Integrated conservation approach for the Australian land snail genus *Bothriembryon* Pilsbry, 1894: curation, taxonomy and palaeontology

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DECLARATION

I declare that this thesis is my own original account of my research and contains as its main content, work which has not previously been submitted for a degree at any tertiary education institution and as author, I reserve the right of copyright under the *Copyright Act 1968*, Commonwealth of Australia.

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Corey Whisson

"Probably the most intriguing land shells in Australia are the bulimoid forms inhabiting the south-west corner. A large number of species and races has developed, and probably only a tithe has been described. It is unfortunate these have not yet been studied by anyone conversant with local conditions, and it is certain that they will provide future students with much research. No more exciting subject could be chosen by the student, but the unravelling of the many problems will necessitate much investigation."

Mr Tom Iredale

(cited in Iredale, 1939)

Abstract

Native land snails are important to ecosystems given their role in the decomposition process through herbivorous feeding of primarily decaying plant matter; calcium recycling and soil nitrification, and as a food source for larger predators. They also serve as a valuable bio-indicator group, especially in Western Australia where they are critical to Environmental Impact Assessments surveys. One conspicuous genus of native land snail found in Western Australia is *Bothriembryon* Pilsbry, 1894, a Gondwanan group endemic to the southern half of Australia and most diverse in the south-west of Western Australia. Eight species of *Bothriembryon* are listed as threatened at state and international level. Modern comprehensive reviews of land snails are needed to form good conservation policy however there are a number of knowledge gaps that are hindering the development of an effective conservation management plan for *Bothriembryon*. Most taxonomic studies on the genus have been based on shell morphology and the group requires modern molecular treatment to help clarify taxonomy. Additionally the group has been subjected to limited biogeographical and ecological studies, particularly those examining diet, predation and life span.

In this study legacy data of the seven nominally threatened south-west Western Australia *Bothriembryon* species was collated from Australian museums and institutes. This data set was compared with new data gathered through curation of the WAM *Bothriembryon* collection and targeted fieldwork. Together this augmented data set was designed to improve conservation initiatives, specifically an updated assessment of these species International Union for Conservation of Nature status. Additionally, during curation of the WAM *Bothriembryon* collection, genetically useful material of all described species was earmarked for DNA extraction toward the first molecular phylogeny of the genus.

This study addressed a major nomenclatural issue with the genus name *Bothriembryon* with case 3748 submitted to the ICZN to conserve the current genus usage. To promote nomenclatural stability, it was proposed that all type species fixations for the nominal genus *Liparus* Albers, 1850 and *Bothriembryon* Pilsbry, 1894 be set aside, and to designate *Helix melo* Quoy and Gaimard, 1832 as their type species.

Many undescribed species of *Bothriembryon* are known, some likely requiring conservation management, but only one species has been named in the last 30 years (as of 2016). In this study *Bothriembryon sophiarum* was described, based on shell and anatomical morphology, the latter using 3D scanning for the first time in this group. Because of its limited distribution, *B. sophiarum* Whisson and Breure, 2016 qualifies as a short range endemic.

Little published data on the fossil biogeography of *Bothriembryon* exists. In this study, fossil and modern data of *Bothriembryon* from Australian museums and institutes were mapped for the first time. The fossil *Bothriembryon* collection in the Western Australian Museum was curated to current taxonomy. Using this data set, the geological age of fossil and extant species was documented, and where material was available, shell sizes compared between fossil and modern populations. Twenty-two extant *Bothriembryon* species were identified in the fossil collection, with 15 of these species having a published fossil record for the first time. Several fossil and extant species had range extensions. The geological age span of *Bothriembryon* was determined as a minimum of Late Oligocene to recent, with extant endemic Western Australian *Bothriembryon* species determined as younger, traced to Pleistocene age. Extant *Bothriembryon* species from the Nullarbor region were older, dated Late Pliocene to Early Pleistocene. Most extant *Bothriembryon* species have similar fossil and modern shell sizes, except for *B. fuscus* Thiele, 1930, *B. notatus* Iredale, 1939, *B. sayi* (Pfeiffer, 1847), *B. perobesus* Iredale, 1939 and *B. indictus* Iredale, 1939, which had generally more elongate shells during the Pleistocene. This study did not significantly expand the biogeography or geological age of the group but the data set provided insights into the origin and radiation of *Bothriembryon*, and will enable future phylogenetic dating.

Collectively, data generated in this study will enable better conservation outcomes for *Bothriembryon*. This data will also contribute toward the first molecular phylogeny of *Bothriembryon*.

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List of Abbreviations and Acronyms

ALA	Atlas of Living Australia
AM	Australian Museum
DPaW	Departments of Parks and Widlife
EIA	Environmental Impact Assessment
EPA	Environmental Protection Authority
GA	Geoscience Australia
GWA	Government of Western Australia
GSSA	Geological Survey of South Australia

ICZN	International Code of Zoological Nomenclature
IUCN	International Union for the Conservation of Nature
KYA	thousand years ago
MAGNT	Museum and Art Gallery of the Northern Territory
MYA	million years ago
NRETAS	Natural Resources, Environment, Arts and Sport (Northern Territory).
QM	Queensland Museum
QVMAG	Queen Victoria Museum and Art Gallery
SAM	South Australian Museum
SCTIG	South Coast Threatened Invertebrate Group
TEC	Threatened Ecological Communities
TMAG	Tasmanian Museum and Art Gallery
UWA	University of Western Australia
SRE	short-range endemic
SWWA	south-western Western Australia
WA	Western Australia
WAM	Western Australian Museum

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PUBLICATIONS

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Whisson, C.S. and Breure, A.S.H. (2016) A new species of *Bothriembryon* (Mollusca, Gastropoda, Bothriembryontidae) from south-eastern Western Australia. *ZooKeys* **581,** 127–140.

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Kirkendale, L. and **Whisson, C.S.** (2018) Wheatbelt *Bothriembryon*. *Landscope* **34**: 37.

STATEMENT OF AUTHORSHIP FOR PUBLISHED PAPERS INCLUDED IN THESIS

Title: Review of the Western Australian Museum's extant *Bothriembryon* Pilsbry, 1894 collection to aid conservation

CW reviewed the literature; curated the WAM collections; assembled electronic data, prepared bar graph; prepared all tables; planned and conducted most of the fieldwork; provided descriptions of live animals and drafted the manuscript

CW: 90%

Title: Case 3748 - *Bothriembryon* Pilsbry, 1894 (Mollusca, Orthalicoidea, BOTHRIEMBRYONTIDAE): proposed conservation of the name by designation of *Helix melo* Quoy & Gaimard, 1832 as the type species of *Liparus* Albers, 1850

CW reviewed the literature; investigated ICZN rules and drafted the manuscript

CW: 95%

Title: A new species of *Bothriembryon* (Mollusca, Gastropoda, Bothriembryontidae) from south-eastern Western Australia

CW reviewed the literature; curated the WAM collections; undertook shell measurements and descriptions; prepared distributional figure and drafted large sections of the manuscript particularly Introduction; Type Material; Other Material Examined; Diagnosis (part); Habitat; Remarks and Discussion.

CW: 75%

Title: Review of the fossil record of the Australian land snail genus *Bothriembryon* Pilsbry, 1894 (Mollusca: Gastropoda: Bothriembryontidae): new distributional and geological data

CW reviewed the literature; curated the WAM collection; assembled electronic data, prepared all tables, distributional maps and bar charts; undertook shell measurements; undertook SEM imaging and drafted the manuscript

CW: 95%

Title: The presumed extinct *Bothriembryon whitleyi* Iredale, 1939 remains elusive

CW reviewed the literature, planned and conducted fieldwork; undertook photography of shell and largely drafted the manuscript

CW: 85%

Title: Wheatbelt *Bothriembryon*

CW reviewed the literature; planned and conducted fieldwork and helped draft the manuscript

CW: 50%

By signing the Statement of Authorship, each author certifies that the candidate's stated contribution to the publication is accurate to the best of their knowledge (as detailed above), and permission is granted to include the publication in this thesis.

Corey Whisson	Lisa Kirkendale	Abraham Breure
Ben Schneider	Helen Ryan	Mikael Siversson

NOTE ON THESIS STRUCTURE

This thesis is composed of a series of four papers: Chapters 3 and 4 have been peer-reviewed and published; Chapter 5 has been submitted for publishing, and Chapter Two is in preparation to be submitted for publishing. For those chapters already published, the format and referencing style has been slightly modified from the published version to allow consistency throughout the thesis. The order of the chapters reflects the general workflow of the study and does not reflect the date published or submitted for corresponding papers. Appendices A and B are published popular articles relating to Chapter 2.

Chapter 1: General Introduction

1.1 Biodiversity and Conservation in Western Australia

Taxonomy, the formal description of new species, underpins biodiversity science (Kim and Byrne 2006; Tahseen 2014). Estimating biodiversity is important as it drives the selection of conservation areas. However, this is most challenging for highly diverse groups of small-bodied taxa, such as the majority of invertebrates (Régnier *et al.* 2015). The decline in global biodiversity is a result of many threats e.g. invasive species and urban development (Lovejoy 2002) but recent research suggests that biodiversity loss is due principally to two factors: overexploitation (harvesting) of species and agriculture (Maxwell *et al*. 2016).

In Western Australia (WA), there are a range of legislative and management policies in place to help conserve species, habitats, communities and natural biodiversity (e.g. Commonwealth Environmental Protection and Biodiversity Conservation Act 1999, Wildlife Conservation Act 1950, Conservation and Land Management Act 1984 and Environmental Protection Act 1986). On a finer scale, many conservation reserves and parks have been created within WA based on high biodiversity and endemism of the biota (Burbidge 2004), with a number of Threatened Ecological Communities (TEC) now also listed under the Environmental Protection and Biodiversity Conservation (EPBC) Act 1999.

As it is not feasible to evaluate all invertebrates, proponents of development proposals in WA are required to assess whether short-range endemic (SRE) species are present (Environmental Protection Authority 2009). SREs are defined as species with naturally small distributions (usually less than or equal to 10,000 km^2) and these species have been generally found to possess similar characteristics such as poor dispersal capability, slow growth, low fecundity and restriction to specific, discontinuous habitats. In WA, many of these species have been found to be niche-conserved Gondwanan ‘relicts’ (Hopper *et al.* 1996; Harvey 2002). Land snails are a noted SRE group in Western Australia (Harvey 2002; Environmental Protection Authority 2004, 2009) or are known more broadly in Australia as narrow range taxa (Ponder and Colgan 2002; Ponder 1997; Parkyn and Newell 2013). However, while some terrestrial SRE invertebrates are becoming increasingly well-known, such as the northern camaenid land snails (Harvey 2002; Cameron *et al*. 2005; Köhler 2011; Harvey *et al.* 2011; O’Neill *et al.* 2014; Taylor *et al.* 2015) and polydesmid and spirostreptid millipedes (Moir *et al.* 2009), many are not (Harvey *et al.* 2011).

1.2 Genus *Bothriembryon* Pilsbry, 1894

The native land snail genus *Bothriembryon* Pilsbry, 1894 (Solem 1998; Breure and Whisson 2012) forms a large and characteristic component of the Australian terrestrial molluscan fauna, particularly in WA (Iredale 1939; Kershaw 1985; Solem 1998). Iredale (1939) suggests *Bothriembryon* are perhaps the most intriguing land snails in Australia on account of their diversity and form. The conspicuous large-bodied snails typically have ovate to oblong-conic shells, 15-50 mm in height (Pilsbry 1894; Iredale 1939). In WA they are regarded as an SRE group in WA (EPA 2009) but are poorly studied (Breure and Whisson 2012).

The genus is endemic to the southern half of Australia and significant because it forms part of an ancient Gondwanan element (family Bothriembryontidae) within the superfamily Orthalicoidea (Breure and Romero 2012). Besides *Bothriembryon*, only one other Bothriembryontid genus is known from Australia: *Placostylus* H. Beck, 1837 which has a single species on Lord Howe Island (Smith 1992). A total of 10 names have been created at the subgeneric level, but only *Bothriembryon* and *Tasmanembryon* Iredale, 1933 are currently in use (Smith 1992; Smith *et al.* 2002).

The genus *Bothriembryon* currently contains seven fossil species and a maximum of 40 extant, described species (Iredale 1939; Wells 1977; Breure 1979a; Smith 1992; Richardson 1995; Breure and Whisson 2012; Breure and Ablett 2012; Schneider and Morrison 2018, Stanisic *et al.* 2018) but many synonyms exist. Species numbers have been considered to be much higher (Solem 1998) and the presence of allopatric species (Kendrick 1983) may suggest fine scale structuring.

The majority of *Bothriembryon* species (31) are limited to the cooler, moist areas of south-western Western Australia (SWWA), a global biodiversity hotspot (Myers *et al.* 2000), broadly defined as extending from Shark Bay to Israelite Bay (Gole 2006; Rix *et al.* 2014) (Figure 2.1). Four species have distributions across to South Australia, with three endemics in South Australia, one in the Northern Territory and one in Tasmania (Whisson and Breure 2016; Schneider and Morrison 2018; Stanisic *et al.* 2018). In SWWA, *Bothriembryon* species occupy a range of habitats from coastal heath and scrubland over sandy soils (e.g. Geraldton and Swan Coastal Plains) to rocky outcrops in more rugged and exposed terrain (e.g. Darling and Stirling Ranges), as well as inter-lying sclerophyllous forests and woodlands. While the diversity and abundance of *Bothriembryon* is highest in the coastal fringe areas of SWWA, they also penetrate inland (up to 250 km) and inhabit numerous islands between Shark Bay and the Recherche Archipelago (Iredale 1939; Smith 1992; Smith *et al.* 2002; Stanisic *et al.* 2018).

Detailed phylogenetic, taxonomic and ecological studies have been made on many bothriembryontid genera including the Pacific *Placostylus* (Ponder *et al.* 2003; Brescia *et al.* 2008) but *Bothriembryon* has largely been neglected (Hill *et al.* 1983; Breure and Whisson 2012).

1.3 Aims and structure of thesis

The overall aim of this study is to improve knowledge about the genus *Bothriembryon* in Australia, particularly within the SWWA biodiversity hotspot, to enable better conservation of the group. A range of tools are used in this study: taxonomy and nomenclature including species descriptions; collection curation and fieldwork. Additionally, material generated from this study will enable the development of the first molecular phylogeny for *Bothriembryon*.

Chapter 2 comprises a literature review of *Bothriembryon* ecology and conservation knowledge as well as legacy data of the seven nominally threatened SWWA *Bothriembryon* species. The preserved extant *Bothriembryon* collection at the WAM is curated. Additionally the dry and preserved extant collections at the WAM are curated for the seven nominally threatened SWWA *Bothriembryon* species. Fieldwork is also conducted to target live specimens and gather ecological data on the seven nominally threatened SWWA *Bothriembryon* species.

Chapter 3 addresses a major nomenclatural issue detected during the literature review conducted in Chapter 2. As a result, Case 3748 is submitted to the International Code of Zoological Nomenclature (ICZN) to correct this issue and to conserve the current genus usage of *Bothriembryon*.

In Chapter 4 *Bothriembryon sophiarum* is described, based on shell and anatomical morphology. This new species was discovered whilst curating the preserved extant *Bothriembryon* collection at the WAM as detailed in Chapter 2.

Whilst investigating records of *Bothriembryon* species in Chapter 2, the size and value of the WAM fossil collection was discovered. In Chapter 5, a literature review of fossil *Bothriembryon* studies is documented. The fossil *Bothriembryon* collection at the WAM is curated, with records mapped for the first time. Additionally the biogeography of extant *Bothriembryon* records is mapped for the first time. Using this data set, the geological age of fossil and extant species is documented, and where material is available, shell size compared between fossil and modern populations.

Chapter 6 summarises the work completed in this thesis with recommendations for future studies.

Chapter 2: Review of the Western Australian Museum's extant *Bothriembryon* Pilsbry, 1894 collection to aid conservation

This chapter will be published in:

Whisson C.S., Kirkendale, L., Schneider, B. and Breure, A.S.H. (in prep.) Review of the Western Australian Museum's extant *Bothriembryon* Pilsbry, 1894 collection to aid conservation. *Australian Journal of Zoology* **XX,** XX-XX.

2.1 Introduction

Myers *et al.* (2000) declared 25 terrestrial biodiversity global hotspots based on areas with exceptionally high levels of species endemism (plants and vertebrates) paired with a high degree of threat. This included just one hotspot from Australia, the south-western land division of Australia (SWWA), also referred to as the south-west Australia ecoregion (SWAE), a large area of land (300,000 km^2) broadly defined as extending from Shark Bay to Israelite Bay (Gole 2006; Rix *et al.* 2014) (Figure 2.1). Mittermeier *et al.* (2004) using similar criteria expanded the count to 34 global biodiversity hotspots, and recently a second Australia hotspot was recognised, the Forests of East Australia (Williams *et al.* 2011). On a national level, 15 biodiversity hotspots have been recognized within Australia, with a large proportion (one-third) being in the SWWA region (Morton *et al.* 1995).

The native genus *Bothriembryon* Pilsbry, 1894 is most diverse in the SWWA biodiversity hotspot, where 77.5% of described species occur (Breure and Whisson 2012; Breure and Ablett 2012; Stanisic *et al.* 2018). However, little work has been done on the group with reviews being morphological, predominantly shell-based with

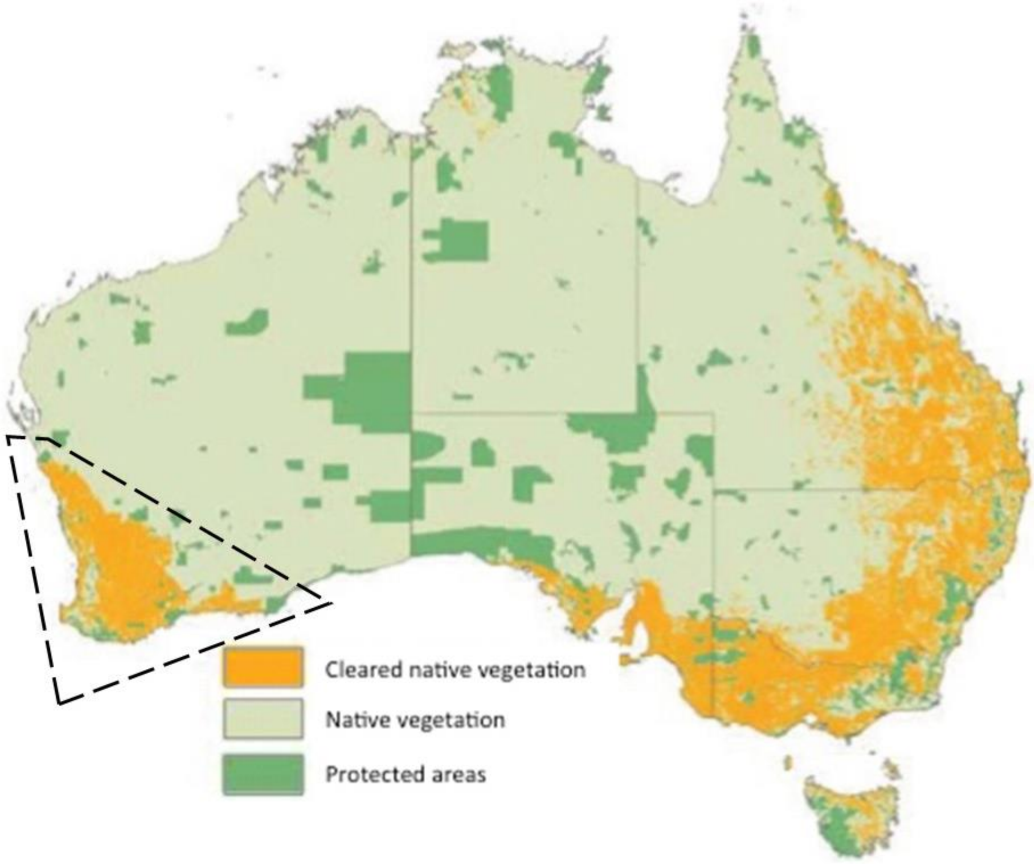

Figure 2.1 Map of Australia, defining south-western Western Australia (SWWA) (black dashed triangle) and showing areas of native and cleared vegation, and protected zones (Department of the Environment and Energy 2016).

few specimens and limited anatomical work (Pilsbry 1900; Iredale 1939; Smith 1992; Stanisic *et al.* 2018). Shell form can be variable in land snails and may not be a good taxonomic character (Goodfriend 1986; Heller 1987; Stankowski 2011; Criscione and Köhler 2015). The genus has never been studied using molecular methods (Breure and Whisson 2012), except for a few species (Breure and Romero 2012) and has been subjected to limited biogeographical and ecological studies, particularly those examining diet, predation and life span.

It has been widely recognised that modern comprehensive reviews of land snails are needed to form good conservation policy (Ponder 1998a; Ponder and Colgan 2002; Harvey 2002; Cameron *et al.* 2005). It is important that the taxonomy of *Bothriembryon* is resolved to help conservation and management of this important and vulnerable group. Native land snails are important to ecosystems given their role in the decomposition process through herbivorous feeding of primarily decaying plant matter; calcium recycling and soil nitrification, and as a food source for larger predators.

2.1.1 Historical Collecting

Museums are responsible for the long term care and maintenance of faunal collections, carefully recording details such as collecting locality and date (Ponder 1998b; Stanisic *et al.* 2010, 2018). Museum collections offer a wealth of data for conservation assessment (Reigner *et al.* 2015) but caution should be used, as the data reflects presence and not necessarily absence. An extant mollusc collection can comprise dry shells (i.e. dead-taken) or preserved specimens (i.e. live-taken) but is seldom completely curated to modern taxonomy (Ponder 1998b; Stanisic *et al.* 2010, 2018).

