along some coasts and gravels in stream beds. The type species *Nedsia douglasi* is described from Cape Range, WA (we note that access to the type locality has been destroyed), and a further 15 species are described from Barrow Island and across the Pilbara in WA.

Pilbarana, with two species, is also described from alluvial aquifer systems in the Pilbara region [43]. Unpublished data suggest several additional undescribed species.

The described species of *Nedsia* and *Pilbarana* are identified as short-range endemics, as defined by Harvey [70] to be taxa with ranges <10,000 km^2. Thus, it is likely that considerably more species will be found as additional molecular data from broader geographic areas across the Pilbara are examined.

An additional monotypic genus, *Aenigmata* (*A. megabranchia*) described alongside this publication in same volume [39], is now described from a very limited distribution (1–2 bores) on Barrow Island.

3.3. Hadziidae S. Karaman, 1943 [71]

The Hadziidae are a cosmopolitan family with marine, freshwater, epigean, and hypogean taxa [69]. Two Australian hadziid species (*Hadzia branchialis* [41] and *Hadzia subthalassicus* [41] are described from anchialine cave systems in North West Cape and Barrow Island (WA) (Table 1, Figure 1). Both are true stygobionts. They were originally described within *Liagoceradocus* but moved when this genus was later synonymized with *Hadzia* [72].

3.4. *Melitidae Bousfield, 1973 [73]*

The Melitidae are diverse and cosmopolitan, with marine, freshwater, epigean, and hypogean taxa [69]. Three melitid species from separate genera are found in groundwater habitats across eastern and southern Australia (NSW, SA, and WA) (Table 1, Figure 1).

The monotypic *Brachina* (for *Brachina invasa* [40]), from alluvial aquifers in the Flinders Ranges in SA, is a true stygobiont.

Nurina poulteri [45], also a true stygobiont, is described from a groundwater pool in Nurina cave in the Nullarbor karst in WA.

Josephosella plumulosa [44] is recorded from a groundwater-fed artificial freshwater lake in NSW.

Additional species of melitids have been identified (Leijs, unpublished data) from alluvial aquifers in the Flinders Ranges, karst aquifers in the Uley groundwater basin (Eyre Peninsula, SA), and small limestone basins on Yorke Peninsula, SA.

Bogidielloidea Hertzog, 1936 [74].

3.5. *Bogidiellidae Hertzog, 1936 [74]*

The bogidiellids are a family of freshwater, hypogean taxa with a world-wide distribution [69]. Four bogidiellid species in three genera have been recorded from Australia, largely along coastal habitats in WA, SA, and QLD (Table 1, Figure 1).

Bogidomma australis [41] is known from a cave on Barrow Island (WA). This species has eyes, so it is not considered a true stygobiont but considered groundwater dependent.

Bogidiella veneris [46] is a true stygobiont species from a groundwater observation well drilled in an aeolianite limestone formation on the Eyre Peninsula, SA.

Xystriogidiella capricornea [47] and *Xystriogidiella juliani* [48] are both stygobiont species from interstitial waters off marine beaches, Great Barrier Reef, QLD. It is likely that this is a site of groundwater undersea venting.

Crangonyctoidea Bousfield, 1973 [73].

3.6. *Chillagoeidae Lowry and Myers, 2013 [69]*

Lowry and Myers [69] established Chillagoeidae for the monotypic *Chillagoe* (for *Chillagoe thea* [40]), a stygobiont from a freshwater pool in a cave in northern QLD. Two further QLD stygobiont genera and species (*Warregoensis lowryi* [49] and *Carnarvonis katjae* [49]) were recently described from a spring-fed upwelling of groundwater within a gravel creek bed in central QLD (Table 1; Figure 1). With these two new genera and species recently described from a single spring site, it is likely that many additional stygobiont species will be found across QLD as more areas are explored.

3.7. *Giniphargidae Lowry and Myers, 2013 [69]*

Lowry and Myers [69] established Giniphargidae for the monotypic *Giniphargus* (for *Giniphargus pulchellus* [50]), a blind species collected from a freshwater pool (likely spring-fed) in Gippsland in eastern VIC (Table 1, Figure 1).

3.8. *Neoniphargidae Bousfield, 1977 [75]*

The Neoniphargidae are an endemic Australian freshwater amphipod family with both epigean and hypogean species [69]. Currently this family includes five genera and 15 species associated with groundwater: *Jasptorus* and *Neocrypta* (from caves in NSW) [42], *Neoniphargus* (species found in cave pools and spring-fed lakes across NSW and VIC) [42], *Wesniphargus* (from cave pool habitats in WA) [42,53], and *Wombeyanus* (from a cave pool in NSW) [42] (Table 1; Figure 1). We have excluded the monotypic genera *Tasniphargus* and *Yulia* from our list as they are epigean species from high altitude lakes in TAS, not necessarily associated with groundwater [55]

At least three new genera with undescribed species of neoniphargids have been collected from alluvial aquifers and spring habitats in SA: western slopes of the Mount Lofty Ranges (Leijs unpublished), southern Mount Lofty Ranges and Fleurieu Peninsula

(Leijs, King and Schwartz unpublished), and further species occur in the Mount Gambier aquifer, southeast SA (Leijs unpublished).