Extant records of *Bothriembryon* in the Western Australian Museum (WAM) Mollusc Collection can be divided into two categories, as also suggested by Wells (1977): (i) material collected and/or supplied to Tom Iredale, Curator of Molluscs at the Australian Museum (AM), prior to his review on the Western Australian land snail fauna (Iredale 1939); and (ii) material collected post Iredale's review (Figure 2.2). Very few collections were made before Iredale's work, but his seminal paper ushered in a period of heightened collecting. The oldest record of *Bothriembryon* in the WAM Mollusc Collection is from 1892, collected by "Mrs Irvine" at Cape Naturaliste. Important specimens were collected during the early 1910s, namely by shell collectors A.F. Basset Hull, F.R. Bradshaw and S.W. Jackson, who sent some of this material to Iredale at the AM, who later returned representatives to the WAM (Iredale 1939). Ludwig Glauert also made important *Bothriembryon* collections, initially as Keeper of Biological Collections at WAM, then as Curator from 1927 (Johnstone 2008) where he loaned land snail material (including *Bothriembryon*) to Iredale at the AM, sometime during the early 1930s.

In the years following Iredale's review, the WAM *Bothriembryon* collection started to grow, spiking around the early 1950s (with collections by A.R. Main) and again between 1960 and 1980 (namely by G.W. Kendrick, W.H. Butler, A. Solem and P. Kendrick). Many of these previously listed collectors were staff at the University of Western Australia (UWA). WAM staff also continued to build the collection until the present day, notably B.R. Wilson, S. Slack-Smith and H. Merrifield. From about the mid-2000s there was another large spike in *Bothriembryon* records, largely a result of targeted collecting for Environmental Impact Assessments (EIA) associated with the WA mining and resources economic boom (Figure 2.2).

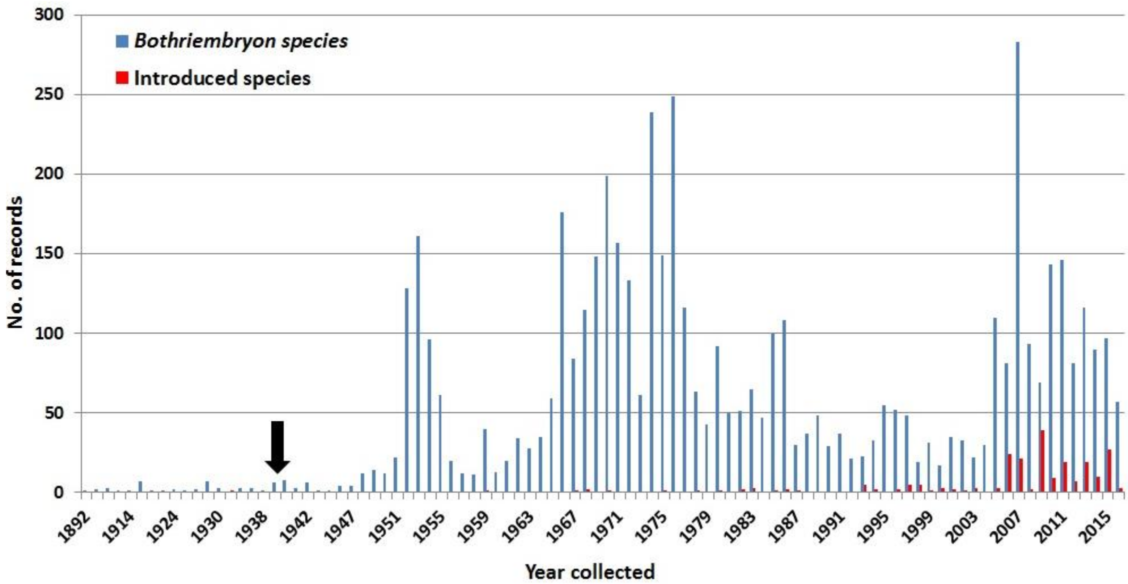

Figure 2.2 Records of *Bothriembryon* (blue, n = 5261) and introduced land snails (red, n = 230) in the WAM mollusc collection through time. The black arrow denotes the year of publication of Iredale (1939).

2.1.2 Ecology

Few ecological studies have been undertaken on *Bothriembryon* species, with most studies focused on the eastern Australia bothriembryontids, *Bothriembryon tasmanicus* (Pfeiffer, 1853) (e.g. Smith and Kershaw 1981; Kershaw 1985, 1987) and *Placostylus* H. Beck, 1837 (e.g. Ponder *et al.* 2003; Brescia *et al.* 2008, Régnier *et al.* 2015; Barker *et al.* 2016). In a recent review of ecological research on Australian land snails, the work on *Bothriembryon*, albeit limited, was not mentioned (Parkyn and Newell 2013). Iredale's (1939) review, where 20 *Bothriembryon* species (or subspecies) were described, was based on shells and contained scant ecological data. Smith (1992) listed ecological categories for all species but his categories were rather broad and in many cases unsubstantiated and did not agree with field observations (C. Whisson, pers. obs.). Main and Carrigy (1953) detailed the ecology of three species in King's Park and Schneider (2014) discussed some ecological aspects of *Bothriembryon perobesus* Iredale, 1939.

2.1.2.1 Habitat niche

Breure (1979*a*,*b*) proposed five generalised habitats for Orthalicoidea: ground dwellers among leaf litter; ground dwellers near or under large stones; those living on rock faces; those living on low shrubs; and those living on trees. Solem (1998) collapsed this to two categories, ground-dwellers or strictly arboreal. *Bothriembryon tasmanicus* has been found across a variety of habitats from the trunks of trees or on shrubs; clustered on rocks or rock walls; in litter; or under fallen bark (Iredale 1933; Smith and Kershaw 1979, 1981; Kershaw 1985, 1987; Smith 1992; Bonham 2006). Main and Carrigy (1953) often observed *Bothriembryon kendricki* Hill, Johnson and Merrifield, 1983 in proximity to the fan flower plant *Scaevola* and *Bothriembryon bulla* (Menke, 1843) near the low shrub *Jacksonia.* The central Australian *Bothriembryon spenceri* (Tate, 1894) has been found in leaf litter under fig trees and/or rocky areas (Solem 1988; Smith 1992). The recently described *Bothriembryon sophiarum* Whisson and Breure, 2016 was commonly found on stones and on low vegetation.

2.1.2.2 Vegetation

It has been suggested that *Bothriembryon* species are strongly linked to both soil and vegetation structure and composition (Iredale 1939; Main and Carrigy 1953; Hill *et al.* 1983). For example, *B*. *bulla* has been shown to be common in marri-tuart woodland, whereas *B*. *kendricki* frequents *Banksia*-jarrah or marri-jarrah woodland (Main and Carrigy 1953; Hill *et al.* 1983).

2.1.2.3 Aestivation

Bothriembryon species aestivate during the hot and dry summer months, either loosely in litter or buried in soil and remain dormant for long periods (Solem 1998). This is primarily to avoid dessication as land snails expel large amounts of water during locomotion through the mucus gland located on their foot (Smith and Stanisic 1998). The presence of living populations is best determined during rainfall in winter (Whisson and Kirkendale 2013) as *Bothriembryon* become active after the first winter rains (Main and Carrigy 1953) or after heavy, consistent rain (Schneider 2014). Most species have a calcareous epiphragm for water conservation (Solem 1998) although Hill *et al.* (1983) reports that *B*. *bulla* produces a mucoid epiphragm. Hartley (1957) remarked that *Bothriembryon barretti* Iredale, 1930 had a calcareous epiphragm which was stuck to a very small area of the foot.

Whisson and Slack-Smith (2011) report that *Bothriembryon glauerti* Iredale, 1939 buries under rocks and boulders. Main and Carrigy (1953) documented *B*. *indutus* (Menke, 1843) burying themselves under limestone rocks on scree slopes but *B*. *bulla* (later to include *B*. *kendricki*) burying themselves in sand beneath litter or under shrubs. They buried into soil using their foot while slowly revolving. *Bothriembryon melo* (Quoy and Gaimard, 1832), *Bothriembryon costulatus* (Lamarck, 1822) and *Bothriembryon onslowi* (Cox, 1864) have been observed aestivating in litter under low plants and shrubs in sandy soils (Kendrick and Wilson 1975; Wilson 2008). Some species such as *Bothriembryon mastersi* (Cox, 1867) are found under vegetation in dry woodland (Smith and Kershaw 1979). The central Australian *B. spenceri* and south-eastern *B. tasmanicus* bury in soil during dry periods (Kershaw 1987; Solem 1988; Smith 1992).

2.1.2.4 Feeding and diet

Limited published data is available on the diet of *Bothriembryon* but Solem (1998) suggests that they feed on encrusted plants by rasping and scraping and in areas of high moisture, some species forage in trees. *Bothriembryon kendricki* was observed consuming dead leaves of the fan flower plant *Scaevola* in the laboratory (Main and Carrigy 1953). Species may be nocturnal or shaded feeders, as observed for *B. bulla* which tended to avoid daylight feeding and preferred shrub cover (Main and Carrigy 1953) and *B. tasmanicus* which descend to ground level at night to forage (Smith and Kershaw 1979; Kershaw 1985).

2.1.3 Potential Threatening Processes

Bothriembryon land snails, like most slow-moving invertebrates, can be more susceptible than those animals that have high dispersal capabilities (Burbidge 2004, Parkyn and Newell 2013; Rix *et al.* 2017).

2.1.3.1 Land clearing

The biggest threat to land snails is likely to be the loss of habitat (Stanisic *et al.* 2010, 2018). Loss of habitat in the SWWA has largely occurred through land clearing for residential or infrastructure growth, or for agriculture and forestry, or in many cases both (Burbidge 2004; Gole 2006; Metcalfe and Bui 2017). In SWWA the clearing of native vegetation is extensive (Gole 2006; Metcalfe and Bui 2017) with just 10.8% of original habitat remaining (Myers *et al*. 2000) (Figure 2.1) and further fragmentation resulting from urban expansion into areas of remnant bushland. In the Perth area, *B. bulla* and *B. kendricki* are threatened by the spread of the metropolitan area (Hill *et al*. 1983).

2.1.3.2 Habitat degradation

Further compounding the problem of land clearing is degradation of some important remnant native vegetation through processes such as salinisation of soils or the introduction of exotic plants and weeds, or plant diseases and viruses. Although untested, introduced plants would presumably be an unsuitable food source for most *Bothriembryon* species. As such, degraded areas are becoming fundamentally different in quality to those undisturbed remnant habitats (Burbidge 2004).

Uncontrolled fire regimes also likely alter the composition of remnant vegetation (Burbidge 2004), particularly the undergrowth and associated litter (Stanisic *et al*. 2010). This is important because a number of *Bothriembryon* species likely feed on the leaf litter but also use it for cover and protection. Additionally some species aestivate directly into leaf litter or bury at shallow depths, and could be susceptible to fires at certain times, e.g. *B. kendricki* (Main and Carrigy 1953). Wilson *et al*. (2006) suggests that the central Australian *B. spenceri* is likely to be threatened by uncontrolled fire regimes, fuelled by exotic grasses.

2.1.3.3 Climate change

The impact of climate change on land snails is not well understood as it has been little studied (although promising methods exist, e.g. Hugall *et al*. 2002). Climate change is nonetheless a plausible threat, particularly for species highly restricted in their distribution (Parkyn and Newell 2013). A reduced rainfall and warmer temperatures in the SWWA may put pressure on some of the biota (Burbidge 2004, Rix *et al*. 2014). The shortening of the wet, cool seasons would likely affect the life history of many land snails including *Bothriembryon*. Only soaking rain creates the humid conditions which allow these soft-bodies animals to emerge, mate, eat, lay eggs and aestivate again – free from the danger of dehydration. Any alterations to this pattern would likely have detrimental effects, as suggested for species of the closely related *Prestonella* from South Africa (Herbert 2007).

2.1.3.4 Predation

Very little is known about predators of *Bothriembryon* species, particularly the impact from exotic animals. The first studies on predation of species of *Bothriembyon* were by S.W. Jackson in 1912 who in his field notes observed squeaker birds (grey currawong, *Strepera versicolour*) feeding on these snails in karri forests (Whittell 1952). Buller (1953) at Phillips River also observed currawong searching through litter and piercing the shells of *Bothriembryon balteolus* Iredale, 1939. Main and Carrigy (1953) did not observe any predators eating *Bothriembryon* species in King's Park but suggested predation by the western magpie (*Gymnorhina dorsalis*), particularly after fire when there is little cover. Solem (1998) suggested from evidence of broken shells that rodents may predate on species of *Bothriembryon*. There are no reports of direct predation by introduced snails, although the introduced carnivorous snail *Oxychilus* spp. may predate on *Bothriembryon* eggs. Species of the closely related bothriembryontid genus *Placostylus* has been significantly impacted by predation from introduced animals such as feral pigs, rats and mice (Brescia *et al.* 2008).

2.1.3.5 Competition from exotics

A potential but poorly studied threat includes competition for resources by exotic snails, particularly those coastal or near coastal *Bothriembryon* species where introduced species such as *Cochlicella acuta* (Muller, 1774) and *Theba pisana* (Muller, 1774) are most abundant (Shea 2007, Blacket *et al.* 2016). Whisson and Kirkendale (2013) noted that both native and introduced species co-occurred in the Perth area. This sympatry may be placing pressure on many *Bothriembryon* species which, it seems, are depending on native plants and associated litter as a source of food, shade, shelter and protection. If we are to take incidence in collections as a proxy for increased encounters – a simplistic but not unreasonable assumption – WAM collections indicate that the presence of introduced snails have increased through time (Figure 2.2). This may place pressure on *Bothriembryon* species and other land snails found in the same wider geographical area.

2.1.3.6 Shell collectors

Many *Bothriembryon* species are endemic to SWWA, some with short-ranges. Paired with an aesthetically pleasing shell colour and sculpture, these restricted species may be targeted by shell collectors. Solem (1998) suggested that *B. spenceri* is vulnerable to extinction through shell collection alone. A comparable marine example could be the southern Australian endemic cowry *Zoila*, a prized item for shell collectors and as such its populations appear to have suffered (Wilson and Clarkson 2004).

2.1.4 Conservation Importance

Many *Bothriembryon* species have short ranges (Solem 1998) and like many invertebrates (Régnier *et al.* 2015) are often known only from the type locality (Smith 1992; Smith *et al.* 2002). Driven in part by this restricted distribution (likely a result of deficient biogeographical data) and a variety of perceived threats (Ponder 1998a; Stanisic *et al.* 2010, 2018), many *Bothriembryon* species are of conservation concern. Eight species of *Bothriembryon* (ca. 20% of described extant species) are listed as threatened at state and international levels, with seven of those species in the SWWA region (Table 2.1, Figure 2.3).

The International Union for the Conservation of Nature (IUCN) lists six species as vulnerable (*Bothrembryon bradshawi* Iredale, 1939*; Bothriembryon brazieri* (Angas, 1871); *B. glauerti; Bothriembryon irvineanus* Iredale, 1939, *B. spenceri* and *Bothriembryon whitleyi* Iredale, 1939) and two species (*B. perobesus* and *Bothriembryon praecelsus* Iredale, 1939) as endangered (Kessner and Ponder 1996; Slack-Smith 1996*a*-*g*;). The IUCN assessment on *Bothriembryon* was completed over twenty years ago (1996) and all species are in need of an updated assessment (including misspellings in the names of two species, i.e. *B. praecelcus* and *B. bradshawi*), as noted for each IUCN species listing. Within Australia, two of these species (*B. praecelsus* and *B. whitleyi*) are regarded as Extinct (Burbidge 2004; Government of Western Australia 2015), five species (*B. bradshawi, B. brazieri*, *B. glauerti*, *B. irvineanus* and *B. perobesus*) are regarded as Priority Fauna (Department of Parks and Wildlife 2015) and one species (*B. spenceri*) is regarded as Vulnerable (Wilson *et al.* 2006).

Table 2.1 Conservation status of Australian *Bothriembryon* species. Abbreviations: DPaW – Department of Parks and Wildlife Western Australia, GWA - Government of Western Australia, IUCN – International Union for the Conservation of Nature, NRETAS – Natural Resources, Environment,the Arts and Sport (Northern Territory).

Taxa	**Type Locality**	**Status (Agency)**
B. bradshawi Iredale,1939	WA, Tambellup	Priority Fauna P1 (DPaW), Vulnerable (IUCN)
B. brazieri (Angas,1871)	WA, Stirling Range	Priority Fauna P2 (DPaW), Vulnerable (IUCN)
B. glauerti Iredale,1939	WA, Stirling Range	Priority Fauna P2 (DPaW), Vulnerable (IUCN)
B. irvineanus Iredale,1939	WA, Cape Naturaliste	Priority Fauna P2 (DPaW), Vulnerable (IUCN)
B. perobesus Iredale, 1939	WA, mouth of Moore River	Priority Fauna P1 (DPaW), Endangered (IUCN)
B. praecelsus Iredale,1939	WA, Kellerberrin District (see results)	Schedule 4 Fauna Presumed, Extinct (GWA), Endangered (IUCN)
B. whitleyi Iredale, 1939	WA, Geraldton, Bluff Point (see results)	Schedule 4 Fauna Presumed, Extinct (GWA), Vulnerable (IUCN)
B. spenceri (Tate, 1894)	NT, Glen of Palms by the junction with Palm Creek	Vulnerable B2 (NRETAS), Vulnerable (IUCN)

However, effort to re-collect these species appears low, or in many cases absent. Recently, Whisson and Breure (2016) and Schneider and Morrison (2018) described new *Bothriembryon* species from the south-eastern coast of Western Australia which are likely to be SRE, indicating the presence of further sensitive taxa. Currently no *Bothriembryon* species are listed under the Federal EPBC Act 1999, however, 16 species of land snails are listed from the Northern Territory or Eastern Australia, including the closely related *Placostylus bivaricosus* (Gaskoin, 1855) (Bothriembryontidae) which is endemic to Lord Howe Island (Smith 1992).

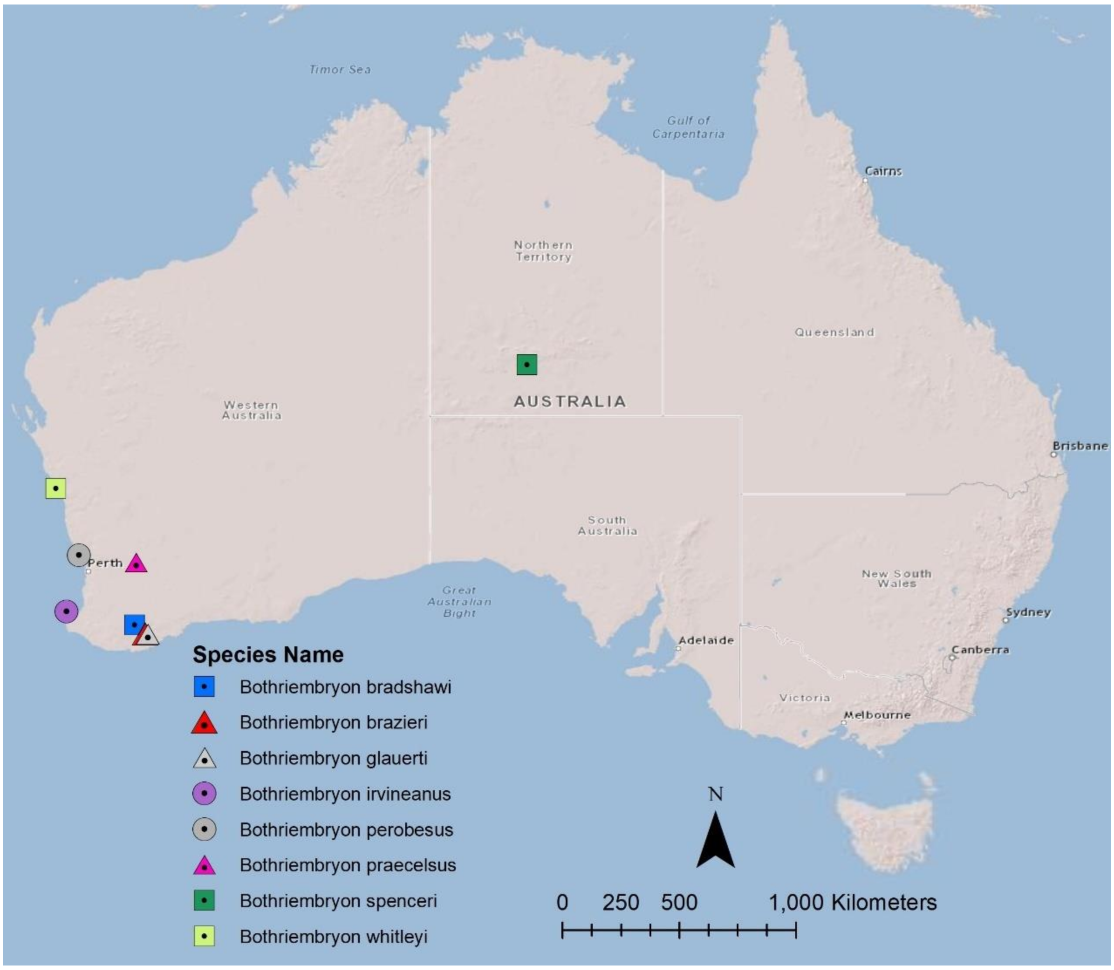

Figure 2.3. Type localities of threatened *Bothriembryon* species.

2.1.5 Aims

The aims of this study were twofold:

(i) curate the preserved *Bothriembryon* collection at WAM to current taxonomy so data could be uploaded to the Atlas of Living Australia (ALA) portal (http://www.ala.org.au).

(ii) collate existing (or legacy) data of the seven nominally threatened SWWA *Bothriembryon* species in Australian museum and institute collections. Then compare this legacy data set with new data that has become available, through curation of the dry and preserved WAM collection and targeted fieldwork. This augmented data set will contribute to improved conservation initiatives, specifically an updated assessment of IUCN status.

2.2 Materials and Methods

2.2.1 Curation of WAM *Bothriembryon* Collection

Bothriembryon specimens at the WAM were examined using a Leica MZ95 microscope and compared with type material at WAM and/or with descriptions and type figures in relevant publications (Iredale 1939; Smith 1992; Breure and Ablett 2012; Breure and Whisson 2012; Stanisic *et al.* 2018). Most type material was dry, including all of the seven nominally threatened SWWA *Bothriembryon* species (Figure 2.4). Identification was based exclusively on shell characters, specifically maximum shell height (H); maximum shell diameter (D); H/D ratio; number of shell whorls (W), number of protoconch whorls (P) and colour and sculpture of the whorls (protoconch and teleoconch). All WAM specimens were registered in the WAM Mollusc database. The term record is defined as a registered lot which contains one or more specimens.

Dry shells were assumed dead-taken, whilst preserved specimens were live-taken. Freshly dead-taken specimens were defined as shells showing a trace of colour and sculpture (not bleached white or eroded). Sub-adult and adult specimens were defined by size of shell and possession of a slightly thickened body whorl and outer lip.

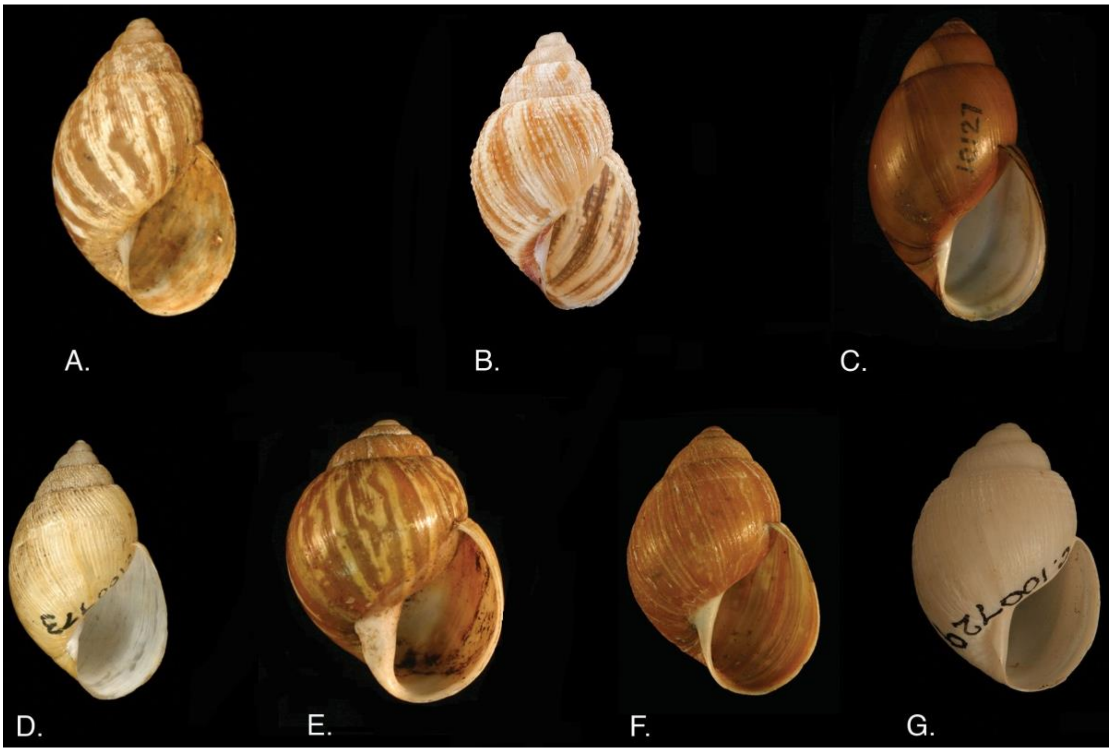

Figure 2.4. Type specimens of *Bothriembryon* species from SWWA. Institutional abbreviations: AM – Australian Museum, Sydney, NHMUK - Natural History Museum, London, WAM = Western Australian Museum, Perth. A. *B. bradshawi* Iredale, 1939, syntype, AM C.100749 (H = 19.0 mm). B. *B. brazieri* (Angas, 1871), lectotype, NHMUK 1870.11.5.8. (H = 14.3 mm). C. *B. glauerti* Iredale, 1939, syntype, WAM S14466 (H = 36.7 mm). D. *B. irvineanus* Iredale, 1939, syntype, AM C.100773 (H = 24.2 mm). E. *B. perobesus* Iredale, 1939, holotype, WAM S14467 (H = 24.2 mm). F. *B. praecelsus* Iredale, 1939, holotype, WAM S14468 (H = 27.1 mm). G. *B. whitleyi* Iredale, 1939, syntype, AM C.100729 (H = 14.4 mm).

2.2.1.1 Inter-state loans

Where WAM did not hold preserved representatives of *Bothriembryon* species, requests were made to other Australian Museums (e.g. SAM; MAGNT) to loan or exchange specimens, particularly those specimens suitable for genetic work.

2.2.2 Threatened SWWA *Bothriembryon* data

2.2.2.1 Legacy data

At the beginning of this study (2014), a count was made of registered specimens of the seven nominally threatened SWWA *Bothriembryon* species in Australian museums and institutes. For non-WAM records, this was done using ALA. Identification of specimens in non-WAM Institutions was not verified by the authors, although the status of any preserved specimens was checked with relevant staff.

As *Bothriembryon* material in the WAM Mollusc Collection was not available on ALA, the wet and dry collections were searched to locate previously identified material of the seven nominally threatened SWWA *Bothriembryon* species. The specimen identifications were re-checked and material was registered into the WAM Mollusc database if found to be unregistered.

2.2.2.2 New data

Over a six year period (ca. 2014–mid 2019), curation of the WAM Mollusc Collection was undertaken with the aim of locating additional (previously unidentified or newly deposited) specimens of the seven nominally threatened SWWA *Bothriembryon* species. This material was identified and registered where needed.

Over the same period, fieldwork was undertaken to target live individuals of the seven nominally threatened SWWA species to better understand their ecology, and where needed, to obtain genetically viable tissue. The emphasis was on resurveying type localities and/or re-collecting at suitable sites identified during the curation process, particularly those records that were live-taken or contained shells from recently living snails.

Fieldwork generally coincided with mid- to late winter rains, i.e. in the July to

September period and during daylight (Table 2.2). Visual searching (e.g. rock and log turning; litter scraping and bark peeling) for live and dead specimens was undertaken, generally for about an hour per site. At each site approximately 500ml of leaf litter was collected and sieved *in situ* and examined with a hand lens for *Bothriembryon* shells. At sites where specimens were found, one litre of leaf litter was collected and examined more closely in the laboratory. Site data including coordinates and detailed habitat information were recorded, as well as observations on land snail biology such as colour of the foot, body and tentacles of live animals. Site coordinates were not included in this paper due to the threatened status of the species.

Table 2.2 Fieldtrip localities targeting the seven nominally threatened SWWA *Bothriembryon* species, including managing authority and year of fieldtrip.

Locality	Managing Authority	Year(s)
Moore River National Park	DPaW	2014
Tambellup area	Tambellup Shire	2014
Peringillup Nature Reserve	DPaW	2015
Beekeepers Nature Reserve	DPaW	2016
Busselton District	Busselton Naturalists Club Club	2016
Geraldton	Shire of Geraldton	2017
Kellerberrin District	Shire of Kellerberrin	2015; 2018
Stirling Range National Park	DPaW	2011; 2019

Live specimens were photographed before being relaxed via drowning overnight (ca. 16 hours) and then transferred into 70% ethanol for future anatomical studies. For some specimens, a small piece of tissue (ca. 5 x 5 mm) was taken from the rear of the foot before relaxation, transferred into 100% ethanol and stored in a Ultra-Low Temperature Freezer (-80°C) for future molecular work.

2.3 Results

2.3.1 Legacy data

A total of 226 records were located for the seven nominally threatened SWWA *Bothriembryon* species across all Australian museums and universities, with most comprising dry shells (165, 73.0%). However, some records were on live-taken specimens (61, 27.0%) (Table 2.3).

Bothriembryon brazieri, *B. glauerti* and *B. perobesus* were most numerous. For some species, records were largely (*B. irvineanus*, *B. bradshawi*) or entirely (*B. praecelsus*) dead-taken, type shells. Only four species were known from live collections, *B. brazieri*, *B. glauerti*, *B. irvineanus* and *B. perobesus,* and other than *B. brazieri* (collected 14/2/2011, WAM S34795) and *B. glauerti* (collected 17/11/2007, WAM S34993), there was little recently collected material. Most preserved collections were, on average, twenty years old or older, were fixed in 10% formalin and as such, are challenging candidates for molecular study. Enquiries with relevant Institutions revealed that ALA records of *B. whitleyi* (collected 1978, QVM:9:18618) and *B. perobesus* (collected 1990, WINC 045214) were dry shells (dead-taken) and not preserved specimens (i.e. live-taken). Records of each species were almost exclusively from the type locality, which are generally large geographical areas.

2.3.2 New data

After curation of the WAM Mollusc Collection and targeted fieldwork (ca. 2014–mid 2019), 159 new records (70.4% increase) across the seven nominally threatened SWWA *Bothriembryon* species were located, with over half being live-taken (82, 51.6%) (Tables 2.3 and 2.4). Five of the species, *B. brazieri*, *B. bradshawi*, *B. glauerti*, *B. irvineanus* and *B. perobesus*, were successfully re-collected alive during fieldwork, at or in close proximity to their respective type localities. Live specimens tentatively identified as *B. praecelsus* were also successfully found.

Table 2.3 Australian museums and university records of the seven nominally threatened SWWA *Bothriembryon* species (legacy and new data). Abbreviations: P - preserved specimen with soft anatomy and D - dry specimens, empty shells only.

	Legacy data (No. records)		New data (No. records)		Increase in collection records due to new data (%)	
Species	P	D	P	D	P	D
B. bradshawi Iredale,1939	0	7	5	10	100.0	142.9
B. brazieri (Angas, 1871)	23	39	24	22	104.3	56.4
B. glauerti Iredale,1939	29	53	8	11	27.6	20.8
B. irvineanus Iredale,1939	3	7	16	8	533.3	114.3
B. perobesus Iredale,1939	6	38	9	7	150.0	18.4
B. cf. *praecelsus* Iredale,1939	0	1	20	12	100.0	1200.0
B. whitleyi Iredale,1939	0	20	0	7	0	35.0
Total	61	165	82	77	134.4	46.7
Grand Total	226		159		70.4	

2.3.2.1 Bothriembyon bradshawi Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4A, 2.5A and 2.6A)

15 new records of *B. bradshawi* were located during the study. Shells or live specimens were not common during fieldwork however, 4 live-taken specimens were found during fieldwork in 2015. They were found at two sites in open wandoo (*Eucalyptus wandoo*) woodland in proximity to the type locality at Tambellup. Live specimens (juveniles, sub-adults) were found among damp leaf litter at only one of these sites. A search for *B. bradshawi* in 2014 in close proximity to Tambellup failed to yield any specimens.

Table 2.4 Legacy and new ecological (habitat) and biological (animal colour) data for the seven nominally threatened SWWA *Bothriembryon* species. Abbreviations: B - body, F - foot, CT - cephalic tentacle, NS - neck nape stripe. Source: [1]Smith 1992; [2]Schneider 2014.

Taxa	**Legacy Habitat Data**	**New Data**		
		Date Coll., Reg. No. (WAM S)	**Habitat Data**	**Animal Colour: Body (B), Foot (F), Cephalic Tentacle (CT), Neck Nape Stripe (NS)**
B. bradshawi	Under rocks, open scrub[1]	24/08/2015, 66268	Among loose leaf litter and bark. Brown loamy soil. Mixed Wandoo (*Eucalyptus wandoo*) and Swamp Sheoak (*Casuarina obesa*) woodland with scattered *Santalum acuminatum*, over *Dianella revoluta*, sedges and grasses. Edge of wetland area.	Light grey (B), light cream (F), inner black, outer light grey (CT), black (NS)
B. brazieri	Litter, open woodland[1]	18/08/2011, 81345	In leaf litter among decomposing wood and quartzite rocks in creek gully near scree slope. In open jarrah (*Eucalyptus marginata)* and marri (*Corymbia calophylla*) woodland with mallee eucalypts (e.g. *E. vegrandis*), *Trymalium odoratissimum*, *Thomasia* sp. Toolbrunup (G.J. Keighery 9895), *Banksia formosa* and *B.* cf. *baueri*, over sparse dwarf shrubs, orchids and mosses.	Light grey to cream (B), cream (F), inner dark grey, outer cream (CT), dark black, thick (NS)
B. glauerti	Litter, woodland[1]	24/05/2011, 65732	From under schistose rocks. Sparsely vegetated water-filled gully surrounded by dense Stirling Range mallee-thickets (*Eucalyptus* spp.). Associated gully species include *Trymalium odoratissimum* [tall shrubs], *Xanthosia rotundifolia* [low shrubs] and *Cheilanthes austrotenuifolia* [fern], with sedges and mosses.	Light grey to brown (B), light cream (F), inner mottled grey, outer cream (CT), dark grey to black, thick (NS)

B. irvineanus	On bushes, open scrub, open heath[1]	21/08/2016, 99124	Among loose leaf litter and on limestone pebbles. Plain with dark grey, sandy soil. Burned within previous 5 years [probably]. Open marri (*Corymbia calophylla*) woodland with scattered jarrah (*Eucalyptus marginata)*, over *Xanthorrhoea preissii*, *Kingia australis*, *Hypocalymma angustifolium* and Hibbertia cf. *hypericoides*, over sedges and herbs.	Light cream (B), cream (F), inner dark brown, outer cream (CT), dark brown, thick (NS)
B. perobesus	Under rocks, saxicoline[1]; On sand[2]	26/07/2014, 66910	On bare sand and low vegetation and among leaf litter. Deep white sand in *Banksia menziesii* dominated woodland with *Eucalyptus todtiana*, over *Xanthorrhoea preissii* and mixed low shrubland of *Stirlingia latifolia*, *Conospermum stoechadis* and species of *Melaleuca*, *Leucopogon*, *Acacia* and *Hibbertia*, over sedges	Light grey to light cream (B), cream (F), inner dark grey, outer light grey (CT), dark brown, thick (NS)
B. cf. *praecelsus*	Litter, open scrub, woodland[1] (as for *B. bulla*)	03/08/2015, 66236	On pale brown loamy soils under fallen mallee (*Eucalyptus* cf. *rigidula*) branches. Plain with open mallee (*Eucalyptus* spp.) woodland with scattered *Acacia* and *Melaleuca* (*M*. cf. *scalena*).	Grey (B), light cream (F), inner, outer grey (CT), Absent (NS)
B. whitleyi	Under rocks, open heath, saxicoline[1]	14/07/2009, 60323	On white sand. Coastal dune system with moderately dense *Acacia cyclops* and *Acacia* sp. medium to tall shrubs and *Olearia axillaris* low shrubs, over *Spinifex longifolius, Scaevola crassifolia* and **Tetragona decumbens*. Leaf litter sparse to almost absent. (* = naturalised)	N/A

Figure 2.5. Live specimens of *Bothriembryon* species from SWWA. Abbreviations: BS - Ben Schneider personal collection, WAM – Western Australian Museum A. *B. bradshawi*, WAM S66268 (H = 7.7 mm), on wandoo bark in laboratory. B. *B. brazieri*, BS-BOTH-L0097 (H = 17.5 mm), on garden leaf in laboratory. C. *B. glauerti*, BS-BOTH-L0063 (H = 35.9 mm), on garden leaf in laboratory. D. *B. irvineanus*, WAM S99124 (H = 23.6 mm), crawling on post in field (placed). E. *B. perobesus*,

WAM S66911 (H = 18.7 mm), on garden leaf in laboratory. F. *B*. cf. *praecelsus*, WAM S66236 (H = 15.5 mm), on garden bark in laboratory.

Figure 2.6. Examples of habitat shots from which specimens of *Bothriembryon* were

collected: A-F. live-taken specimens G. dead-taken shells. A. *B. bradshawi*, wandoo woodland. B. *B. brazieri*, jarrah-marri woodland, Toolbrunup Peak. C. *B. glauerti*, slatey-shale rock gully edged with mallee thickets. D. *B. irvineanus*, marri-jarrah woodland. E. *B. perobesus*, Banksia woodland F. *B.* cf. *praecelsus*, mallee woodland. G. *B. whitleyi*, coastal dune system with wattle shrubs.

2.3.2.2 Bothriembryon brazieri (Angas, 1871)

(Tables 2.3 and 2.4, Figures 2.4B, 2.5B and 2.6B)

A large number of new records (46) of *B. brazieri* were located during the study, including 4 live-taken specimens from two sites during fieldwork in 2011 and 2019. The Toolbrunup Peak specimens, within the Stirling Range type locality, were found on a quartzite scree slope in open jarrah-marri woodland. Adult specimens were found in leaf litter among decomposing wood and rocks.

2.3.2.3 Bothriembyon glauerti Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4C, 2.5C and 2.6C)

Nineteen new records of *B. glauerti* were found during the study, including 3 live-taken specimens during fieldwork in 2011 and 2019. *Bothriembryon glauerti* was collected from the type locality of Stirling Range on a steep gully, from under quartzite slabs in marri-jarrah thickets. Live individuals were not uncommon, often found sealed to the underside of rocks. They were also observed crawling on marri leaves that showed signs of rasping.

2.3.2.4 Bothriembyon irvineanus Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4D, 2.5D and 2.6D)

Twenty-four new records of *B. irvineanus* were found during the study, including 5 live-taken specimens during fieldwork in 2016. Specimens were found at three sites within a small area near Busselton, a short distance (ca. 30 km) from the Cape Naturaliste type locality. They were found on grey sandy soils in open marri-jarrah woodland, often under fallen branches or among leaf litter near small grasses. *Bothriembryon irvineanus* was observed on damp, decomposing marri leaf litter that appeared to have been rasped. Introduced plants, e.g. *Zantedeschia aethiopica* (arum lily), and land snails e.g. *Prietocella barbara* (WAM S99129) were noted on the edges of the site.

2.3.2.5 Bothriembyon perobesus Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4E, 2.5E and 2.6E)

Sixteen new records of *B. perobesus* were found during the study, including 6 live-taken specimens from two sites in 2014 and 2016. Those specimens from Moore River National Park, in close proximity to the type locality, were found on white sandy soils in *Banksia* woodland and scattered eucalypt trees (*E. todtiana*), often among low shrubs (see also Schneider 2014). At the second site, on a limestone escarpment north of Leeman many shells had broken spires. While searching for *B. perobesus* in a nearby area, a smaller, putative new species of *Bothriembryon* was found.

2.3.2.6 Bothriembyon praecelsus Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4F, 2.5F and 2.6F)

Specimens tentatively identified as *B. praecelsus* were discovered from existing WAM collections and during fieldwork. Thirty-two new records were found during the study, including 27 live-taken specimens during fieldwork in 2015 (see also Kirkendale and Whisson 2018), and two existing previously unidentified WAM live-taken specimens collected between 1971 and 1985 (WAM S3824, WAM S4258). A search within the Kellerberrin township in 2015 and 2018 failed to yield any specimens, however live-taken specimens were found during fieldwork at three sites adjacent (ca. 60 km) from the type locality of Kellerberrin. All specimens found during fieldwork were juvenile or sub-adult and were relatively abundant, with many other specimens observed but not collected. They were found in mallee-form

Eucalyptus woodland on or partially buried in loamy soils, almost exclusively under fallen branches or debris. Examination of legacy catalogue books in the WAM Mollusc Collection revealed a less specific type locality for *B. praecelsus*, with the original record entry denoted as Kellerberrin District (rather than Kellerberrin) and included a collection date of 12th of August 1915. During fieldwork in proximity to Kellerberrin another much smaller, putative new species of *Bothriembryon* was discovered.

2.3.2.7 Bothriembyon whitleyi Iredale, 1939

(Tables 2.3 and 2.4, Figures 2.4G and 2.6G)

Seven new records of *B. whitleyi* were found during the study, comprising entirely of dead-taken empty shells. No live-taken specimens were located during this study. Freshly dead-taken specimens were identified in the collection during detailed curation at WAM (WAM S60323) near the type locality of Geraldton. This record contained 35 shells found on white sand in a coastal dune system with moderately dense wattle (*Acacia* spp.) shrubs. At the same site, a presumably native *Succinea* species (WAM S60338) and the introduced *Prietocella barbara* (WAM S60922) were also found. Examination of syntype labels in the Australian Museum (AM C.127615 and AM C.127713) revealed a more specific type locality for *B. whitleyi*, denoted as "Sand Dunes, Bluff Point near Geraldton". Fieldwork to Bluff Point in 2017 failed to yield any live specimens, with this area under threat from dense residential development and numerous introduced plants and land snails (see also Whisson and Kirkendale 2017).