3.9. Paramelitidae Bousfield, 1977 [75]

The Paramelitidae include freshwater epigean and hypogean amphipod genera distributed across Australia and South Africa [76]. Twelve genera and 38 species associated with groundwater are currently described from Australia: *Austrogammarus* and *Austrocrangonyx* from spring habitats in southern Australia (SA, VIC, NSW, and TAS) [55]; *Hurleya*, *Protocrangonyx*, *Totgammarus*, *Toulrabia*, and *Uroctena* from southwestern WA [52,57,59]; and *Pilbarus*, *Maarrka*, *Molina*, *Chydaekata*, and *Kruptus* from the Pilbara, WA [24,40,42,56,58] (Table 1, Figure 1). Habitats include southern springs in VIC and SA, aquifers in the Pilbara, and springs in south-west WA. We have excluded *Antipodeus* species from our list as they are epigean species from high altitude lakes in TAS, not necessarily associated with groundwater [55], although we note that Bradbury and Williams [42] referred to *Antipodeus* species as "troglophiles".

Unpublished data document 50+ potential species across several new genera in WA (King, unpublished data). Sixteen evolutionary lineages/species have also been identified in the Yilgarn calcretes [25] and more are likely to be known given numerous unexplored calcretes remain. There is also at least one blind *Austrogammarus* species collected from bore holes in the Mount Gambier Aquifer in south-east SA (Leijs unpublished).

3.10. Perthiidae Williams and Barnard, 1988 [55]

The Perthiidae are an Australian endemic freshwater amphipod family, distributed across temperate habitats. There is one known genus of the family, *Perthia*, with two epigean species described from groundwater-fed habitats in southwestern WA [53,61] (Table 1, Figure 1).

There is evidence of greater species diversity within *Perthia*, with four additional undescribed *Perthia* species, including stygobionts, from southwestern WA [77] and species reported from SA (Scott Creek, Mount Lofty Ranges and Lower SE), Lake Condah area, VIC (Leijs unpublished data), as well as other locations in NSW and VIC [78].

3.11. Uronyctidae Lowry and Myers, 2013 [69]

Lowry and Myers [69] established Uronyctidae for the monotypic and former crangonyctid taxon *Uronyctus longicaudus* [62] from SA. This species was collected from rotting wood inside a sinkhole and limestone cave habitat in Mount Gambier and is a true stygobiont (Table 1, Figure 1).

Unpublished data suggest several additional species occur in the Mount Gambier limestone aquifer, SA (Leijs unpublished).

4. Discussion

Globally, amphipod crustaceans have substantial biodiversity, with total species estimates of 10,500, including around 2100 freshwater species [79]. Updated estimates of total global subterranean amphipod species are lacking; however, older estimations indicated 197 species from 10 families in the North American–West Indian region and 376 species from 12 families in the central and southern European–Mediterranean region [16]. At that time, the Australian stygobiont fauna was considered to comprise ten species from nine genera and six families [16]. Later, Bradbury and Williams [17,42] estimated around 30 Australian subterranean species. In the current review of Australian fauna, we show that 103 formally described freshwater amphipod species representing 11 families are reported as subterranean or associated with groundwater habitats, and we estimate a further 170 amphipod species have been documented but not yet formally described (Table 1). Indeed, based on the current taxonomy, we estimate that Australian groundwater-associated species represent 12% of the global freshwater amphipod fauna, compared to the 6% estimated by Väinölä in 2008 [15]. Given this updated review, here, we describe the current hypotheses on the origins of this amphipod biodiversity in Australia, highlight possible regions of high biodiversity for future exploration, and identify specific taxon groups for future focus (Table 1).

It has been argued that the presence of significant Australian invertebrate stygobiont communities has been overlooked in the past because of assumptions over the overall aridity of Australia, as well as the lack of widespread carbonate rocks, and the lack of widespread historical glaciation events [10,27,67]. Glacial events, in particular, were deemed to be necessary for the evolution of diverse invertebrate communities in subterranean hotspots of the northern hemisphere [80,81]. Emerging research indicates aridity may be the main driver of stygobiont radiations across the Australian continent, and that Australian subterranean aquatic habitats of exceptional invertebrate biodiversity exist in atypical/unusual geologic settings, such as the isolated calcrete aquifers of the Yilgarn (WA) [82,83] and Amadeus and Ngalia Basins (NT) [84], Miocene limestone aquifers with scattered alluvial deposits of Barrow Island and Cape Range (WA), the Cambrian limestone aquifer system of Beetaloo Basin (NT), the Tertiary limestone aquifer of the Lower South East (SA), a number of small limestone groundwater basins on the Eyre Peninsula (SA), numerous confined and unconfined alluvial aquifers in the Pilbara (WA) and eastern Australia (NSW and QLD) [20,85,86], alluvial and fractured rock aquifers in the Flinders and Mount Lofty Ranges (SA) and NSW, anchialine cave systems in north-west Australia (WA), artesian springs (GAB spring groups in SA, NSW, and QLD), and springs and spring-fed seeps and marshes (largely in southern temperate regions).

The predominant picture forming for the evolution of Australian stygofauna generally indicates that it is an ancient fauna, many with Gondwanan affinities [87]. In the arid zone, there is evidence for significant radiations that align with tributaries (Pilbara, WA) [19], spring groups (Great Artesian Basin) [26,65,88], and individual confined aquifers (Yilgarn, WA [89–91]), as well as the Ngalia, Amadeus, and Beetaloo basins, NT [22]. There is also evidence for repeated patterns of colonization and isolation of invertebrates within groundwater systems across the arid zone [92], likely linked to climatic changes starting in the Miocene that have led to increased aridity across central and northern Australia [25,65,93]. It should be noted that exploration efforts for groundwater-associated invertebrates have been uneven across Australia, with a recent intense focus on areas of resource mining (i.e., the Pilbara region of WA), where exploration wells and bores can provide exceptional access to aquifers as well as providing specimens from legislated environmental reporting that requires biological survey work. Recent surveys of springs across non-arid regions of SA (Leijs, King and Schwartz, unpublished data) indicate that springs associated with fractured rock aquifers are core habitats for diverse invertebrate stygobiont communities, with springs existing as important but poorly surveyed interfaces between groundwater and surface habitats [94].

As predicted by Väinölä et al. [15], Australian stygobiont amphipods are now being demonstrated to show exceptional patterns of distribution and diversity [18,25,26,32,37]. Many species have distributions that are restricted to localized habitats (individual aquifers, tributaries, or springs) and are considered ultrashort-range endemics (uSREs), taxa with distributions less than 100 km^2 [88]. Considering the described species, the Chiltoniidae, Giniphargidae, Melitidae, Neoniphargidae, Paramelitidae, Perthiidae, and Uronyctidae are largely distributed across temperate eastern and southern Australia, although some (Chiltoniidae, Paramelitidae) are also successful within groundwater systems across arid zones in WA and SA. Other groups are more restricted: the Eriopisidae are represented by taxa in the arid north-west of Australia; the Chillagoeidae in tropical north-east QLD; the Bogidiellidae from coastal anchialine (i.e., freshwater habitats with subterranean connections to the ocean) habitats in the north-west (WA), coastal SA, and interstitial beaches in north-east Australia; and the Hadziidae from coastal (anchialine) habitats in the north-west. As noted by Humphreys [28], groups distributed in subterranean habitats across the arid zones, tropics, and subtropics comprise only stygobiont species, whereas combinations of epigean and stygobiont species are common in groundwater-associated groups in the southern temperate regions.

5. Conclusions

Australian groundwater habitats contain exceptional invertebrate biodiversity, particularly for amphipod crustaceans (both stygobiont and associated epigean species). One hundred and three described freshwater amphipod species are classified herein as associated with groundwater habitats, and we estimate a further 170 amphipod species have been documented but not yet formally described. Additional species from poorly explored areas (especially QLD, and springs across temperate southern Australia) are still likely to be found and will increase species numbers significantly.

The predominant hotspot of stygobiont amphipod biodiversity are the alluvial aquifers of the Pilbara region (WA). However, numerous diverse habitats are identified as emerging biodiversity hotspots: the isolated calcrete aquifers of the Yilgarn (WA), Amadeus Basin, and Ngalia Basins (NT); limestone aquifer systems of the Beetaloo Basin (NT); the limestone aquifers of the Lower South East of SA; numerous confined and unconfined alluvial aquifers in eastern Australia (NSW and QLD); alluvial and fractured rock aquifers in the Flinders and Mount Lofty Ranges (SA) and NSW; anchialine cave systems in north-west Australia (WA); artesian springs (Great Artesian Basin spring groups in SA, NSW, and QLD); and springs and spring-fed seeps and marshes in southern temperate regions.

It is likely that many of the true stygobiont amphipod taxa, and many epigean associates dependent on the subterranean systems, are uSREs, with severely restricted distributions of less than 100 km^2, and often within confined aquifer systems. Amphipods form an important ecological constituent within subterranean habitats and should be a primary focus of water and landscape conservation management plans. Also, their evolutionary relationships provide significant palaeoecological information on landscape and biodiversity changes over time, which is of particular importance as we navigate global climatic and biodiversity crises.

Author Contributions: Conceptualization, R.A.K., R.L., B.S. and S.J.B.C.; methodology, R.A.K., D.N.S., R.L., S.J.B.C. and M.T.G.; validation, R.A.K.; investigation, R.A.K.; data curation, R.A.K. and J.T.; writing—original draft preparation, R.A.K. and D.N.S.; writing—review and editing, R.A.K., D.N.S., S.J.B.C., R.L., B.S., W.F.H., J.T. and M.T.G.; visualization, R.A.K. All authors have read and agreed to the published version of the manuscript.

Funding: Several sources of external funding have contributed to the generation of much of the authors' published and unpublished data referred to in this review paper. Australian Biological Resources Study (ABRS) National Taxonomy Research Grant Program (RF 211-20) to R.A.K., S.J.B.C. and W.F.H. (with funding support from the South Australian Museum, The University of Adelaide's School of Biological Sciences and the Australian Centre of Evolutionary Biology and Biodiversity, Subterranean Ecology and Bennelongia). ABRS National Taxonomy Research Grant (No. 208-61) to S.J.B.C. Hermon Slade Foundation research project funding (HSF11-8) to R.A.K. and S.J.B.C. Bush Blitz Tactical Taxonomy Grant from the Australian Government through ABRS (2017–2018) to R.L. and R.A.K. Landscape SA Hills and Fleurieu, 2023 grassroots funding to R.L. and R.A.K. M.T.G. was supported by Australian Research Council Linkage Project Grant LP190100555 (linkage partners: Rio Tinto, BHP, Chevron, South Australian Museum, Western Australian Museum, Department of Biodiversity, Conservation and Attractions, Department for Water and Environmental Regulation, and Western Australian Biodiversity Science Institute). DNS was supported by the Western Australian Biodiversity Science Institute (WABSI), with funding provided by BHP Billiton Iron Ore Pty Ltd. and Rio Tinto Ltd., as well as funding from The University of Adelaide's Faculty of Sciences, Engineering and Technology (SET) Research Transition Support Scheme.