2.3. 3 Data sets

Excel files of the following are available upon request to the WAM Mollusc Section:

(i) the curated preserved WAM *Bothriembryon* collection

(ii) legacy and new data of the seven nominally threatened SWWA *Bothriembryon* species

2.4 Discussion

This study almost doubled the number of records of the seven nominally threatened SWWA *Bothriembryon* species found in Australian museum and university collections, with fieldwork resulting in the discovery of living populations of five of these species. In addition and most significantly, the presumed extinct *B. praecelsus* may have been collected live-taken for the first time awaiting more detailed analysis, and freshly dead-taken shells were located for the presumed extinct *B. whitleyi*. The new morphological and ecological data generated through this project, particularly during fieldwork, has not only increased knowledge about the seven nominally threatened SWWA *Bothriembryon* species, but has assisted in the identification of specimens in the WAM collection (Table 2.3). These results have shown not only the importance of new collections but also the importance of ongoing curation and digitization of valuable legacy material. It is recognised that taxonomic expertise coupled with identification of natural history museum collections can provide valuable data for evaluation of conservation status (Régnier *et al*. 2015).

2.4.1 Type Localities and Conservation Areas

Most *Bothriembryon* species descriptions, including the seven nominally threatened SWWA species, were based solely on shell material (e.g. Figure 2.4) and usually comprise specimens from single localities, the type locality (the only exceptions being *B. kendricki* and B. *sophiarum*). It proved difficult to re-collect species from type localities as in most cases, the landcape has become vastly different since original collection and description, containing few areas of remnant vegetation. Although needing more rigorous fieldwork to compare populations in modified and undisturbed habitats, all species collected live during fieldwork were found among remnant vegetation in nature reserves or conservation areas, highlighting their ecological significance. The conservation areas, however, are generally quite small and are scattered among vast expanses of increasingly cleared or modified land (Figure 2.1).

The only other areas that contain some remnant vegetation include road-side verges, hilltops or uncleared farm land. Remnant native vegetation it seems provides a food source and a refuge for *Bothriembryon*.

Additionally, none of the seven nominally threatened SWWA species were found across two or more vastly different habitat types, but this requires more sampling. This has conservation outcomes, as if the preferred habitat is extensive (e.g. jarrah-marri woodlands) then the species could be expected to have a large biogeographic range. Conversely, if the preferred habitat is restricted (e.g. high altitude scree slope) then a smaller biogeographic range might be expected. This fits the model of an SRE proposed by Harvey (2002). Given just 10.8% of remnant vegetation remains in SWWA (Myers *et al*. 2000) (Figure 2.1) and continued urban expansion into remnant bushland, it is hard to imagine any habitat type will remain extensive for long. Most of the seven nominally threatened SWWA *Bothriembryon* species have pressures on their preferred remnant vegetation habitat, largely land clearing for agriculture (*B*. *irvineanus*, *B*. *bradshawi* and *B*. *praecelsus*); land salinization (*B*. *bradshawi*, *B*. *praecelsus*) and the introduction of exotic plants or plant disease and viruses e.g. *Phytopthora cinnamomi* (*B*. *irvineanus*).

Re-collection of the seven nominally threatened SWWA species was also difficult as type localities were often broadly-termed e.g. Stirling Range. Whilst this presented one problem, the discovery of a broader type locality for *B*. *praecelsus* during this study could have assisted re-collection, as the search focus shifted from the somewhat small (ca. 4 km^2) developed Kellerberrin township, to a broader Kellerberrin district (ca. 15,000 km^2) that borders the area where *B.* cf. *praecelsus* was collected during fieldwork. Detailed work needs to be undertaken to confirm the identifications of these specimens as *B*. *praecelsus*. The holotype of *B*. *praecelsus* is a large shell with a height 27.1 mm, width 17.9 mm (Figure 2.4F) (Iredale 1939; Breure and Whisson 2012) and those collected during fieldwork were consistently smaller (Figure 2.5F, height 15.5 mm). The specimens were collected in late winter (August) from the inland wheatbelt region, which has a much lower, shorter rainfall season than areas closer to the coast. It is feasible the specimens collected were a younger cohort, with larger adult specimens already deeper into aestivation (see also Kirkendale and Whisson 2018).

Conversely, restricting a type locality made re-collection more difficult. Research during this study narrowed the type locality of *B. whitleyi* from Geraldton to Bluff Point. This coastal area is now subject to large port and residential growth and is highly disturbed with introduced flora and fauna, making re-collection of this presumed extinct species from its type locality unlikely (see also Whisson and Kirkendale 2017).

2.4.2 Ecology

In general, most of the seven nominally threatened SWWA species were found living at ground level among leaf litter, occasionally in proximity to small rocks or pebbles or under fallen branches or debris. The exceptions were *B. glauerti* which was found underneath large quartzite slabs and rocks, and *B. perobesus* which was also noted on low shrubs. The shade offered by rocks, branches or other debris would likely help retain ground moisture and offer cooler temperatures during daylight. It may also provide increased cover from predators (Stanisic *et al.* 2010).

As fieldwork during this study was undertaken in the wetter months, there were few observations made on aestivating activities for the seven nominally threatened SWWA *Bothriembryon* species. However, *B.* cf. *praecelsus* was noted emerging from small shallow depressions in loamy soils and *B. perobesus* was observed emerging from under white sandy soils (see also Schneider 2014).

During fieldwork *B. irvineanus* and *B. glauerti* were observed crawling on decomposing marri (*Corymbia calophylla*), with some leaves having been rasped. The rasping of marri leaves has also been noted in other species such as *B. kendricki* and *Bothriembryon serpentinus* Iredale, 1939 (C. Whisson, pers. obs.). *Bothriembryon* snails, particularly large-bodied species, may prefer the large surface area of *Eucalyptus* leaves for attachment, particularly marri, as opposed to smaller, narrower leaves. Like many land snails that feed on leaf litter (Bocock and Gilbert 1957; Grime *et al.* 1996; Cornelissen *et al.* 1999), *Bothriembryon* species presumably rely on other organisms (e.g. fungi) to start the decomposition process before they start to feed. The apparent preference for marri leaves by many *Bothriembryon* species may be important, given the rise of *Quambalaria coyrecup* (marri fungus).

2.4.3 Competition and Predation

A potential but poorly studied threat includes competition for resources by exotic snails, particularly coastal or near coastal *Bothriembryon* species (*B. perobesus*, *B. whitleyi* and *B. irvineanus*) where introduced species such as *Cochlicella acuta* (Muller, 1774) and *Theba pisana* (Muller, 1774) appear most abundant (Shea 2007, Blacket *et al*. 2016). At one site where *B. perobesus* was found, the predation of snails was inferred by the consistently broken apex of dead adult shells, most likely by native or introduced rats (B. Schneider, pers. comm.).

2.4.4 Summary and Future Directions

It is clear from data generated in this study that the conservation status of the seven nominally threatened SWWA *Bothriembryon* species needs updating. It is likely that many of these species have not been resurveyed since initial collection, and sampling effort needs to be carefully considered in conservation assessment. I therefore call for a new study that incorporates a quantitative ecological survey of each species, as well as molecular and anatomical work. Future efforts must also recognize the importance of remnant bushland at the margins of large agricultural lands in offering appropriate refugia. Additionally, the importance of searching for *Bothriembryon* following significant rains is critical for locating live animals.

Chapter 3: Application to the International Commission of Zoological Nomenclature – Case 3748

This chapter was published in:

Whisson C.S., Kirkendale, L. and Breure, A.S.H. (2018) Case 3748 - *Bothriembryon* Pilsbry, 1894 (Mollusca, Orthalicoidea, BOTHRIEMBRYONTIDAE): proposed conservation of the name by designation of *Helix melo* Quoy & Gaimard, 1832 as the type species of *Liparus* Albers, 1850. *Bulletin of Zoological Nomenclature* **75**: 44-48.

3.1 Introduction

The genus-group name *Liparus* Albers, 1850 (p. 172) was first proposed as a subgenus of *Bulimus* Scopoli, 1777, and originally included two land snail species, *Bulimus atomatus* Gray, 1834 [currently *Pygmipanda atomata* (Gray, 1834), Caryodidae, from New South Wales, Australia] and *Bulimus favannii* Lamarck, 1822 [currently *Leucotaenius favannii* (Lamarck, 1822), Clavatoridae, from Madagascar] but no type species was designated (Albers 1850). *Liparus* Albers, 1850 is a junior homonym of *Liparus* Olivier, 1807 (Coleoptera: Curculionidae), which is currently in use as a valid genus. Albers passed away shortly thereafter in 1857, but E. von Martens completed his work, where a re-description of the subgenus *Liparus* was provided, titled "*Liparus* Albers" (Albers and Martens 1860, p. 229). This re-description was based solely on Australian land snails, with *Bulimus atomatus* Gray, 1834 listed along with eight varieties or species previously included in *Bulimus* (currently *Bothriembryon*). Albers and Martens (1860) designated *Buliminus inflatus* Lamarck, 1822 [error for *Bulimus inflatus*, currently *Bothriembryon costulatus* (Lamarck, 1822) from Australia, not *Bulimus inflatus* Olivier, 1801, currently *Albinaria corrugata* (Bruguière, 1792) from Greece] as the type species of *Liparus* Albers, 1850, but this is an invalid designation as it was not an originally included nominal species.

Pilsbry (1894, p. 36) proposed the name *Bothriembryon* expressly as a new replacement name for *Liparus* Albers, 1850, which was preoccupied by *Liparus* Olivier, 1807 and designated as type species of *Bothriembryon* the nominal species *Helix melo* Quoy and Gaimard, 1832, which was included in *Liparus* Albers, 1850 by Albers and Martens (1860) but was not an originally included species of *Liparus* Albers, 1850. Pilsbry (1894, p. 35–36) clearly intended *Bothriembryon* as a replacement name for *Liparus* Albers, 1850 as he stated "The name *Liparus* in Mollusca is preoccupied by *Liparus* Olivier, Entomologie, ou Hist. Nat. des Insectes, Vol. V, pp. 73, 283 (1807), for a genus of *Rynchophorous* Coleoptera. I therefore suggest as a new name for the Australian group BOTHRIEMBRYON, the type being *Bul. melo*". Pilsbry (1900, p. 2) later clarified the proposal of *Bothriembryon* and emphasized that *Helix melo* Quoy and Gaimard, 1832 should be the type species.

When discussing the systematics of *Bothriembryon* Pilsbry, 1894, many authors have failed to cite the original description of *Liparus* Albers, 1850 (e.g. Kendrick 1978, 2005; Smith 1992; Smith *et al*. 2002) or presumably treated Albers and Martens (1860) as a separate, new description of *Liparus* (e.g. Pilsbry 1900; Iredale 1937*a*,*b*, 1939; Zilch 1959; Kendrick and Wilson 1975; Burch 1976; Breure 1979; Richardson 1995; Schileyko 1999). All taxonomic revisions of the genus *Bothriembryon* Pilsbry, 1894 have followed Pilsbry (1894) in citing the type species as *Helix melo* Quoy and Gaimard, 1832 (e.g. Pilsbry 1900; Iredale, 1937*a*,*b*, 1939; Zilch 1959; Kendrick and Wilson 1975; Burch 1976; Kendrick 1978, 2005; Smith 1992; Richardson 1995; Schileyko 1999; Smith *et al*. 2002; Whisson and Breure 2016).

There is no valid type designation for *Liparus* Albers, 1850 or its replacement name *Bothriembryon* Pilsbry, 1894. As *Bulimus atomatus* Gray, 1834 and *Bulimus favannii* Lamarck, 1822 were the only species included in *Liparus* when it was first named by

Albers (1850), only those species are available to be selected as type species. Acceptance of either as the type species of *Liparus* would mean that *Bothriembryon* would share the same type species (Article 67.8). Acceptance of *Bulimus atomatus* Gray, 1834 as the type species of *Liparus* would mean that *Liparus* and *Bothriembryon* would be the senior synonym of *Pygmipanda* Iredale, 1933 (currently in Caryodidae, a different family) as they would all share the same type species. This would result in the two species of *Pygmipanda* (see Smith 1992; Smith *et al*. 2002) being transferred to *Bothriembryon* and all 36 species of *Bothriembryon* (see Breure and Whisson 2012; Whisson and Breure 2016) being transferred to one of *Hartogembryon* Iredale, 1933 (type species *Bulimus onslowi* Cox, 1864 by original designation), *Larapintembryon* Iredale, 1933 (type species *Liparus spenceri* Tate, 1894 by original designation), *Satagembryon* Iredale, 1933 (type species *Bulimus gratwicki* Cox, 1899 by original designation) or *Tasmanembryon* Iredale, 1933 (type species *Bulimus tasmanicus* Pfeiffer, 1853 by original designation), all currently treated as junior synonyms or subgenera of *Bothriembryon* (see Smith *et al*. 2002). Acceptance of *Bulimus favannii* Lamarck, 1822 as the type species of *Liparus* would mean that *Liparus* and *Bothriembryon* would be senior synonyms of *Leucotaenius* Albers and Martens, 1860 (currently Clavatoridae, a different family). Again, this would result in considerable disruption with the one species of *Leucotaenius* being transferred to *Bothriembryon*, and all 36 species of *Bothriembryon* transferred to *Hartogembryon*, *Larapintembryon*, *Satagembryon* or *Tasmanembryon*.

Both of these actions threaten the current usage of *Bothriembryon*, the name and concept of which have been frequently and consistently used for more than a century. A different type species for *Bothriembryon* other than *Helix melo* Quoy and Gaimard, 1832 would create significant nomenclatural instability and confusion. For example, many *Bothriembryon* species are included on the IUCN Red List of Threatened Species and on the Western Australian (WA) Threatened and Priority Fauna list. Additionally *Bothriembryon* is an iconic group of short-range endemic species in the

WA Environmental Protection Authority (EPA) Guidance Statement. The name *Bothriembryon* has been used in numerous publications dealing with: taxonomy and systematics (a list of 39 publications has been provided to the Secretariat); biology, ecology, biogeography and behavior (11 publications provided to the Secretariat); catalogs, checklists, keys and servers (18 publications provided to the Secretariat); and the threatened status of some species (13 publications provided to the Secretariat). I seek stabilization of these issues to allow current usage of *Bothriembryon* to continue.

3.2 Conclusion

The International Commission on Zoological Nomenclature is accordingly asked:
(1) to use its plenary power to set aside all type species fixations for the nominal genus *Liparus* Albers, 1850 and to designate *Helix melo* Quoy and Gaimard, 1832 as its type species;
(2) to use its plenary power to set aside all type species fixations for the nominal genus *Bothriembryon* Pilsbry, 1894 and to designate *Helix melo* Quoy and Gaimard, 1832 as its type species;
(3) to place on the Official List of Generic Names in Zoology the name *Bothriembryon* Pilsbry, 1894 (gender: masculine), type species *Helix melo* Quoy and Gaimard, 1832, as ruled in (2) above;
(4) to place on the Official List of Specific Names in Zoology the name *melo* Quoy and Gaimard, 1832 as published in the binomen *Helix melo* (specific name of the type species of *Bothriembryon* Pilsbry, 1894), as ruled in (2) above.

Chapter 4: A new species of *Bothriembryon* (Mollusca, Gastropoda, Bothriembryontidae) from south-eastern Western Australia

This chapter was published in:
Whisson, C.S. and Breure, A.S.H. (2016) A new species of *Bothriembryon* (Mollusca, Gastropoda, Bothriembryontidae) from south-eastern Western Australia. *ZooKeys* **581,** 127–140.

4.1 Introduction

Along with the diverse and generally more northern and eastern Camaenidae, the endemic Australian genus *Bothriembryon* (Bothriembryontidae) forms a large and characteristic component of the Australian terrestrial molluscan fauna, particularly in Western Australia (Iredale 1939; Kershaw 1985; Solem 1998). Thirty five extant and seven fossil *Bothriembryon* species are currently known from Australia (Iredale 1939; Breure 1979*b*; Smith 1992; Richardson 1995; Smith *et al*. 2002; Breure and Whisson 2012) but many undescribed species have been proposed based on specimen identifications by former Western Australian Museum malacologists.

Recent taxonomic work on this group has been limited, with the last description of a new extant species being over thirty years ago (Hill *et al*. 1983). The majority of *Bothriembryon* species are limited to mesic south-western Western Australia with two species endemic to South Australia, one species to the lower Northern Territory and one species to south-eastern Tasmania. During the 1970's a somewhat slender shell from the Caiguna and Cocklebiddy areas was identified as a new species by Western Australian Museum malacologist Hillary Merrifield but was never named. This taxon is described herein.

4.2 Materials and Methods

A total of 22 lots comprising 242 specimens were examined from the malacological collection of the Western Australian Museum. Three relaxed formalin-fixed specimens were used for 3D visualisation (Walker *et al*. 2014) and stained in a solution of 1% iodine in 70% ethanol for four days. Due to the narrowly elongated shape of the shells the staining of the upper whorls is less than those of the animal extending outside the shell (Figure 4.3A). Subsequently they were scanned using the Nikon Metrology HMX ST 225 micro-CT scanner at the Imaging and Analysis Centre at the Natural History Museum, London. This system is equipped with a detector panel (2000 x 2000 pixels) with a maximum resolution of 5 μm and a maximum energy of 225 kV. A tungsten reflection target was used with the following parameters: 180 kV, 180 μA, 500 ms exposure time and 3,142 projections were taken. Images acquired during the scanning process were subsequently reconstructed using CT Pro (Nikon Metrology, Tring, UK), which employs a modified version of the back-projection algorithm created by Feldkamp *et al*. (1984). Output files were used with ImageJ 2.0.0-rc-9 (2D), and Avizo 8.1 and Mimics 15.01 (3D).

Shell dimensions followed the methods figured by Breure (1974: figure 2) and Kendrick and Wilson (1975: figure 1) for whorl counts. Measurements were made through digital calipers to 0.1 mm for maximum shell height (H) and maximum shell diameter (D); a Leica M80 Dissecting Microscope for number of shell whorls (W), number of protoconch whorls (P), number of ribs on the penultimate whorl (RP), number of nodules on the penultimate whorl (NP) and number of spiral lines on the penultimate whorl (SP). Finer measurements of height of aperture (HA), width of aperture (WA) and height of last whorl (LW) were taken from digital photographs using a Leica MZ16A microscope with Leica DFC500 camera. Photographs of live and preserved specimens were also taken with this equipment. Anatomical features are following the terminology by Tompa (1984), and—contrary to Breure (1978)—proximal and distal refer to organ (or parts of organs) positions relative to the direction of the gamete flow, i.e. from tip of flagellum (proximal) to genital pore (distal).

Abbreviations of depositories: AM, Australian Museum, Sydney, Australia; RMNH, Naturalis Biodiversity Center, Leiden, the Netherlands; WAM, Western Australian Museum, Perth, Australia.

Data for material examined has been transcribed as per specimen labels and distributional maps were plotted using ArcGis 10.1 software.

4.3 Systematics

Superfamily Orthalicoidea Albers, 1860

Family Bothriembryontidae Iredale, 1937*a*

Subfamily Bothriembryontinae Iredale, 1937*a*

Genus *Bothriembryon* Pilsbry, 1894

Subgenus *Bothriembryon* Pilsbry, 1894

Type species: *Helix melo* Quoy and Gaimard, 1832 by original description

Remarks. The use of subgenera within this genus is disputed. Breure (1978, 1979*b*) recognized *Bothriembryon* (*Bothriembryon*) and *B.* (*Tasmanembryon*). Kershaw (1986), after a detailed study of external and internal morphology, concluded that his evidence suggested only one generic unit. I follow the opinion of Breure (1978, 1979*b*) supported in recent reviews (Smith 1992, Richardson 1995, Smith *et al.* 2002) and recognise two subgenera. Support for subgenera within *Bothriembryon* will be examined in a near-comprehensive molecular systematic assessment of the genus (Kirkendale *et al*. in prep.)

***Bothriembryon* (*Bothriembryon*) *sophiarum* sp. n.**

http://zoobank.org/2EE13185-B302-42DC-9E55-DAFAB0B44899

Table 4.1, Figures 4.1 to 4.6

4.3.1 Type Material

Holotype Western Australia, Nullabor Plain, Baxter Cliffs near Burnabbie Ruins, 32º07'30"S 126º20'45"E, V. Kessner collector (ex J. Hemmen collection) 6 October 1989, dry, WAM S66478. **Paratypes** (from type locality) WAM S66479 (2 dry specimens) and RMNH.MOL.334653 (2 dry specimens); Western Australia, Nullabor Plain, Baxter Cliffs near Burnabbie Ruins, 32º07'30"S, 126º20'45"E, V. Kessner collector, 6 October 1989, WAM S30768 (6 dry specimens), AM C.477954 (3 dry specimens), RMNH.MOL.334654 (1 dry specimen).

Table 4.1 Shell measurements of the type material of *Bothriembryon* (*B.*) *sophiarum* sp. n.