Data Availability Statement: No new data were created or analyzed in this study. Data sharing is not applicable to this article.

Acknowledgments: Thanks to Andrea Crowther and Shirley Sorokin (Collection Managers, Marine Invertebrates, South Australian Museum) for tireless collections support. Thanks also to Andrew Hosie (Curator of Crustacea, Western Australian Museum), Melanie Mackenzie (Collection Manager, Marine Invertebrates, Museum Victoria), and Marissa McNamara (Collection Manager, crustacea, Queensland Museum) for providing information on type specimens and available material as well as collections support.

Conflicts of Interest: The authors declare no conflicts of interest in the subject matter or materials discussed in this manuscript.

References

1. Gleeson, T.; Befus, K.M.; Jasechko, S.; Luijendijk, E.; Cardenas, M.B. The global volume and distribution of modern groundwater. *Nat. Geosci.* **2016**, *9*, 161–167. [CrossRef]
2. Lall, U.; Josset, L.; Russo, T. A snapshot of the world's groundwater challenges. *Annu. Rev. Environ. Resour.* **2020**, *45*, 171–194. [CrossRef]
3. Griebler, C.; Hahn, H.J.; Mammola, S.; Niemiller, M.L.; Weaver, L.; Saccò, M.; Bichuette, M.E.; Hose, G.C. Legal frameworks for the conservation and sustainable management of groundwater ecosystems. In *Groundwater Ecology and Evolution*, 2nd ed.; Malard, F., Griebler, C., Retaux, S., Eds.; Elsevier: Amsterdam, The Netherlands, 2023; pp. 551–571.
4. Hartland, A.; Fenwick, G.D.; Bury, S.J. Tracing sewage-derived organic matter into a shallow groundwater food web using stable isotope and fluorescence signatures. *Mar. Freshw. Res.* **2011**, *62*, 119–129. [CrossRef]
5. Griebler, C.; Avramov, M. Groundwater ecosystem services: A review. *Freshw. Sci.* **2015**, *34*, 355–367. [CrossRef]
6. Hose, G.C.; Stumpp, C. Architects of the underworld: Bioturbation by groundwater invertebrates influences aquifer hydraulic properties. *Aquat. Sci.* **2019**, *81*, 20. [CrossRef]
7. Chen, L.; Tan, L.; Zhao, M.; Sinha, A.; Wang, T.; Gao, Y. Karst carbon sink processes and effects: A review. *Quat. Int.* **2023**, *652*, 63–73. [CrossRef]
8. Saccò, M.; Mammola, S.; Altermatt, F.; Alther, R.; Bolpagni, R.; Brancelj, A.; Brankovits, D.; Fišer, C.; Gerovasileiou, V.; Griebler, C.; et al. Groundwater is a hidden global keystone ecosystem. *Glob. Chang. Biol.* **2024**, *30*, e17066. [CrossRef]
9. Boulton, A.J.; Bichuette, M.E.; Korbel, K.; Stoch, F.; Niemiller, M.L.; Hose, G.C.; Linke, S. Recent concepts and approaches for conserving groundwater biodiversity. In *Groundwater Ecology and Evolution*, 2nd ed.; Malard, F., Griebler, C., Retaux, S., Eds.; Elsevier: Amsterdam, The Netherlands, 2023; pp. 525–550.
10. Humphreys, W.F. Rising from Down Under: Developments in subterranean biodiversity in Australia from a groundwater fauna perspective. *Invertebr. Syst.* **2008**, *22*, 85–101. [CrossRef]
11. Koch, F.; Blum, P.; Korbel, K.; Menberg, K. Global overview on groundwater fauna. *Ecohydrology* **2024**, *17*, e2607. [CrossRef]
12. Dauvin, J.C. Twenty years of application of Polychaete/Amphipod ratios to assess diverse human pressures in estuarine and coastal marine environments: A review. *Ecol. Indic.* **2018**, *95*, 427–435. [CrossRef]
13. Podlesińska, W.; Dąbrowska, H. Amphipods in estuarine and marine quality assessment–a review. *Oceanologia* **2019**, *61*, 179–196. [CrossRef]
14. Navarro-Barranco, C.; Ros, M.; de Figueroa, J.M.T.; Guerra-García, J.M. Marine crustaceans as bioindicators: Amphipods as case study. *J. Fish. Aquac.* **2020**, *9*, 435–463.
15. Väinölä, R.; Witt, J.D.S.; Grabowski, M.; Bradbury, J.H.; Jazdzewski, K.; Sket, B. Global diversity of amphipods (Amphipoda; Crustacea) in freshwater. *Hydrobiologia* **2008**, *595*, 241–255. [CrossRef]
16. Holsinger, J.R. Biodiversity of subterranean amphipod crustaceans: Global patterns and zoogeographic implications. *J. Nat. Hist.* **1993**, *27*, 821–835. [CrossRef]
17. Bradbury, J.H.; Williams, W.D. *Key to and Checklist of the Inland Aquatic Amphipods of Australia*; Technical Reports of the Australian Museum No. 14; Australian Museum: Darlinghurst, Australia, 1999; pp. 1–21.
18. King, R.A.; Fagan-Jeffries, E.P.; Bradford, T.M.; Stringer, D.N.; Finston, T.L.; Halse, S.A.; Eberhard, S.M.; Humphreys, G.; Humphreys, B.F.; Austin, A.D.; et al. Cryptic diversity down under: Defining species in the subterranean amphipod genus *Nedsia* Barnard & Williams, 1995 (Hadzioidea: Eriopisidae) from the Pilbara, Western Australia. *Invertebr. Syst.* **2022**, *36*, 113–159.
19. Finston, T.L.; Johnson, M.S.; Humphreys, W.F.; Eberhard, S.; Halse, S. Cryptic speciation in two widespread subterranean amphipod genera reflects historical drainage patterns in an ancient landscape. *Mol. Ecol.* **2007**, *16*, 355–365. [CrossRef]
20. Eberhard, S.M.; Halse, S.A.; Humphreys, W.F. Stygofauna in the Pilbara region, north-west Western Australia: A review. *J. R. Soc. West. Aust.* **2005**, *88*, 167–176.
21. Hose, G.C.; Sreekanth, J.; Barron, O.; Pollino, C. *Stygofauna in Australian Groundwater Systems: Extent of knowledge*; CSIRO: Canberra, Australia, 2015.
22. Rees, G.N.; Oberprieler, S.; Nielsen, D.; Watson, G.; Shackleton, M.; Davis, J.A. *Characterisation of the Stygofauna and Microbial Assemblages of the Beetaloo Sub-Basin, Northern Territory*; CSIRO: Canberra, Australia, 2020.
23. Thurgate, M.E.; Gough, J.S.; Spate, A.; Eberhard, S. Subterranean biodiversity in New South Wales: From rags to riches. *Rec. West. Aust. Mus.* **2001**, *64*, 37–48. [CrossRef]