B. sophiarum Registration number	***n***	**Shell Height** mm (sd)	**Shell Diameter** mm (sd)	**H/D Ratio** (sd)	**No. Whorls** (range)
WAM S66478 (Holotype)	1	14.4	5.0	2.9	6.75
WAM S66479	2	12.7 (0)	4.7 (0)	2.7 (0)	6.28 (6.20-6.35)
RMNH.MOL.334653	2	13.7 (0.35)	5.0 (0)	2.7 (0.07)	6.48 (6.20-6.75)
WAM S30768	6	15.3 (1.07)	5.4 (0.30)	2.8 (0.07)	6.62 (6.25-7.00)
AM C.477954	3	15.2 (0.06)	5.4 (0.21)	2.8 (0.12)	6.57 (6.50-6.60)
RMNH.MOL.334654	1	16.2	5.7	2.8	6.85
Grand Mean	15	**14.7 (1.23)**	**5.2 (0.35)**	**2.8 (0.09)**	**6.56 (6.20-7.00)**

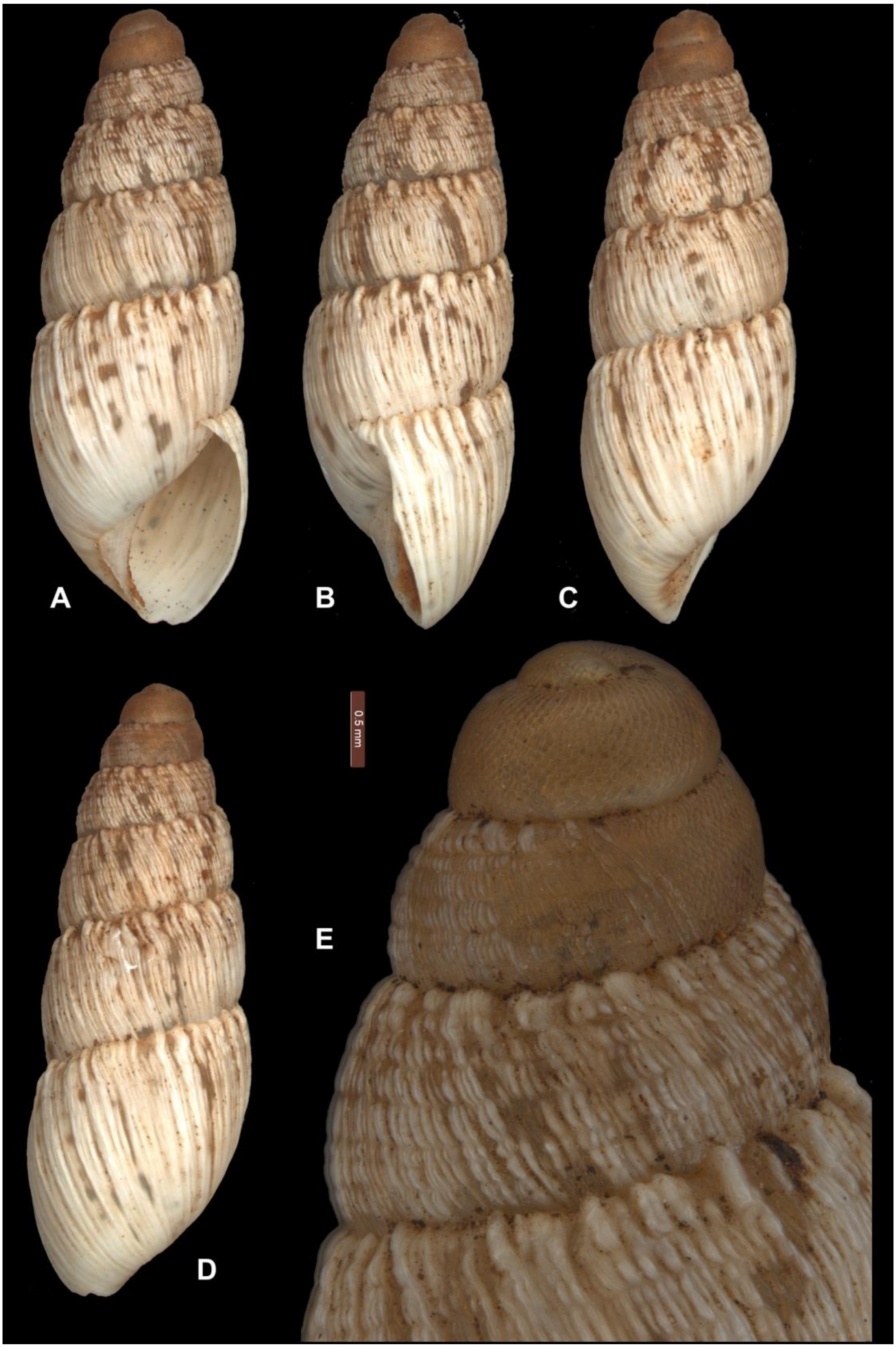

Figure 4.1 *Bothriembryon* (*B.*) *sophiarum* sp. n. holotype WAM S66478 (H = 14.4 mm) E Protoconch and early teleoconch sculpture; scale line 0.5 mm.

4.3.2 Other material examined

Western Australia: Israelite Bay, W.G. Buick Collection No. 13096, Pre June 1992, WAM S7972 (2 dry specimens); Israelite Bay area, start of cliffs at E end, Point Culver area, A. Longbottom, 21 October .1983, WAM S7977 (46 dry specimens); Nuytsland Nature Reserve, Toolina Cove, A. Cummings, 31 August.2010, WAM S64829 (4 preserved specimens); Top of Toolina Cliff, J. Lowry, 07 November 1966, WAM S7978 (8 dry specimens); Nuytsland Nature Reserve, Baxter Cliffs, near Baxter Memorial, A. Cummings, 30 August 2010, WAM S64824 (6 preserved specimens); South of Baxter Memorial, 50 feet from edge of cliff, P. Bridge and B. Robinson, 19 December 1966, WAM S7968 (6 dry, 24 preserved specimens); 38 km S of Caiguna, sea cliff top, K.A. Lance, 07 January 1976, WAM S7966 (25 dry specimens); S of Caiguna, between the Baxter Memorial and coast, P. Bridge and B. Robinson, 19 December 1966, WAM S7971 (8 dry specimens); S of Caiguna; near coast, B. Robinson, April 1966, WAM S8006 (2 dry specimens); 6 km SE of Baxter Memorial, top of Baxter Cliffs, A. Saar and K. Lance, 07 January 1976, WAM S7970 (10 dry, 4 preserved specimens); Twilight Cove, on cliff slope east of the cave, J. Lowry, 05 November 1966, WAM S7973 (33 dry specimens); 13 miles SE of Cocklebiddy, 7 miles N of Eyre, K. Thies, 21 May 1971, WAM S7974 (12 dry specimens); Eyre Homestead, escarpment face, W. Humphreys, March 1985, WAM S7969 (1 dry specimen); 14 miles ESE of Cocklebiddy, on face of Hampton Escarpment, A. Baynes and W. Youngsen, 04 September 1969, WAM S8031 (25 dry, 2 preserved specimens); Eyre, foot of escarpment, E. Sedgwick, August 1977, WAM S8053 (8 dry specimens); Baxter Cliffs 1.3 km E of Burnabbie Ruins, 32º07’6.54”S 126º21’4.50”E, R. Phillips, 6 March 2015, WAM S67680 (1 wet specimen).

4.3.3 Diagnosis

A slender shell characterised by plicate teleoconch whorls, often with pillared sculpture formed from incised spiral lines which become less frequent on the body whorl, and a strongly crenulate suture.

4.3.4 Description

4.3.4.1 Shell Morphology

Shell slender, mostly turriform, diameter 4.7–6.7 mm (mean 5.5 mm, sd 0.45), height 12.7–24.4 mm (mean 16.2 mm, sd 2.39) with 6.20–8.50 whorls (mean 7.05, sd 0.63) and a H/D ratio of 2.4–3.8 (mean 2.9, sd 0.26), rimate. Protoconch of 1.80–2.45 whorls (mean 2.18, sd 0.14) with very short, separate oblique wrinkles extending from suture before reticulating into a dense pattern of uniform punctated thimbles (honeycomb pattern). Teleoconch consisting of slightly convex, but regularly rounded plicate whorls, sculptured with narrow, crowded (often bifurcate) flattened or slightly raised axial ribs that are smooth and often translucent. The axial ribs become irregularly spaced on the last whorl, fading away towards the lower part of the whorl. Axial ribs usually crossed by only a few (mean 5, sd 1.0 on penultimate whorl) faint incised spiral lines creating a pillared sculpture that becomes less obvious on the body whorl. Suture irregularly but strongly crenulate formed from axial ribs terminating as large, rectangular nodules at the suture line, with a single nodule often forming from multiple axial ribs. Colour reddish-brown at the protoconch, the teleoconch cream with irregular blotches of reddish- to greyish-brown. Aperture relatively small, skewed elongate-ovate, lip thin, simple, basal margin slightly angular at the transition to the columellar margin, which is triangular dilated above; parietal callus thin and transparent.

4.3.4.2 Animal External Morphology

Body and foot sculptured with regular honeycomb pattern. Upper body and tentacles dark brown to black with an olive to green foot base and sides, the latter relatively wide (Figure 4.2A).

4.3.4.3 Genital Morphology (Based on micro-CT images, see Figures 4.3A-B, 4.4A–E)

Phallus gradually becoming narrower, with the distal part of the epiphallus and the proximal part of the flagellum subcylindrical. Distal part of penis lumen star-shaped (five-legged), lined with a high epithelium and gradually changing into the epiphallus, of which the narrow lumen is also star-shaped. Near the transition to the flagellum the lumen becomes three-legged star-shaped with five very narrow side-branches; more proximally the lumen is rectangular with five very narrow side-branches. The vagina is externally swollen, internally the lumen is elongated and undivided in its distal part, becoming forked at the tail-ends near the split into the spermathecal duct and spermoviduct. The spermathecal duct is comparatively broad with a club-shaped bursa copulatrix. The spermoviduct is slender (as far as traceable). In 3D (Figure 4.3A) the genitalia are extruded outside the body of the animal; the female part cannot be traced towards its distal end, the phallus is heavily curled towards its distal end.

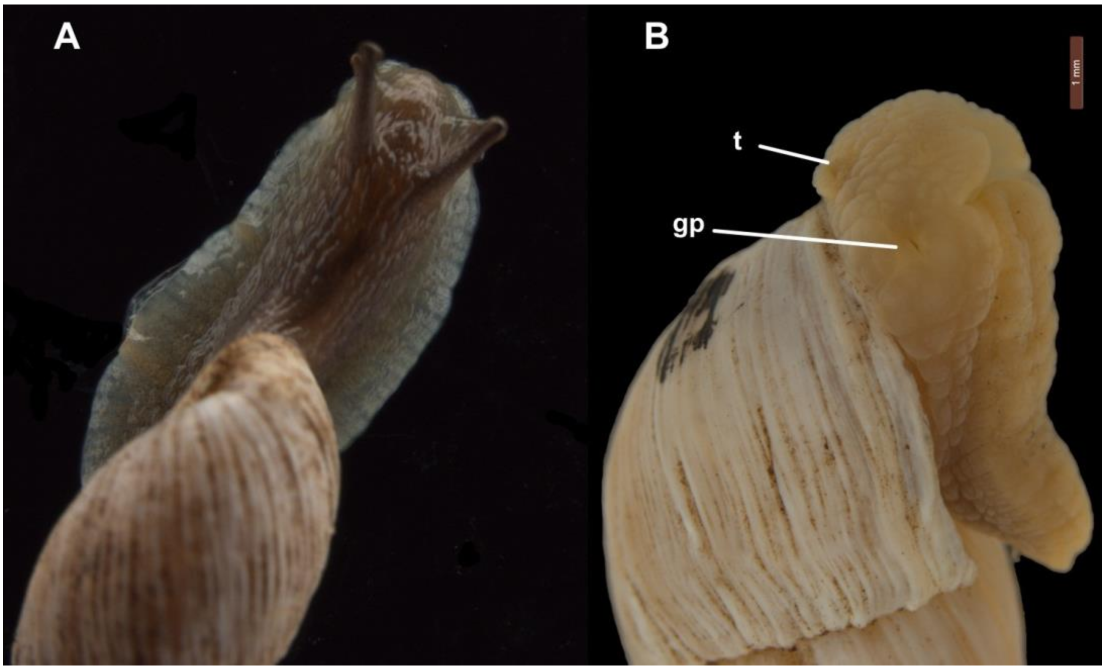

Figure 4.2 *Bothriembryon* (*B.*) *sophiarum* sp. n. A. living animal WAM S67680 B. relaxed narcotized specimen showing the genital pore, WAM S7968. Scale lines 1.0 mm (B). Abbreviations: gp, genital pore; t, retracted tentacle.

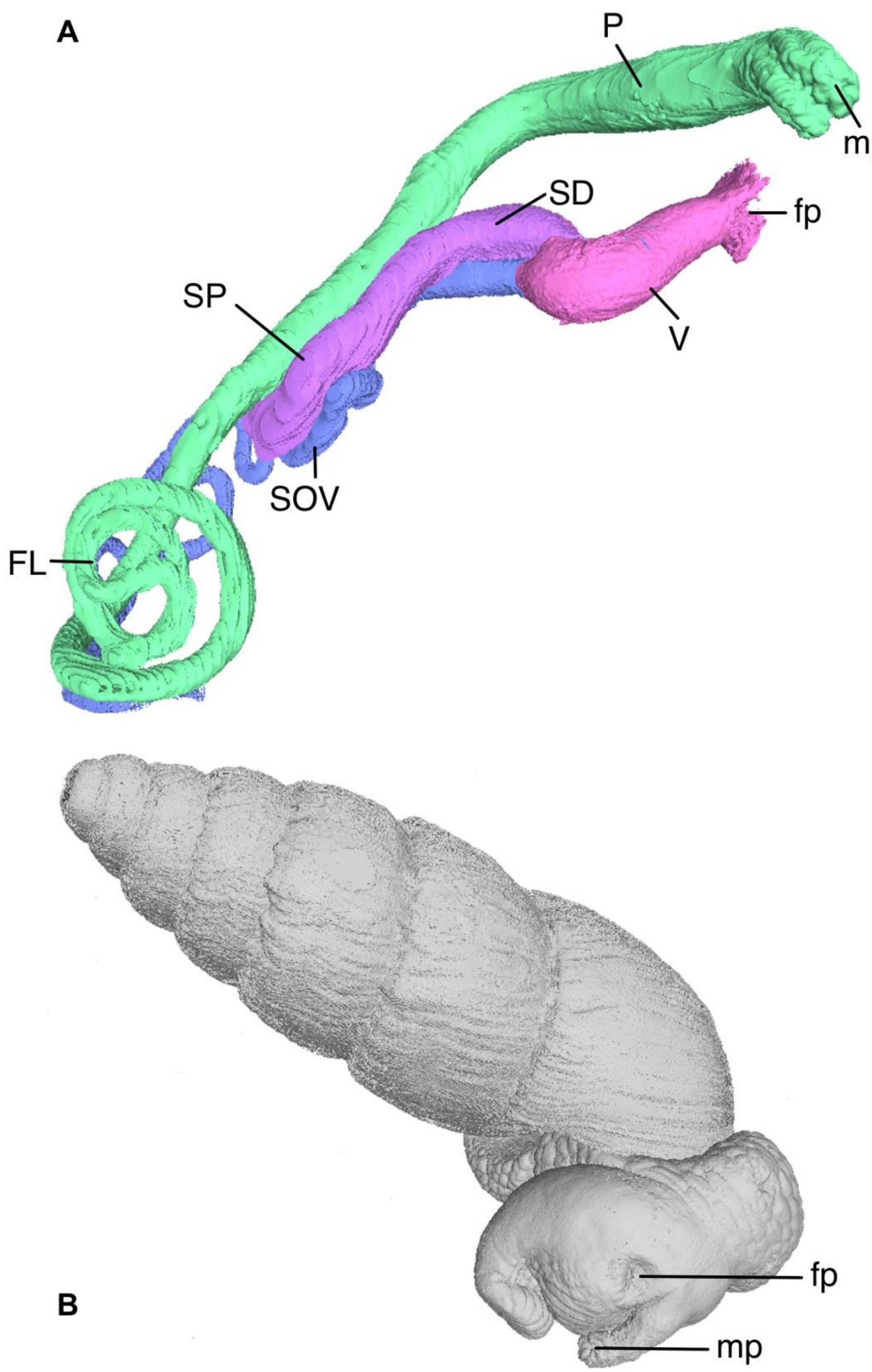

Figure 4.3 *Bothriembryon* (*B.*) *sophiarum* sp. n., WAM S7968, genitalia (extruded) A. segmented in mimics to show the different parts B. in situ. Abbreviations: FL, flagellum; fp, female pore; mp, male pore; P, penis (or phallus); SD, spermathecal duct; SOV, spermoviduct; SP, spermatheca (or bursa copulatrix); V, vagina.

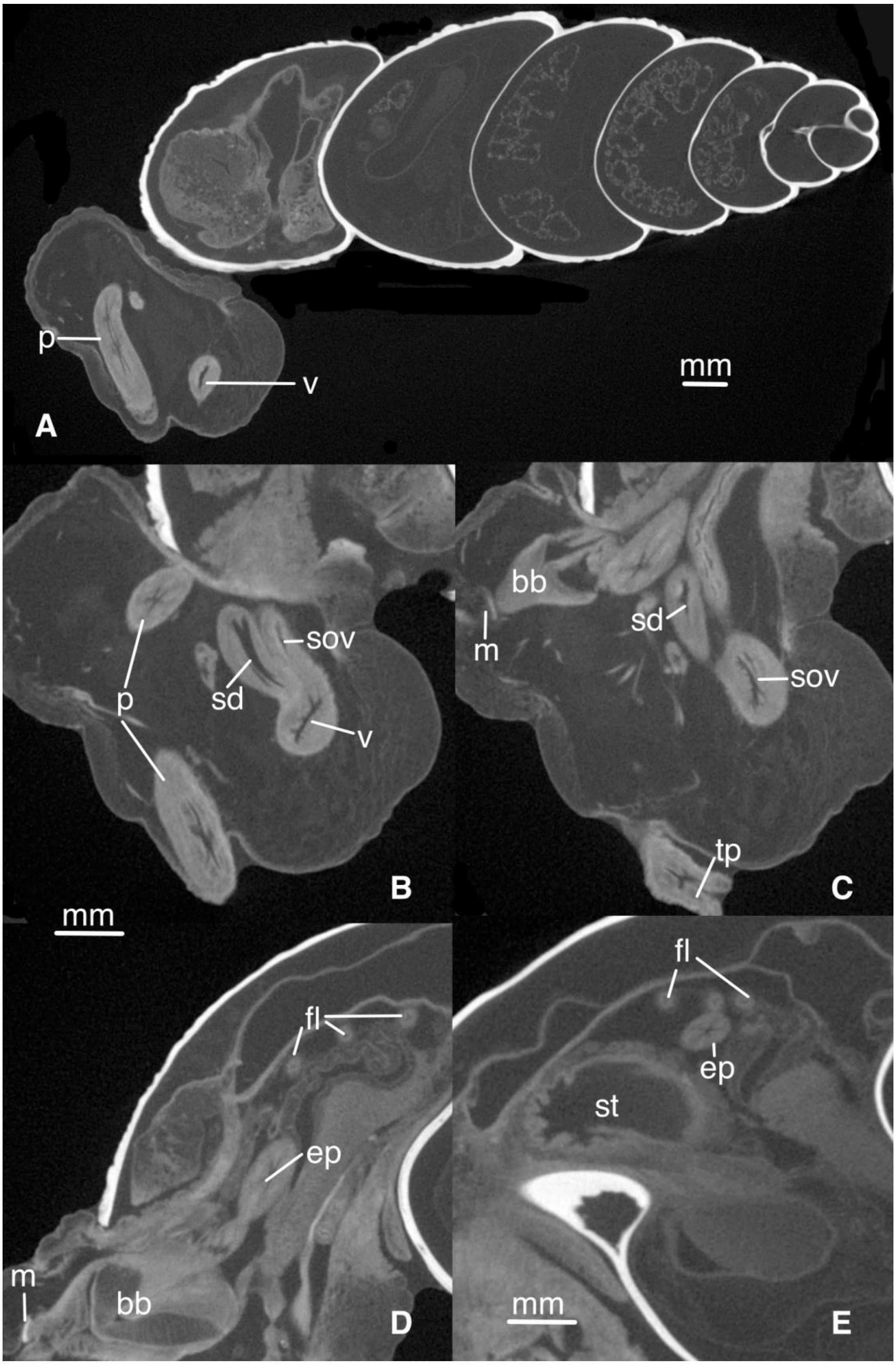

Figure 4.4 *Bothriembryon* (*B.*) *sophiarum* sp. n., WAM S7968, anatomy shown with micro-CT. A. Longitudinal view of snail B–E. Details showing parts of genitalia at different cross-sections. Abbreviations: bb, buccal bulb; ep, epiphallus; fl, flagellum;

m, mandibula; p, penis; sd, spermathecal duct; sov, spermoviduct; st, stomach; tp, tip of penis; v, vagina.

4.3.5 Distribution

Western Australia; along the escarpment and cliff tops of the Baxter Cliffs and Hampton Ranges from the Point Culver area eastward to the Burnabbie Ruins, a linear distance of 180 kilometres (Figure 4.5). Museum records (WAM S7972) suggest it might occur further westward to Israelite Bay (townsite) but the veracity of the location data is questionable.