24. Finston, T.L.; Johnson, M.S.; Eberhard, S.M.; Cocking, J.S.; McRae, J.M.; Halse, S.A.; Knott, B. A new genus and two new species of groundwater paramelitid amphipods from the Pilbara, Western Australia: A combined molecular and morphological approach. *Rec. West. Aust. Mus.* **2011**, *26*, 154–178. [CrossRef]
25. Cooper, S.J.B.; Bradbury, J.H.; Saint, K.M.; Leys, R.; Austin, A.D.; Humphreys, W.F. Subterranean archipelago in the Australian arid zone: Mitochondrial DNA phylogeography of amphipods from central Western Australia. *Mol. Ecol.* **2007**, *16*, 1533–1544. [CrossRef]
26. Murphy, N.P.; Adams, M.; Guzik, M.T.; Austin, A.D. Extraordinary micro-endemism in Australian desert spring amphipods. *Mol. Phyl. Evol.* **2013**, *66*, 645–653. [CrossRef] [PubMed]
27. Guzik, M.T.; Austin, A.D.; Cooper, S.J.B.; Harvey, M.S.; Humphreys, W.F.; Bradford, T.; Eberhard, S.M.; King, R.A.; Leys, R.; Muirhead, K.A.; et al. Is the Australian subterranean fauna uniquely diverse? *Invertebr. Syst.* **2011**, *24*, 407–418. [CrossRef]
28. Humphreys, W.F. Diversity Patterns in Australia. In *Encyclopedia of Caves*; White, W.B., Culver, D.C., Pipan, T., Eds.; Academic Press: Chennai, India, 2012; pp. 203–219.
29. Rafinesque, C.S. *Analyse de la Nature ou Tableau de L'univers et des Corps Organisés*; Self-Published: Palermo, Italy, 1815; pp. 1–224.
30. Barnard, J.L. Gammaridean Amphipoda of Australia, Part 1. *Smithsonian Contrib. Zool.* **1972**, *103*, 1–333. [CrossRef]
31. QGIS Development Team. QGIS Geographic Information System. Open Source Geospatial Foundation Project. 2024. Available online: https://qgis.osgeo.org (accessed on 1 October 2024).
32. King, R.A. Two new genera and species of chiltoniid amphipods (Crustacea: Amphipoda: Talitroidea) from freshwater mound springs in South Australia. *Zootaxa* **2009**, *2293*, 35–52. [CrossRef]
33. Sayce, O.A. Description of some new Victorian fresh-water Amphipoda. *Proc. R. Soc. Vic.* **1901**, *13*, 225–242; pls. 36–40.
34. Zeidler, W. A new species of freshwater amphipod, *Austrochiltonia dalhousiensis* sp. nov. (Crustacea: Amphipoda: Hyalellidae) from Dalhousie Springs, South Australia. *Trans. R. Soc. South Aust.* **1997**, *121*, 29–42.
35. King, R.A.; Leys, R. Molecular evidence for mid-Pleistocene divergence of populations of three freshwater amphipod species (Talitroidea: Chiltoniidae) on Kangaroo Island, South Australia, with a new spring-associated genus and species. *Aust. J. Zool.* **2014**, *62*, 137–156. [CrossRef]
36. Zeidler, W. A new genus and species of phreatic amphipod (Crustacea: Amphipoda) belonging in the chiltonia generic group, from Dalhousie springs, South Australia. *Trans. R. Soc. South Aust.* **1991**, *115*, 177–187.
37. King, R.A.; Bradford, T.; Austin, A.D.; Humphreys, W.F.; Cooper, S.J.B. Divergent Molecular Lineages and Not-So-Cryptic Species: The First Descriptions of Stygobitic Chiltoniid Amphipods (Talitroidea: Chiltoniidae) from Western Australia. *J. Crust. Biol.* **2012**, *32*, 465–488. [CrossRef]
38. Murphy, N.P.; King, R.A.; Delean, S. Species, ESUs or populations? Delimiting and describing morphologically cryptic diversity in Australian desert spring amphipods. *Invertebr. Syst.* **2015**, *29*, 457–467. [CrossRef]
39. Stringer, D.N.; King, R.A.; Austin, A.D.; Guzik, M.T. An elusive new genus and species of subterranean amphipod (Hadzioidea: Eriopisidae) from Barrow Island, Western Australia. *Diversity* **2024**, *in press*.
40. Barnard, J.L.; Williams, W.D. The taxonomy of Amphipoda (Crustacea) from Australian fresh waters: Part 2. *Rec. Aust. Mus.* **1995**, *47*, 161–201. [CrossRef]
41. Bradbury, J.H.; Williams, W.D. Two new species of anchialine amphipod (Crustacea: Hadziidae: *Liagoceradocus*) from Western Australia. *Rec. West. Aust. Mus.* **1996**, *17*, 395–410.
42. Bradbury, J.H.; Williams, W.D. Amphipod (Crustacea) diversity in underground waters in Australia: An Aladdin's Cave. *Mem. Mus. Vic.* **1997**, *56*, 513–519. [CrossRef]
43. Stringer, D.N.; King, R.A.; Austin, A.D.; Guzik, M.T. *Pilbarana*, a new subterranean amphipod genus (Hadzioidea: Eriopisidae) of environmental assessment importance from the Pilbara, Western Australia. *Zootaxa* **2022**, *5188*, 559–573. [CrossRef] [PubMed]
44. Zeidler, W. A new species of *Melita* (Crustacea: Amphipoda: Melitidae) from northern New South Wales with a note on the genus *Abludomelita* Karaman, 1981. *Proc. Linn. Soc. N. S. W.* **1989**, *110*, 327–338.
45. Bradbury, J.H.; Eberhard, S. A new stygobiont melitid amphipod from the Nullarbor Plain. *Rec. West. Aust. Mus.* **2000**, *20*, 39–50.
46. Leijs, R.; Bloechl, A.; Koenemann, S. *Bogidiella* veneris, a new species of subterranean Amphipoda (Bogidiellidae) from Australia, with remarks on the systematics and biogeography. *J. Crust. Biol.* **2011**, *31*, 566–575. [CrossRef]
47. Stock, J.H. First record of Bogidiellidae (Crustacea, Amphipoda) from the Pacific: *Bogidiella* (*Xystriogidiella* n. subgen.) capricornea new species from the Great Barrier Reef. *Bull. Mar. Sci.* **1984**, *34*, 380–385.
48. Coleman, C.O. Bogidiellidae. *Zootaxa* **2009**, *2260*, 279–284. [CrossRef]
49. King, R.A.; Stringer, D.N.; Leijs, R. *Carnarvonis* gen. nov. and *Warregoensis* gen. nov.: Two new genera and species of subterranean amphipods (Crangonyctoidea: Chillagoeidae) described from north-eastern Australia. Festschrift in Honour of James K. Lowry. *Rec. Aust. Mus.* **2023**, *75*, 447–457. [CrossRef]
50. Sayce, O.A. Art. XVII.-*Niphargus pulchellus*, a new Victorian blind amphipod. *Proc. R. Soc. Vic.* **1899**, *112*, 152–159.
51. Sayce, O.A. Description of some new Victorian fresh-water Amphipoda. no. 2. *Proc. R. Soc. Vic.* **1902**, *15*, 47–58; pls. 4–7.
52. Nicholls, G.E. *Protocrangonyx fontinalis*, a new blind freshwater amphipod from Western Australia. *J. R. Soc. West. Aust.* **1926**, *12*, 71–78.
53. Straškraba, M. *Perthia* n. g. (Amphipoda, Gammaridae) from fresh water of Western Australia, with remarks on the genera *Neoniphargus* and *Uroctena*. *Crustaceana* **1964**, *7*, 125–139. [CrossRef]