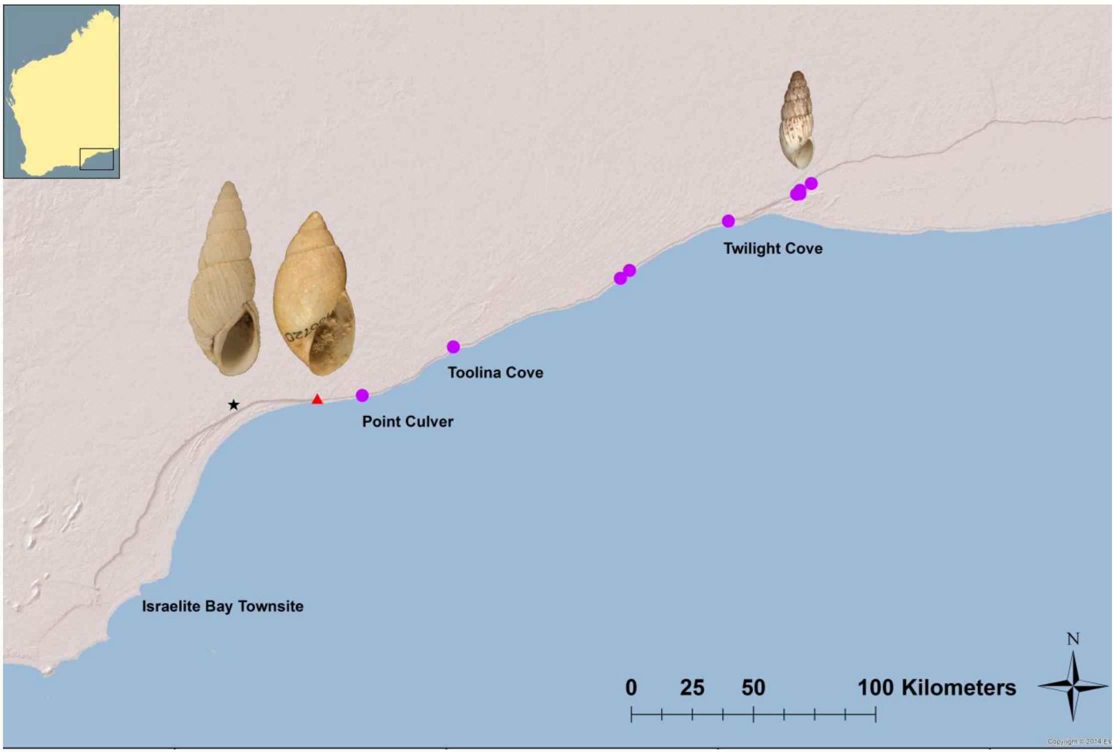

Figure 4.5 Distribution map of *Bothriembryon* (*B.*) *sophiarum* sp. n. (dot) including photo of holotype (WAM S66478, H = 14.4 mm) and type localities and photos of nearby coastal species *B.* (*B.*) *perditus* Iredale, 1939 (triangle, AM C.100720, H = 23.2 mm) and *B.* (*B.*) *gratwicki* (Cox, 1899) (star, AM C.127559, H = 29.5 mm); Inset: Western Australia highlighting enlarged area

4.3.6 Habitat

Very open, low coastal scrub on limestone cliff-edge or slope scattered (often densely) with low limestone rocks and stones (Figure 4.6). Dominant plant species were *Westringia dampieri*, *Correa backhouseana* var. *coriacea* and *Carpobrotus virens* and very occasionally *Melaleuca* and *Eucalyptus* trees. In dry conditions living specimens are commonly found in rock crevices or fissures; under stones or around tree roots, occasionally in litter. When wet, crawling snails have been observed on soil and stones and on branches of scrub.

4.3.7 Remarks

Bothriembryon sophiarum can be distinguished from most other *Bothriembryon* species by its shell morphology, notably its slender turriform shape and a teleoconch sculpture of coarsely plicate whorls and strongly crenulate suture. Most *Bothriembryon* species are elongate-conical in shape and have a teleoconch sculpture of faint or narrow axial growth lines. The geographically nearby *Bothriembryon* (*B.*) *perditus* Iredale, 1939 has similar shell morphology but its shell is much broader being elongate-conical in shape and has sutures which are more finely crenulate. The other nearby species *Bothriembryon gratwicki* (Cox, 1899) is similar in shape but its shell is broader and usually more elongated, with a coarse nodulose teleoconch sculpture (Figure 4.5). Only one fossil species occurs nearby, *Bothriembryon kremnobates* Kendrick, 2005 which is found further east on the Roe Plain and is ovate-conical in shape.

Anatomically *B. sophiarum* differs slightly from known data of *Bothriembryon* (*Bothriembryon*) species which have a long, narrow spermathecal duct and a short rounded bursa copulatrix. The short and broad spermathecal duct and relatively broad, elongate bursa copulatrix of *B. sophiarum* agrees more with *Bothriembryon* (*Tasmanembryon*) *tasmanicus* (Kershaw 1986, Breure 1978). The specimens examined have their genitalia somewhat extruded, hence the male and female genital

Figure 4.6 *Bothriembryon* (*B.*) *sophiarum* sp. n., habitat for WAM S64824 A. Inland view B. Detail showing host plants *Westringia dampieri*, *Carpobrotus virens* and *Correa backhouseana* var. *coriacea* among limestone (photos courtesy Andrew Cummings and Ben Schneider).

pores seem to be separated; in other preserved, non-extruded specimens these pores are united inside the atrium (Figure 4.3). It is interesting to note that *B. sophiarum* specimens from Point Culver (WAM S7977) at the western edge of its range, are slightly taller (mean height 20.3 mm, sd 2.11) with a higher H/D ratio (mean 3.4). This collection is a large series (n = 46) and most likely represents population variation due to local environmental conditions, a common occurrence within *Bothriembryon* as suggested by Main and Carrigy (1953).

4.3.8 Etymology

Named in honour of Sophie Jade Whisson, first daughter of the senior author and Sophie J. Breure, spouse of the second author; noun in pleural genitive case.

4.3.9 Data set

An excel file of *Bothriembryn sophiarum* records at the WAM are available upon request to the WAM Mollusc Section.

4.4 Discussion

Bothriembryon (*B.*) *sophiarum* appears to have a restricted range with a linear distribution of ca. 180 km and as it currently occupies an area less than 10000 km^2 qualifies as a Short Range Endemic (SRE) (Harvey 2002). Like many land snail species in arid environments (Slatyer *et al*. 2007) *B. sophiarum* has developed strategies to avoid desiccation. It occupies a niche of rocky near coastal cliff-edges and escarpments, an environment that would support higher rainfall and lower temperatures as well as provide shelter and shade. Live *Bothriembryon* (*B.*) *sophiarum* collected in the hot dry months suggests they mostly aestivate within rocks fissures or loosely under rocks on the soil surface, being a free-sealer with a white calcareous epiphragm for long-term aestivation. Resting specimens that were recently active have been observed with a clear mucoid seal over the aperture. This observed aestivation pattern of *B. sophiarum* fits the definition of a rock-dweller provided by Heller (1987), where rock-dwelling land snails aestivate during summer in rock crevices, cliffs, among boulders or beneath stones. This pattern also contains those species that burrow in soil but will rest temporarily beneath stones or between crevices of boulders.

Bothriembryon sophiarum has a slender, high-spired shell shape which is intriguing and differs from almost all known members of *Bothriembryon* which are predominantly ovate to elongate-conical in shape. Breure and Whisson (2012) remarked that the nearby and similarly shaped *B. gratwicki* (Cox, 1899) was “aberrant within the genus *Bothriembryon*” (see Figure 4.5). Heller (1987) found that there were differences in shell shape depending on what habitat a species occupied and that shell form was largely governed by the foot size requirements for each habitat and the ability to move easily within a habitat. The rocky limestone substrate in which *B. sophiarum* is found is often fractured with narrow cracks and fissures, and the slender shell shape would allow easy access into these cavities and/or under rocks. It would also aid climbing the vertical surface of the rocks. Additionally, the shell colour of *B. sophiarum* (cream with red/grey brown blotches) may provide camouflage from predators while in or on the similarly coloured limestone rocks.

Chapter 5: Review of the fossil record of the Australian land snail genus *Bothriembryon* Pilsbry, 1894 (Mollusca: Gastropoda: Bothriembryontidae): new distributional and geological data

This chapter has been submitted as:

Whisson, C.S. and Ryan, H. (Submitted) Review of the fossil record of the Australian land snail genus *Bothriembryon* Pilsbry, 1894 (Mollusca: Gastropoda: Bothriembryontidae): new distributional and geological data. *Records of the Western Australian Museum* **XX,** XX-XX.

5.1 Introduction

Molluscs are important in understanding changes in biodiversity over time due to the high preservation rate of their hard calcareous shells and consequently long fossil record, compared to other invertebrates (Jell and Darragh 1998). Fossilised molluscs not only provide information on the geological past through shell dating methods such as Uranium-series or Radiocarbon dating, but can provide past information on the ecology (e.g. predation = praedichnia); morphology (e.g. morphological stasis) and evolution of a group (Peppe and Deino 2013). While the use of molluscs for paleoecological studies is on the rise, taxonomy has become less recognised, despite being inextricably intertwined with it (Forey *et al*. 2004). Not all fossils are preserved and/or collected, and as such the global fossil record is imperfect (Behrensmeyer *et al*. 1992; Harper and Brenchley 1998).

In Australia, most molluscan fossils are of marine origin with the terrestrial and freshwater component relatively sparse (Jell and Darragh 1998; Smith and Stanisic 1998). This is not unexpected as terrestrial mollusc deposits are less common in the southern hemisphere (Smith and Stanisic 1998) possibly due to the deletory effect of physical, chemical and particularly biological processes (Behrensmeyer *et al*. 1992). Environmental conditions in Australia during the Tertiary were generally poor for preserving fossils and hence few faunal deposits are known from this time period (Breed and Ford 2007). Bishop (1981) remarked that few Australian land snail fossils are known and the prospect of discovering more are not good, indicating this is not a sampling bias. Despite this, large fossil mollusc collections remain unstudied in most Australian museums and universities (Jell and Darragh 1998). This includes fossil material of the endemic land snail genus *Bothriembryon* Pilsbry, 1894, a member of the Gondwanan family Bothriembryontidae containing seven fossil and at least 37 extant species (Breure and Ablett 2012; Breure and Whisson 2012; Schneider and Morrison 2018; Stanisic *et al*. 2018).

5.1.1 Taxonomic History of Fossil *Bothriembryon* Pilsbry, 1894 species

The first described fossil species of *Bothriembryon* was *Bulinus gunnii* (Sowerby II in Strzelecki, 1845) from south-east Tasmania, later clarified as genus *Bulimus* (misspelt) and distinct from the extant *Bothriembryon tasmanicus* (Pfeiffer, 1853) (Kershaw 1981). Similar to the extant fauna (Breure and Whisson 2012), fossil *Bothriembryon* have received little to no recent taxonomic attention, with only six fossil species described in over 170 years since *B. gunnii* was first discovered in Tasmania. Five of these species were from south-western Western Australia (SWWA): *Bothriembryon consors* Kendrick, 1978 and *Bothriembryon gardneri* Kendrick, 1978 from the Windy Harbour area; *Bothriembryon douglasi* Kendrick, 1978 and *Bothriembryon ridei* Kendrick, 1978 from the Shark Bay area and *B. kremnobates* Kendrick, 2005 from the Roe Plains. The remaining species *Bothriembryon praecursor* McMichael, 1968 was described from central Australia. Ludbrook (1980) later redescribed *B. praecursor*.

McNamara *et al*. (1991) listed Western Australian Museum type material and Richardson (1995) treated all fossil species. Later Breure and Whisson (2012) listed all fossil type material and illustrated all fossil species, some for the first time.

5.1.2 Geological Age

According to available literature, the oldest geological age of *Bothriembryon* has been determined as minimum Late Oligocene (Kershaw 1981) or broadly tertiary (McMichael and Iredale 1959; McMichael 1968), based on the stratigraphy at the Tasmanian type locality of *B*. *gunnii*. Similarly, stratigraphy at the Northern Territory type locality of *B*. *praecursor* has been dated as broadly tertiary (McMichael 1968; Ludbrook 1980). Additional material of this species from South Australia narrowed the geological age to tentatively Miocene (Ludbrook 1963) or middle Miocene (Ludbrook 1980). Based on *B*. *praecursor* material, Kendrick and Wilson (1975) summarised the oldest age of *Bothriembryon* as tentatively Miocene, whilst Solem (1998) interpreted it as late tertiary but remarked that more records were needed to accurately determine the age of the *Bothriembryon* group. Kendrick (2005) suggested the age of *B*. *praecursor* needs clarification.

Based on unknown fossil specimens, Zilch (1959) tentatively placed the oldest age of *Bothriembryon* as Pliocene. Kershaw (1981) discussed an early Miocene age for the whole group (pers. comm. from Ludbrook).

5.1.3 Fossil Biogeography

Considering only type material, a total of just 41 lots which are all holotypes and paratypes (note: *B*. *gardneri* erroneously listed as syntypes in Breure and Whisson 2012), the fossil distribution of *Bothriembryon* is restricted to the seven type localities around Australia (Breure and Whisson 2012) or in some cases, also in close proximity to them.

Available literature enhances this biogeography. In northern Western Australia (WA), an interesting record from the coastal part of Cape Range extends the known distribution much further north (Slack-Smith 1993). Kendrick and Wilson (1975) documented *Bothriembryon costulatus* (Lamarck, 1822) from the mainland as well as insular Shark Bay, with *Bothriembryon onslowi* (Cox, 1864) restricted to the mainland. Wilson (2008) later found fossil shells of *B. onslowi* from Faure Island in Shark Bay. Other *Bothriembryon* specimens have been analysed for dating at Shark Bay (Hearty 2003). Whisson and Kirkendale (2017) identified Holocene *Bothriembryon whitleyi* Iredale, 1939 from the Geraldton area.

In south-east WA and eastward, fossil *Bothriembryon barretti* Iredale, 1930 specimens were noted from the Roe Calcarenite and Bridgewater formations (Ludbrook 1978), with a very similar specimen noted from St Francis Island in South Australia (Kershaw 1985, 1986). This latter record extends the mainland distribution eastward significantly and offshore. A fossil record was documented from the Kent Group to the north of Tasmania (Kershaw 1981).

In lower SWWA, subfossils of *Bothriembryon rhodostomus* (Gray, 1834) (tentative identification) were recorded from near Esperance, apparently exposed in large numbers (Cram 2010). Kendrick and Wilson (1975) recorded *Bothriembryon melo* (Quoy and Gaimard, 1832) at Bremer Bay and Limestone Head. On the Leeuwin-Naturaliste ridge unidentified *Bothriembryon* fossils were noted from soil pockets at Hamelin Bay (Fairbridge 1967), and *Bothriembryon sayi* (Pfeiffer, 1847) was recorded from a cave deposit near Margaret River and used for dating (Prideaux *et al*. 2010).

In central Australia, McMichael (1968) and Ludbrook (1980) listed specimens of *B. praecursor* from north-east inland South Australia (SA). Lowry (1970) discusses an isolated fossil specimen inland ca. 80 miles north of Rawlinna, on the southern edge of the Great Victoria Desert.

5.1.4 Aims

In this study I aim to curate the large Western Australian Museum (WAM) *Bothriembryon* collection to current taxonomy (Breure and Ablett 2012; Breure and Whisson 2012; Stanisic *et al*. 2018) and to define the geological age of identified *Bothriembryon* species (where available). I test whether these geological ages are concordant with previous literature. These data are to be used for divergence timing in a molecular phylogeny of the genus (Kirkendale *et al.*, unpublished data).

I also assess the biogeography of fossil *Bothriembryon* in Australia and compare it with modern biogeography. I hypothesise that these data might provide some insights into the origin and radiation of *Bothriembryon*. Finally, using available material I test the hypothesis that *Bothriembryon* shell size did not change over time within a species (Kendrick and Wilson 1975).

5.2 Materials and methods

Fossil and modern *Bothriembryon* data were requested from Australian museums (AM, MV, SAM, WAM, QM, TMAG, MAGNT; see below for abbreviations) and institutes (GA, GSSA). Where locality coordinates were missing (ca. 40% of records) they were approximated using a combination of Google Earth Pro Software (Ver. 7.3.2.5491) and the Geoscience Australia Gazetteer of Australia Place Names website. In many cases erroneous localities or coordinates were corrected. Distributional maps were plotted using ArcGIS 10.1 software.

Only those specimens in the WAM Palaeontology Department were sighted for identification (or confirmation) using shell morphological characters under a Leica M80 dissecting microscope, and compared with available literature and type specimens. Shell dimensions were taken from intact adult shells, typically characterised by a thickened outer lip and a solidified shell. Modern populations were characterised by strong shell colouration internally and externally. Where available, a maximum of 10 modern and 10 fossil adult shells were measured. When more than 10 specimens were available, the largest specimen(s) was chosen. Measurements were taken from specimens at or near type localities using digital callipers to 0.01 mm for maximum shell height (H) and maximum shell diameter (D). The methods followed those figured by Breure (1974: figure 2).

Stratigraphic dating was made using the International Chronostratigraphic Chart (Cohen *et al*. 2013) or the Australian Stratigraphic Units Database (ASUD) (Geoscience Australia and Australian Stratigraphy Commission 2018).

A silicone cast of *Bothriembryon* was produced from a mould found in pisolitic "kankar". The rock sample was first stabilised and sealed using a solution of Butvar B-76 and Ethanol Absolute 100% BP. The mould was then surrounded by NSP Sulphur-free plasticine and the cast was made using a silicone mix of RTV 3428A/B at a ratio of 10:1, with black Biodur AC 55 used for colour. The apex of the cast was scanned using a Desktop Hitachi TM3030 Plus SEM, fixed in position by carbon tape. Shell images were taken using a Canon 6D digital camera, with the silicone cast coated with ammonium chloride prior to imaging.

Abbreviations used for depositories of material are: AM, Australian Museum, Sydney, Australia; FMNH, Field Museum of Chicago, Chicago, United States of America; GA, Geoscience Australia, Canberra, Australia; GSSA, Geological Survey of South

Australia, Adelaide, Australia; MAGNT, Museum and Art Gallery of Northern Territory, Darwin City, Australia; MV, Museum of Victoria, Melbourne, Australia; NHM, Natural History Museum, London, England; QM, Queensland Museum, South Brisbane, Australia; SAM, South Australian Museum, Adelaide, Australia; TMAG Tasmanian Museum and Art Gallery, Hobart, Australia; WAM, Western Australian Museum, Perth, Australia

5.3 Results

5.3.1 Fossil Taxonomy

Fossil *Bothriembryon* were represented by 628 registered lots in Australian museums and institutes: WAM (613 lots); AM (9 lots); GA (4 lots); GSSA (4 lots) and QM (1 lot). No records were located at SAM; TMAG; MAGNT or MV. Additional type material was included from the NHM (1 lot).

Seven described fossil species and 22 extant species were identified from fossil material during this study. Of the 22 extant species, 15 have a fossil record published for the first time: *Bothriembryon jacksoni* Iredale, 1939 and *Bothriembryon notatus* Iredale, 1939 (treated here as distinct species from *Bothriembryon kingii*); *Bothriembryon dux* (Pfeiffer, 1861); *Bothriembryon bulla* (Menke, 1843); *Bothriembryon esperantia* Iredale, 1939; *B. fuscus* Thiele, 1930; *Bothriembryon gratwicki* (Cox, 1899); *Bothriembryon indutus* (Menke, 1843); *Bothriembryon irvineanus* Iredale, 1939; *Bothriembryon kendricki* Hill, Johnson and Merrified, 1983; *Bothriembryon leeuwinensis* (Smith, 1894); *Bothriembryon mastersi* (Cox, 1867); *Bothriembryon naturalistarum* Kobelt, 1901; *Bothriembryon perobesus* Iredale, 1939 and *B. sayi* (Table 5.1).

Sixteen extant species did not have a fossil record: *Bothriembryon angasianus*

(Pfeiffer, 1864); *Bothriembryon balteolus* Iredale, 1939; *Bothriembryon bradshawi* Iredale, 1939; *Bothriembryon brazieri* (Angas, 1871); *Bothriembryon decresensis* Cotton 1940; *Bothriembryon distinctus* Iredale, 1939; *Bothriembryon glauerti* Iredale, 1939; *Bothriembryon kingii* (Gray, 1825); *Bothriembryon perditus* Iredale, 1939; *Bothriembryon praecelsus* Iredale, 1939; *Bothriembryon revectus* Iredale, 1939; *Bothriembryon richeanus* Iredale, 1939; *Bothriembryon sedgwicki* Iredale, 1939; *Bothriembryon serpentinus* Iredale, 1939; *Bothriembryon sophiarum* Whisson and Breure, 2016 and *Bothriembryon spenceri* (Tate, 1894).

The most abundant species in the fossil collection was *B. leeuwinensis* (>170 lots). Additionally, several putative new species were recognised during curation of the WAM collection.

5.3.2 Biogeography

5.3.2.1 Fossils

Based on available registered specimens, the distribution of fossil *Bothriembryon* species is largely restricted to coastal areas within the SWWA region (at the northern, southern and eastern extremities), central South Australia and south-east Tasmania. However, sparse records from inland, lower Northern Territory and inland northern South Australia exist (Figure 5.1).

In WA, fossil *Bothriembryon* specimens have been recorded from along a near continuous distribution from the northern tip of North West Cape south to Rockingham, before a large gap (ca. 165 km) south to the Busselton area. They are recorded from Cape Naturaliste to Cape Leeuwin, and after a small gap (ca. 55 km) intermittently eastward from the Donnelly River mouth to the WA/SA border (including other significant gaps within this range). Records also occur on islands at

Shark Bay (Dirk Hartog, Bernier and Dorre islands); Rottnest Island and some islands of the Recherche Archipelago (Goose; Observatory and Salisbury islands). Significantly, inland records occur near Tallering Peak; Salmon Gums; Balladonia; Forrest Airport near Reid and north of Rawlinna in the lower Great Victorian Desert.

In South Australia, fossil specimens have been found coastal near Point Sinclair and Cape Bauer, and well inland to the north-east at Lake Palankarinna. In the Northern Territory they have been found in the vicinity of Deep Well Homestead, and in Tasmania, at Hobart. There are noticeable absences from Victoria, New South Wales, Australian Capital Territory and Queensland.

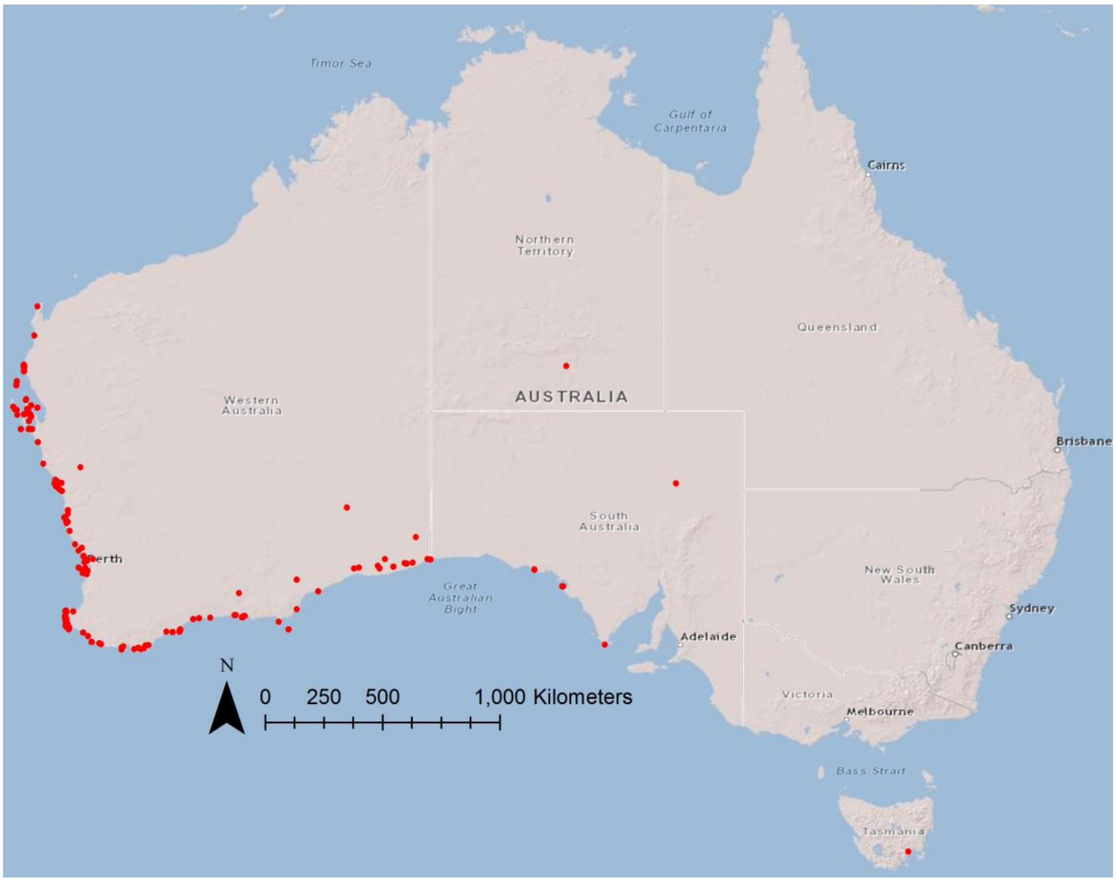

Figure 5.1. Fossil records of *Bothriembryon* species in Australian museums and institutes (ca. 631 lots as of 3rd April 2019).

Table 5.1 Geological age of *Bothriembryon* species in the Western Australian Museum Palaeontology collection based on stratigraphy (note: +extinct taxa, source: [1]WAM Label; [2]Kershaw 1981; [3]ASUD; [4]Shackleton *et al*. 2003; [5]Playford *et al*. 2013; [6]Cohen *et al*. 2003)

Species	**Stratigraphy**	**Epoch/Stage**	**Age**	**WAM No.**	**Remarks**
B. barretti Iredale, 1930	Roe Calcarenite[1]	Late Pliocene to early Pleistocene[3]	2.6 MYA to 1.8 MYA[3]	85.1875	Quarry
B. bulla (Menke, 1843)	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	60.425	Groyne
B. consors Kendrick, 1978+	Calcarenite[1]	Probably Pleistocene[1]	2.58 MYA to 11.70 KYA[6]	00.562	
B. costulatus (Lamarck, 1822)	Peron Sandstone[5]	Probably Middle to Late Pleistocene[5]	133.00 KYA to 11.70 KYA[3]	79.3121	GSWA Locality 1660
B. douglasi Kendrick, 1978+	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	96.410	
B. dux (Pfeiffer, 1861)		Post Eemian[1] (=Late Pleistocene to Holocene[4])	106.00 KYA to Present[4]	72.216	Lake floor
B. esperantia Iredale, 1939		Early to Middle Pleistocene[1]	2.58 MYA to 781.00 KYA[6]	96.360	In bore 19.5-22.0m depth
B. fuscus Thiele, 1930	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	70.1870	Base of cliffs
B. gardneri Kendrick, 1978+	Calcarenite[1]	Probably Pleistocene[1]	2.58 MYA to 11.70 KYA[6]	70.1603	Excavation
B. gratwicki (Cox, 1899)		Probably Holocene[1]	11.70 KYA to Present[6]	88.356	Cliffs
B. gunni (Sowerby, 1845)+	Probably Geilston Bay Travertine[2]	Minimum of Late Oligocene[2]	27.82 MYA to 23.03 MYA[3]	NHMUK PI OR 96907	
B. indictus Iredale, 1939	Roe Calcarenite[1]	Late Plicoene to early Pleistocene[3]	2.6 MYA to 1.8 MYA[3]	70.2161	Excavation
B. indutus (Menke, 1843)		Holocene[1]	11.70 KYA to Present[6]	86.1211	Road excavation
B. irvineanus Iredale, 1939		Middle Pleistocene[1]	781.00 KYA to 126.00 KYA[6]	94.784	Dam excavation 3.1-3.7m
B. jacksoni Iredale, 1939	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	04.242	
B. kendricki Hill *et al*., 1983		Quaternary[1]	2.58 MYA to Present[6]	66.689	Cave

B. kremnobates Kendrick, 2005+	Roe Calcarenite[1]	Late Pliocene to early Pleistocene[3]	2.6 MYA to 1.8 MYA[3]	81.847	Excavation pit
B. leeuwinensis (E.A. Smith, 1894)		Middle Pleistocene[1]	781.00 KYA to 126.00 KYA[6]	03.86	
B. mastersi (Cox, 1867)		Post 5e[1] (=Late Pleistocene to Holoecne[4])	11.70 KYA to Present[6]	03.294	Dune system
B. melo (Quoy & Gaimard, 1832)	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	70.106	
B. naturalistarum Kobelt, 1901	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	65.1178	
B. notatus Iredale, 1939	Below Calcarenite[1]	Holocene[1]	11.70 KYA to Present[6]	86.1503	
B. onslowi (Cox, 1864)	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	03.76	
B. perobesus Iredale, 1939		Holocene[1]	11.70 KYA to Present[6]	77.2770	Cave 2.01-2.10m depth
B. praecursor McMichael, 1968+	Etadunna Formation[1]	Late Oligocene to Miocene[3]	25.7 MYA to 12.5 MYA[3]	70.1801	Lake
B. rhodostomus (Gray, 1834)		Probably Middle Pleistocene[1]	781.00 KYA to 126.00 KYA[6]	05.316	
B. ridei Kendrick, 1978+	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133.00 KYA to 11.70 KYA[3]	05.262	
B. sayi (Pfeiffer, 1847)		Holocene[1]	11.70 KYA to Present[6]	04.29	Excavation
B. whitleyi Iredale, 1939		Pleistocene[1]	2.58 MYA to 11.70 KYA[6]	96.619	

5.3.2.2 Modern

To contrast fossil data, the biogeography of modern records was mapped for the first time. This included a total of 7436 lots from the following museums: WAM (5709 lots); AM (463 lots); MV (326 lots); SAM (513 lots); FMNH (279 lots); TMAG (76 lots); QM (48 lots) and MAGNT (22 lots).

The modern biogeography of *Bothriembryon* largely mirrors the fossil biogeography, having a range from Exmouth in WA (unconfirmed), southward to eastern South Australia, with isolated occurrences in lower Northern Territory and eastern Tasmania (Figure 5.2). A potentially significant, but uncomfirmed specimen, has been found from lower Victoria.

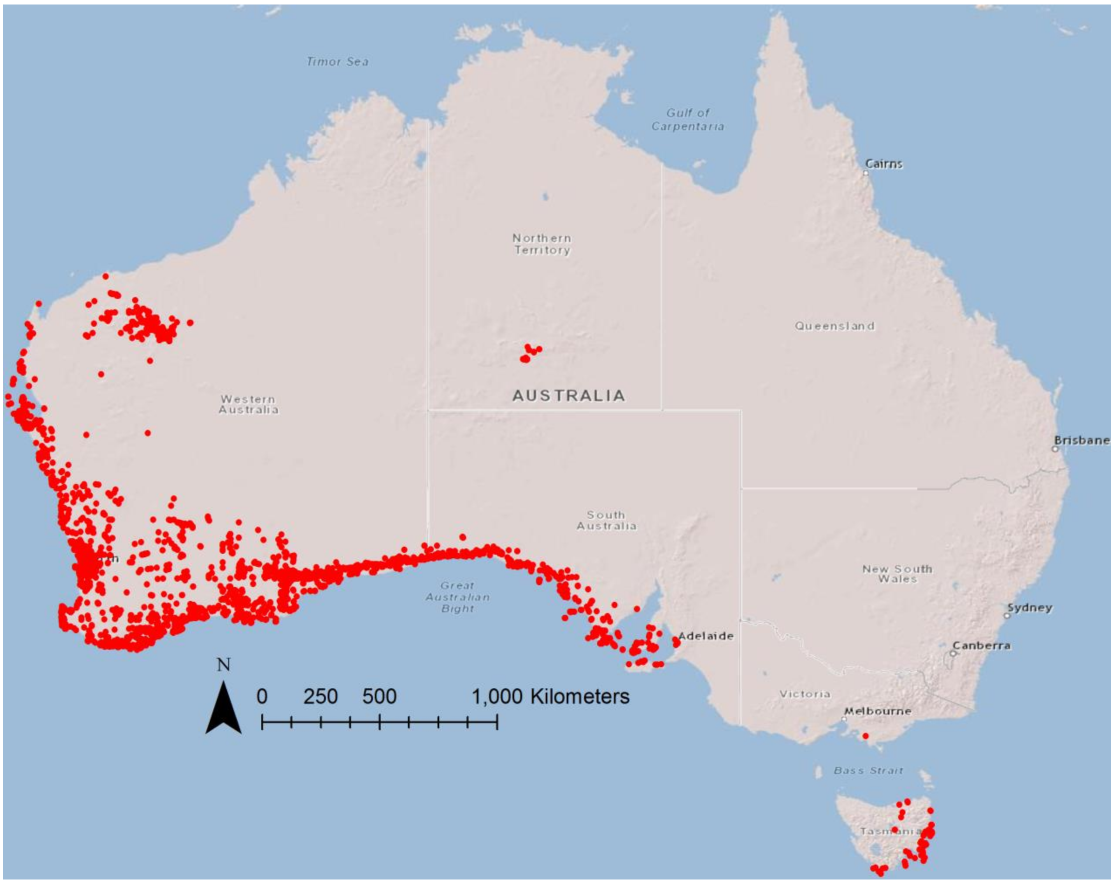

Figure 5.2. Modern records of *Bothriembryon* species in Australian museums and institutes (ca. 7436 lots as of 3rd April 2019).

The modern distribution is more prevalent inland than that of the fossils, with populations in the Pilbara and mid-west regions, and scattered occurrences throughout SWWA. The modern occurences in Tasmania also mirror these trends, with more records and more inland incursions.

5.3.3 Geological Age

The geological age of *Bothriembryon* spans from a minimum Late Oligocene (⩾ 25.70 MYA), based on the stratigraphy of the extinct Tasmanian *B. gunnii*, to recent (= Holocene). Specimens of the extinct *B. praecursor* from the Etadunna Formation in South Australia (WAM 70.1801), are more defined being Late Oligocene to Miocene (25.70–12.50 MYA) (Table 5.1).

All extant, endemic WA species have a wide Pleistocene age (2.58 MYA to 11.70 KYA). Similarly, all extinct, endemic WA species terminate in the wide Pleistocene. Some extant species, which occur across the Nullarbor into South Australia (*B. barretti*, *B. indictus*) were recorded as older, being dated as Late Pliocene to Early Pleistocene (2.60–1.80 MYA) from the Roe Calcarenite formation. The extinct Nullarbor species *B. kremnobates* can be traced back to the late Pliocene. A specimen from ca. 145 km north of Rawlinna (WAM 70.158, Figure 5.4 and 5.5), identified as *B.* cf. *praecursor* during this study, was tentatively dated as Pliocene to Pleistocene (5.333 MYA to 11.70 KYA) (Lowry 1970).

5.3.4 Shell Size

Based on available material, shell sizes for 22 extant species were compared between fossil and modern populations (Figure 5.3). Although limited in sample size, and in many cases, replicated localities, most species had similar maximum H, maximum W and H/W ratios.

However, noticeable size differences were detected in some species, such as the southern *B. fuscus*, *B. notatus* and *B. sayi*; mid-west *B. perobesus* and Nullarbor *B. indictus*, which had larger (generally more elongate) shells during the Pleistocene. In the case of the somewhat rare *B. gratwicki*, available modern material (syntypes) were bleached white; long dead and often contained sediment, likely of a similar age to available fossil specimens.

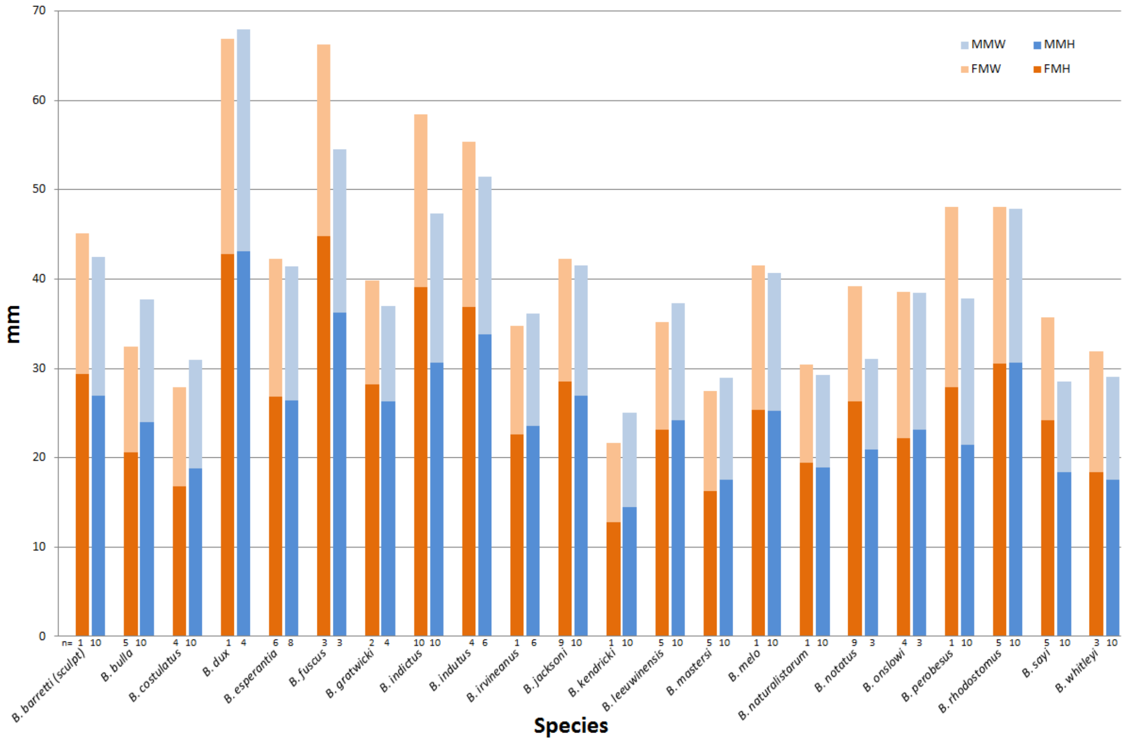

Figure 5.3. Shell size (maximum width MW, maximum height MH) comparisons between fossil (F) and modern (M) populations of various *Bothriembryon* species (Note: n = sample size, x axis).

The adult internal cast from Rawlinna (WAM 70.159) generated in this study measured 21.83 mm H, 12.80 mm W and 1.705 H/W (Figure 5.4I-J). The inland specimen from near Reid, identified as *B.* cf. *praecursor* (WAM 78.297) measured 27.95 mm H, 14.84 mm W and 1.883 H/W (Figure 5.4D-E).

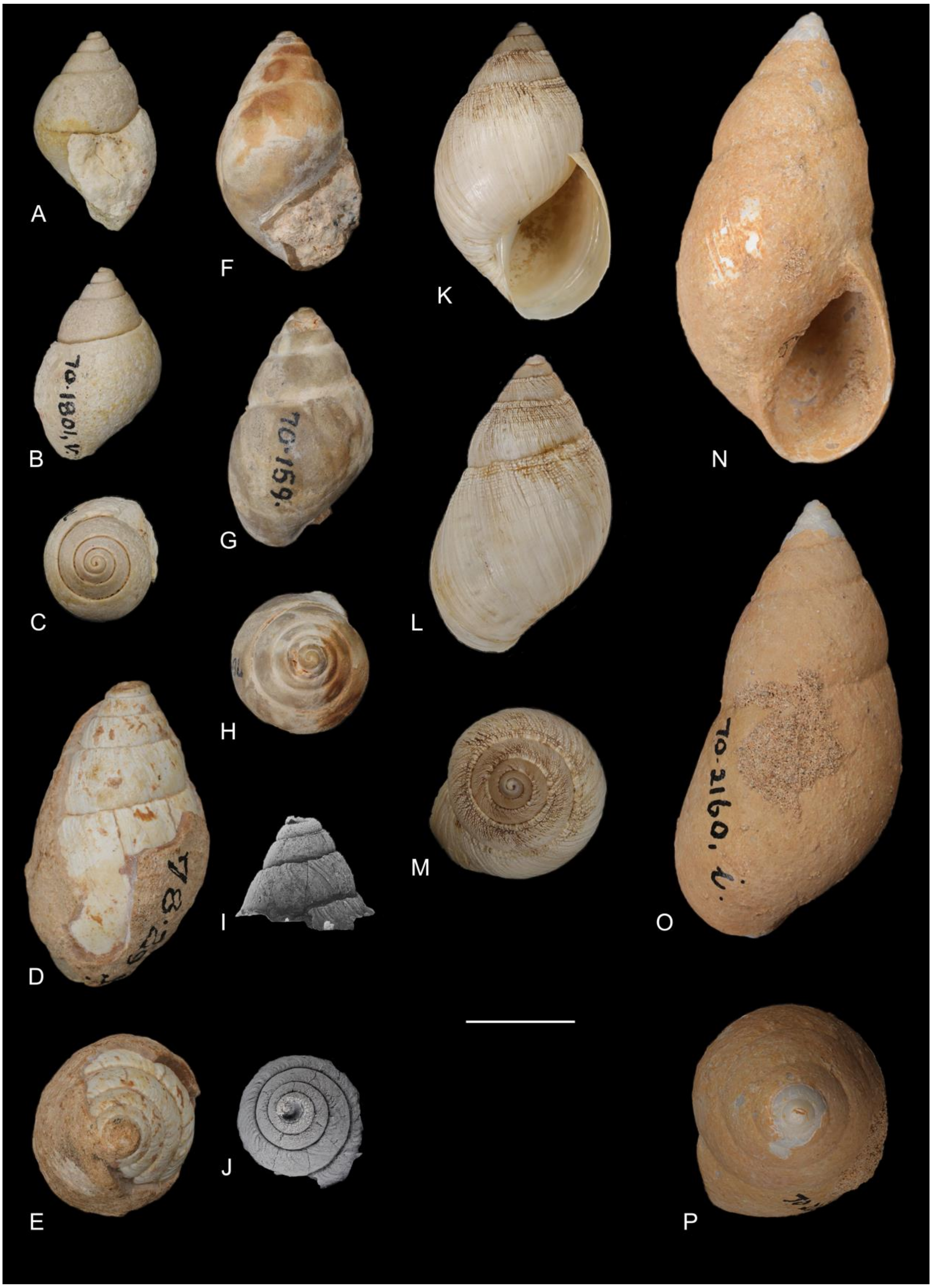

Figure 5.4. Plate of fossil and modern *Bothriembryon* specimens from the Nullarbor region and north-east South Australia. A-C, *B. praecursor*: WAM 70.1801v; D-J, *B.* cf. *praecursor*, D-E: WAM 78.297; F-H: WAM 70.159; I-J: WAM 70.158g (cast); K-M, *B. barretti*, WAM S1635; N-P, *B. indictus*: WAM 70.2160i. Scale bar = 10 mm.