54. Chilton, C. Some Amphipoda and Isopoda from Barrington Tops (4600 ft. alt) N.S.W. *J. Proc. R. Soc. N. S. W.* **1917**, *50*, 82–98. [CrossRef]
55. Williams, W.D.; Barnard, J.L. The Taxonomy of Crangonyctoid Amphipoda (Crustacea) from Australian Fresh Waters: Foundation Studies. *Rec. Aust. Mus.* **1988**, *10*, 1–180. [CrossRef]
56. Bradbury, J.H. Western Australian stygobiont amphipods (Crustacea: Paramelitidae) from the Mt Newman and Millstream regions. *Rec. West. Aust. Mus.* **2000**, *60*, 1–102. [CrossRef]
57. Straškraba, M. *Hurleya kalamundae* ngn sp.(Amphipoda, Gammaridae) from subterranean waters of Western Australia. *Int. J. Speleol.* **1966**, *2*, 1–5. [CrossRef]
58. Finston, T.L.; Johnson, M.S.; Knott, B. A new genus and species of stygobitic paramelitid amphipod from the Pilbara, Western Australia. *Rec. West. Aust. Mus.* **2008**, *24*, 395–410. [CrossRef]
59. Bradbury, J.H.; Williams, W.D. A new genus and species of crangonyctoid amphipod (Crustacea) from Western Australian fresh waters. *Trans. R. Soc. South Aust.* **1995**, *119*, 67–74.
60. Chilton, C. A new blind freshwater amphipod from Western Australia. *J. R. Soc. West. Aust.* **1925**, *11*, 81–84.
61. Nicholls, G.E. *Neoniphargus branchialis*, a new freshwater amphipod from south-western Australia. *J. R. Soc. West. Aust.* **1924**, *10*, 105–111.
62. Stock, J.H.; Iliffe, T.M. A new Australian crangonyctid amphipod with a habit convergent to the Old World genus *Niphargus*. *Stygologia* **1990**, *5*, 137–142.
63. Atlas of Living Australia. Available online: http://www.ala.org.au (accessed on 4 September 2024).
64. King, R.A.; Leys, R. The Australian freshwater amphipods *Austrochiltonia australis* and *Austrochiltonia subtenuis* (Amphipoda: Talitroidea: Chiltoniidae) confirmed and two new cryptic Tasmanian species revealed using a combined molecular and morphological approach. *Invertebr. Syst.* **2011**, *25*, 171–196. [CrossRef]
65. Murphy, N.P.; Adams, M.; Austin, A.D. Independent colonization and extensive cryptic speciation of freshwater amphipods in the isolated groundwater springs of Australia's Great Artesian Basin. *Mol. Ecol.* **2009**, *18*, 109–122. [CrossRef]
66. Bradford, T.; Adams, M.; Humphreys, W.F.; Austin, A.D.; Cooper, S.J.B. DNA barcoding of stygofauna uncovers cryptic amphipod diversity in a calcrete aquifer in Western Australia's arid zone. *Mol. Ecol. Res.* **2010**, *10*, 41–50. [CrossRef]
67. Humphreys, W.F. Groundwater calcrete aquifers in the Australian arid zone: The context to an unfolding plethora of stygal biodiversity. *Rec. West. Aust. Mus. Supp.* **2001**, *64*, 63–83. [CrossRef]
68. Bousfield, E.L. An updated phyletic classification and palaeohistory of the Amphipoda. Crustacean Phylogeny. *Crust. Issues* **1983**, *1*, 257–277.
69. Lowry, J.K.; Myers, A.A. A phylogeny and classification of the Senticaudata subord. nov. Crustacea: Amphipoda. *Zootaxa* **2013**, *3610*, 1–80. [CrossRef]
70. Harvey, M.S. Short-range endemism amongst the Australian fauna: Some examples from non-marine environments. *Invertebr. Syst.* **2002**, *16*, 555–570. [CrossRef]
71. Karaman, S. Die Unterirdischen Amphipoden Südserbiens. *Ohridski zbornik* **1943**, *34*, 163–313.
72. Sawicki, T.R.; Holsinger, J.R.; Iliffe, T.M. Four new species of the subterranean amphipod genus *Hadzia* (Hadziidae) from caves in the western Pacific, with a re-evaluation of the taxonomic status of the genus. *Subterr. Biol.* **2004**, *2*, 65–90.
73. Bousfield, E.L. *Shallow-Water Gammaridean Amphipoda of New England*; Cornell University Press: Ithaca, NY, USA, 1973; 312p.
74. Hertzog, L. Crustacés de biotopes hypogées de la vallée du Rhin d'Alsace. *Bull. Soc. Zool. Fr.* **1936**, *61*, 356–372.
75. Bousfield, E.L. A new look at the systematics of gammaroidean amphipods of the world. In *Studies on Gammaridea*; Brill: Leiden, The Netherlands, 1977; pp. 282–316.
76. Milne, R.; Griffiths, C.L. Additions to and revisions of the amphipod (Crustacea: Amphipoda) fauna of South Africa, with a list of currently known species from the region. *Afr. Nat. Hist.* **2013**, *9*, 61–90.
77. Eberhard, S.M.; Leijs, R.; Adams, M. Conservation of subterranean biodiversity in Western Australia: Using molecular genetics to define spatial and temporal relationships in two species of cave-dwelling Amphipoda. *Subterr. Biol.* **2005**, *3*, 13–27.
78. Lowry, J.K.; Stoddart, H.E. Crustacea: Malacostraca: Peracarida: Amphipoda, Cumacea, Mysidacea. In *Zoological Catalogue of Australia*; Beesley, P.L., Houston, W.W.K., Eds.; CSIRO Publishing: Melbourne, Australia, 2003; Volume 19.2B, pp. xii–531.
79. Horton, T.; De Broyer, C.; Bellan-Santini, D.; Coleman, C.O.; Copilaș-Ciocianu, D.; Corbari, L.; Daneliya, M.E.; Dauvin, J.C.; Decock, W.; Fanini, L.; et al. The World Amphipoda Database: History and progress. *Rec. Aust. Mus.* **2023**, *75*, 329–342. [CrossRef]
80. Peck, S.B. Climatic change and the evolution of cave invertebrates in the Grand Canyon, Arizona. *Nat. Speleo. Soc. Bull.* **1980**, *42*, 53–60.
81. Boutin, C. Stygobiology and historical geology: The age of Fuerteventura (Canary Islands) as inferred from its present stygofauna. *Bull. Soc. Géol. Fr.* **1994**, *165*, 273–285.
82. Humphreys, W.F. Relict stygofaunas living in sea salt, karst and calcrete habitats in arid northwestern Australia contain many ancient lineages. In *The Other 99%: The Conservation and Biodiversity of Invertebrates*; Ponder, W., Lunney, D., Eds.; Royal Zoological Society of New South Wales: Mosman, NSW, Australia, 1999; pp. 219–227.
83. Hyde, J.; Cooper, S.J.B.; Humphreys, W.F.; Austin, A.D.; Munguia, P. Diversity patterns of subterranean invertebrate fauna in calcretes of the Yilgarn Region, Western Australia. *Mar. Fresh. Res.* **2018**, *69*, 114–121. [CrossRef]
84. Ponder, W.F.; Humphreys, W.F.; Shea, M.; Dolman, G.; Criscione, F. Subterranean Tateidae (Gastropoda; Caenogastropoda; Truncatelloidea) from the Ngalia Basin, Northern Territory, Australia. *Mollusc. Res.* **2021**, *42*, 50–72. [CrossRef]

85. Clark, H.; Buzatto, B.; Halse, S.A. Hotspot of Arid Zone Subterranean Biodiversity: The Robe Valley in Western Australia. *Diversity* **2021**, *13*, 482. [CrossRef]
86. Halse, S.A.; Scanlon, M.D.; Cocking, J.S.; Barron, H.J.; Richardson, J.B.; Eberhard, S.M. Pilbara stygofauna: Deep groundwater of an arid landscape contains globally significant radiation of biodiversity. *Rec. West. Aust. Mus. Supp.* **2014**, *78*, 443–483. [CrossRef]
87. Karanovic, I.; Humphreys, W.F. Phylogeny and diversity of Timiriaseviinae ostracods (Podocopida, Cytheroidea) with description of one new species from arid Western Australia. *Syst. Biodiv.* **2014**, *12*, 93–110. [CrossRef]
88. Guzik, M.T.; Stringer, D.N.; Murphy, N.P.; Cooper, S.J.B.; Taiti, S.; King, R.A.; Humphreys, W.F.; Austin, A.D. Molecular phylogenetic analysis of Australian arid-zone oniscidean isopods (Crustacea: Haloniscus) reveals strong regional endemicity and new putative species. *Invertebr. Syst.* **2019**, *33*, 556–574.
89. Cooper, S.J.B.; Hinze, S.; Leys, R.; Watts, C.H.S.; Humphreys, W.F. Islands under the desert: Molecular systematics and evolutionary origins of stygobitic water beetles (Coleoptera: Dytiscidae) from central Western Australia. *Invertebr. Syst.* **2002**, *16*, 589–598. [CrossRef]
90. Cooper, S.J.B.; Saint, K.M.; Taiti, S.; Austin, A.D.; Humphreys, W.F. Subterranean archipelago: Mitochondrial DNA phylogeography of stygobitic isopods (Oniscidea: *Haloniscus*) from the Yilgarn region of Western Australia. *Invertebr. Syst.* **2008**, *22*, 195–203. [CrossRef]
91. Karanovic, T.; Cooper, S.J.B. Explosive radiation of the genus *Schizopera* on a small subterranean island in Western Australia (Copepoda: Harpacticoida): Unravelling the cases of cryptic speciation, size differentiation and multiple invasions. *Invertebr. Syst.* **2012**, *26*, 115–192. [CrossRef]
92. Leys, R.; Watts, C.H.S.; Cooper, S.J.B.; Humphreys, W.F. Evolution of subterranean diving beetles (Coleoptera: Dytiscidae: Hydroporini, Bidessini) in the arid zone of Australia. *Evolution* **2003**, *57*, 2819–2834.
93. Byrne, M.; Yeates, D.K.; Joseph, L.; Kearney, M.; Bowler, J.; Williams, M.A.J.; Cooper, S.; Donnellan, S.C.; Keogh, J.S.; Leys, R.; et al. Birth of a biome: Insights into the assembly and maintenance of the Australian arid zone biota. *Mol. Ecol.* **2008**, *17*, 4398–4417. [CrossRef]
94. Manenti, R.; Piazza, B. Between darkness and light: Spring habitats provide new perspectives for modern researchers on groundwater biology. *PeerJ* **2021**, *9*, e11711. [CrossRef] [PubMed]