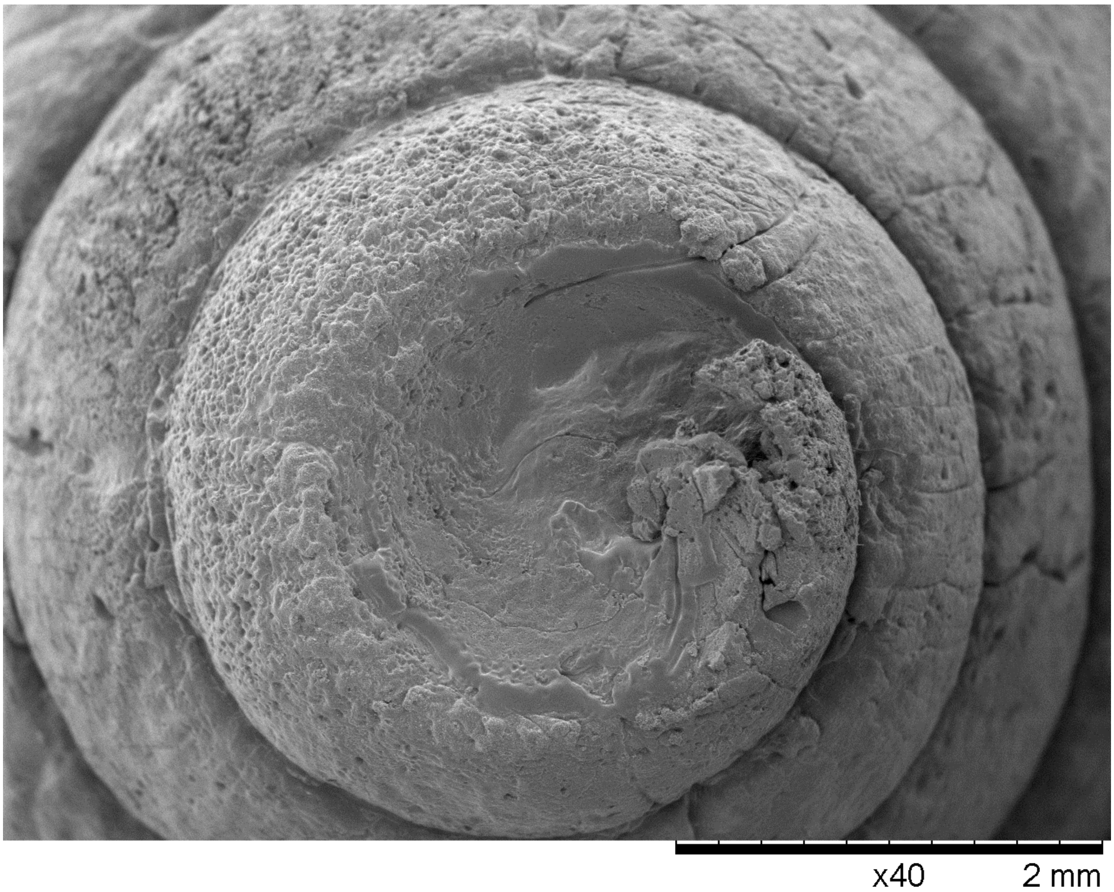

Figure 5.5 SEM image of protoconch and early teleoconch whorls of silcon cast from *B*. cf. *praecursor* fossil found 80-90 miles north of Rawlinna, WA (WAM 70.158g), x40 magnification.

5.3.5 Shell Praedichnia

Fossil shells of several extant species showed signs of extensive predation, typically having the shell spires removed (Figure 5.6). This was most common for the species *B*. *leeuwinensis* in cave deposits along the Cape Leeuwin-Cape Naturaliste Ridge. Similarly, but less frequently, it was noted for the species *B*. *perobesus* in cave deposits near the mid-west coast as well as the rock dwelling *B*. *indutus*. It was also noticed in extinct species such as *B*. *consors* and *B*. *douglasi*.

5.3.6 Data set

An excel file of the curated WAM *Bothriembryon* fossil collection is available upon request to the WAM Palaeontology Section.

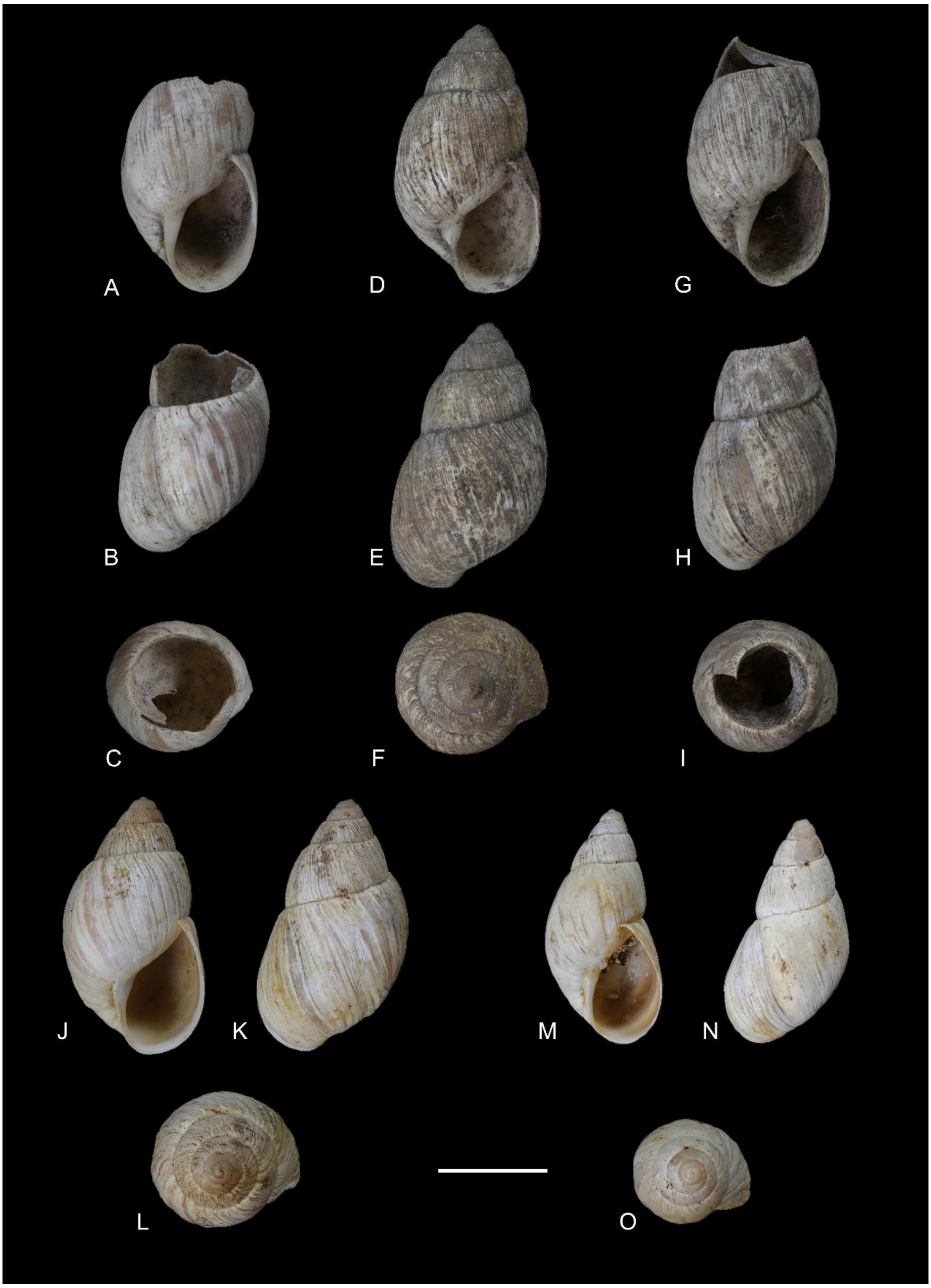

Figure 5.6 Plate of fossil and modern *Bothriembryon* from along the Cape Naturaliste–Cape Leeuwin Ridge. A–I, B. *leeuwinensis* cave subfossils: A–C,

predated shell, WAM 04.25a; D–F, intact adult shell, WAM 04.25b; G–I, predated shell, WAM 04.25c; J–O, *B. leeuwinensis* mixed syntype lot: WAM S15124: J–L, *B. leeuwinensis* adult shell, M–O, *B. sayi* adult shell. Scale bar = 10 mm.

5.4 Discussion

Smith and Stanisic (1998) remarked that no detailed taxonomic analysis had been made on fossil Australian molluscs and this deficit still exists. Furthermore, fossil identification to family and genus level has been based purely on shell characters, a problem exacerbated by the incomplete knowledge of extant taxa. This study treated the relatively large WAM fossil *Bothriembryon* collection (n = 613 lots) using modern taxonomic literature (Breure and Ablett 2012; Breure and Whisson 2012; Stanisic *et al*. 2018), resulting in many specimens being identified or having their identifications corrected. These new data enabled previous evolutionary hypotheses on *Bothriembryon* to be investigated, and demonstrated the value of taxonomic curation of a fossil collection, which are often poorly identified (Smith and Stanisic 1998). For example, numerous fossil records at WAM, previously identified as *B. sayi*, and presumably published as such (e.g. Prideaux *et al*. 2010) were in fact *B. leeuwinensis*. This matter needs further investigation as syntypes of *B. leeuwinensis* at WAM (WAM S15124) contained a mix of *B. leeuwinensis* and *B. sayi* specimens (Figure 5.6). The fossil collection also contained specimens of rare or presumed extinct species, such as *B. gratwicki* (WAM 68.10) and *B. whitleyi* (WAM 68.10).

Assembling fossil *Bothriembryon* data from Australian museums and institutes, combined with curation of the WAM Palaeontology collection, did not significantly expand the overall biogeography or geological age of the group, compared with available literature. However, the study provided accurate identifications and localities, and for available species, defined their oldest geological age and compared shell sizes between geological ages. This large combined data set (and data gaps or absences) may provide new insights into the origin, radiation and past occupation of *Bothriembryon* in Australia. The fossil record for fauna from SWWA is regarded as limited, but inclusion of this material enables phylogenetic dating and may generate new insight into the evolution of SWWA biota (Rix *et al*. 2014).

Fossil pulmonates in Australia are regarded as being late Tertiary or Quaternary in age (Smith and Stanisic 1998), although Bishop (1981) reports no records prior to the Miocene. The oldest geological age of *Bothriembryon* being Late Oligocene i.e. *B*. *gunnii* and *B*. *praecursor*, falls within the Tertiary. The probable young geological age of WA species compared with the slightly older age of Nullarbor species, and much older age of specimens from inland NT and SA and south-east Tasmania, may provide evidence for ancestry and radiation of the group. However, older records may exist (or existed) in more inland parts of WA but did not fossilise well or have not yet been exposed. This is because large parts of inland WA, known as cratons, are tectonically stable, long-term emergent crustal blocks with a thin and poorly preserved sedimentary cover. As such these areas are often overlooked in palaeoenvironmental studies (de Broekert and Sandiford 2005).

It is suggested the occurrence of specimens in tertiary deposits from central Australia (i.e. *B*. *praecursor*) may support the hypothesis that the genus was once more widespread across Australia (McMichael and Iredale 1959; McMichael 1968; Kendrick 1983). It is proposed as the landscape aridified from the mid Miocene, ca. 15 MYA (Byrne *et al*. 2008), *Bothriembryon* contracted to mesic SWWA, leaving a somewhat patchy occurrence in northern areas (McMichael 1968; Kendrick 1983). Whilst this may be the case for some *Bothriembryon* taxa, it could have been an opportunity for expansion of some others.

McMichael (1968) and Ludbrook (1980) suggested *B*. *praecursor* was similar morphologically (and probably ecologically) to the Nullarbor *B*. *barretti* and may be ancestral, although Solem (1988) remarked the fossil specimens were not in appropriate condition for comparison to other species. In my opinion the specimens of *B. praecursor* listed by McMichael (1968) and Ludbrook (1980) more closely resemble the Nullarbor group of species *B. perditus*, *B. barretti*, *B. indictus* and perhaps *B. kremnobates* than other *Bothriembryon* groups (Figure 5.4), although Kendrick (2005) did not include the latter species. Given the slightly older geological age of these Nullarbor species i.e. Pliocene, as opposed to Pleistocene SWWA species (Table 5.1), a radiation of the *B. praecursor* lineage southward may have occurred during the late Miocene glaciation, when the Nullarbor was not inundated by marine waters (Isem *et al*. 2001), combined with favourable aridification through to the Pleistocene (Hill 1994). The inland *Bothriembryon* record located ca. 145 km north of Rawlinna and tentatively aged as Pliocene (Lowry 1970) may further support this hypothesis. Lowry (1970) suggested this fossil resembled the Nullarbor species *B. barretti*, but based on morphology and size of the adult internal cast (WAM 70.159, Figure 5.4F-H), and part silicone external cast (Figures 5.4I-J and 5.5) generated in this study, suggests it could be *B. praecursor*. The adult internal cast from Rawlinna (WAM 70.159) measured 21.83 mm H, 12.80 mm W, 1.705 H/W, and although larger than the holotype (14.17 mm H, 9.00 mm W, 1.574 H/W) (Breure and Whisson 2012), it lies close to the average size range of specimens (22.4 mm H, 13.5 mm W, 1.66 H/W) listed by Ludbrook (1980).

Additionally, an inland (ca. 100 km from coast) undated, strongly lithified fossil from a cave near Forrest Airport, Reid WA was identified as *B.* cf. *praecursor* (WAM 78.297, Figure 3), again being larger (27.95 mm H, 14.84 mm W, 1.883 H/W) than the holotype. The likely late Pleistocene fossil specimen from St Francis Island in South Australia, tentatively identified as *B. barretti* (Kershaw 1985, 1986), suggests expansion of this Nullarbor group eastward during the arid Pleistocene, and may indicate a close relationship to *Bothriembryon* species in South Australia. Another similar species in this Nullarbor group, *B. dux*, was recorded in Pleistocene deposits at

Salmon Gums, toward the west end of its range.

The other major land snail family in Australia is the Camaenidae, long suspected as having an Asian origin (Solem 1997; Hugall and Stanisic 2011). Solem (1993) suggested a "red centre" source for the Camenidae subfamily Sinumeloninae, which then colonised the Nullarbor and mid-west coast of WA. Like *Bothriembryon*, the subfamily is absent from northern Australia and along the east coast (Solem 1993; 1997). Typically Camaenidae and *Bothriembryon* are allopatric, but along the Nullarbor and mid-west coast of WA are broadly sympatric, suggesting a phylogenetic hypothesis may be the same for both Sinumeloninae and *Bothriembryon* (Scott 1997).

The absence of fossil data is perhaps equally as meaningful as the presence of data, with much of eastern Australia i.e. Queensland, New South Wales, Canberra and Victoria void of *Bothriembryon* (Kershaw 1985). The isolated red centre *B. spenceri*, with no continuous connection to the modern or fossil biogeography of *Bothriembryon*, may suggest a different origin for this species, particularly as its shell morphology (shape) is not typical of the SWWA forms and more closely resembles that of South American or African bothriembryontids such as *Prestonella* Connolly, 1929 and *Plectostylus* H. Beck, 1837. Perhaps it is a relictual Gondwanan taxon surving in climatic refugia as suggested by previous authors (Bishop 1981; Kendrick 1983; Solem 1993; Ponder *et al*. 1998). Similarly *B. tasmanicus* appears to lack a fossil or modern connection with mainland Australia species and has shell morphology (shape) with closer affinity to the South American or African Bothriembryontids *Prestonella* and *Plectostylus*. Other workers have also argued that the placement of *B. tasmanicus* within the genus *Bothriembryon* is provisional (McMichael and Iredale 1959; Bishop 1981), including the geographically nearby extinct *B. gunnii* (Solem 1988; Smith and Stanisic 1998). However, McMichael (1968) suggested that *B. gunni* was similar to *B. leeuwinensis* from SWWA. Smith (1984) remarked that the origin of *B. tasmanicus* and a southern South Australian species (name not listed) was unknown, with no fossil record to assist these questions.

Many of the endemic SWWA *Bothriembryon* species were not captured in the fossil record and many geographical areas in SWWA lack *Bothriembryon* fossils. Whilst this might reflect poor fossil record preservation caused by geological activity, it could also offer insight into origin of radiation. In WA a large number of fossils have been found in the Shark Bay area; along the Cape Leeuwin to Cape Naturaliste Ridge, particularly in cave deposits (e.g. Skull Cave) and along the Nullarbor (Figure 5.1). Kendrick (1983) suggested species on the Cape Leeuwin to Cape Naturaliste Ridge originated from a south coast ancestor(s), due to the lack of modern or fossil records to the east and north. The large fossil record gap between Rockingham and Busselton, and east of the Cape Leeuwin to Cape Naturaliste Ridge supports this hypothesis.

New records generated from this study may indicate a previous broader geographical occupation of *Bothriembryon*. The large fossil shells from Salisbury Island, located on the mid continental shelf ca. 50 km from mainland (eastern Recherche Archipelago), tentatively identified as *B. rhodostomus* represent one of the outer-most island records of the group, and likely provide evidence of occupation during past glaciation events. A record of tentatively *B. rhodostomus* from the mainland near Esperance (WAM 67.380) may be ancestral to the island radiation of this group, but requires more work. These specimens resemble the form *B. rhodostomus hullianus* from the type locality Gunton Island. In the northern part of WA, fossil species *B. ridei* and *B. douglasi* were recorded from Bernier Island in Shark Bay (Kendrick 1978), a similar distance offshore as Salisbury Island. The Tallering Peak record, likely an un-named species, represents a significant inland occupation (ca. 120 km from Geraldton) at northern latitudes. Slack-Smith (1993) suggested an unidentified *Bothriembryon* fossil of Pleistocene age from the Cape Range area may indicate that the northern range of *Bothriembryon* has contracted.

In SWWA, fossil records of *B. fuscus* have been recorded from coastal areas such as Point D'Entrecasteaux (WAM 04.40, undated) and Broke Inlet (WAM 70.1870, Pleistocene), which is west of the type localities of Walpole and Denmark (Breure and Whisson 2012). As *B. fuscus* is a karri forest species (Iredale 1939; Stanisic *et al*. 2018), these records might indicate larger coastal stands of karri during more mesic times. A slightly broken specimen of *B. gardneri* was identified during this study from just south of Albany (WAM 69.428) extending its known range some 175 km eastward. Kendrick (1978) remarked the slightly larger *B. gardneri* may have been ancestral to *B. fuscus*, and as such this record from Albany may indicate past occupation of this karri associated species group further eastward. On the Cape Leeuwin-Cape Naturaliste Ridge, *B. irvineanus* was recorded from as far south as the Boranup area and south-east to Nannup, which sits outside of its type locality of Cape Naturaliste.

The comparison of shell sizes of species between geological ages, albeit limited in this study (often few fossil replicates) may provide some insight into ancestral relationships among *Bothriembryon* and past climatic conditions. Kendrick and Wilson (1975) suggested that as a result of increasing aridity during the Pleistocene, the Shark Bay species *B. onslowi* and *B. costulatus* reduced in shell size, whilst the larger *B. douglasi* and *B. ridei* became extinct, unable to cope with decreasing humid conditions (Kendrick 1978). During this study, a considerable number of the specimens previously identified as larger-sized Pleistocene *B. costulatus* (e.g. WAM 74.532, 66.1037, 66.288, 05.298) and *B. onslowi* (e.g. WAM 05.262, 79.3120, 87.247), presumably discussed by Kendrick and Wilson (1975) and listed by Kendrick (1978) were re-identified. They were mostly re-identified as the larger fossil species *B. douglasi* and *B. ridei*, or in the case of *B. costulatus*, sometimes the larger *B. onslowi*. Presumably Kendrick (1978) did not revisit the *B. costulatus* and *B. onslowi* material when describing the new fossil species *B. douglasi* and *B. ridei* and discussing size differences. Therefore the hypothesis of decreased shell size in a *Bothriembryon* species over time, due to increasing aridity as suggested by Kendrick and Wilson (1975) requires further work. In this study though, some species were found to be larger (more elongate) during the Pleistocene, such as *B. fuscus*, *B. indictus*; *B. notatus* and *B. sayi*. Whether these populations are conspecific needs further investigation, as in all cases the compared fossil and modern shells were geographically far apart.

An additional hypothesis is that ancestors of some *Bothriembryon* taxa were larger in shell size. For example, large Pleistocene specimens of *B. consors* were identified during this study from near the coast south-west of Albany (WAM 07.495), extending its known range some 165 km eastward. The shells possess axial stripes and are similar in size to the larger *B. jacksoni* in the *B. kingii* group. Perhaps *B. consors* was ancestral to the *B. kingii* group as suggested by Kendrick (1978), who also proposed a young (i.e. Quaternary) radiation for the *B. kingii* group. *Bothriembryon consors* may have been more widespread during mesic times, but with increasing aridity during the Pleistocene became disjunct due to a fragmenting habitat. Aridity, likely to be more extreme to the eastern parts of its range, could have resulted in the extinction of larger lineages, with smaller, more xeric tolerant lineages able to survive. Rix *et al.* (2014) suggests that *Bothriembryon* may have contained susceptible mesic-adapted lineages that became isolated due to increasing aridificiation, driving allopatric speciation. There are numerous examples of relatively large species confined to the Pleistocene aridification such as *B. gardneri*, *B. ridei*, *B. douglasi* and *B. consors* (Kendrick 1978).

This study demonstrated that cave desposits provide an excellent source of fossil *Bothriembryon* material for a range of species (e.g. *B. leeuwinensis*; *B. perobesus* and *B. dux*). This is not unexpected as caves provide a favourable environment (i.e. stable temperature and humidity) for the preservation of animal fossils (van der Geer and Dermitzakis 2013). The observations of predation seen in many fossil *Bothriembryon* shells (largely those in caves) may have been be caused by rodents, given the nature of the broken shells (i.e. apex removal) as suggested by Solem (1998). Rodents often build dens and middens in caves, which are usually accumulations of the surrounding biota (Breed and Ford 2007).

Chapter 6: General Conclusion

The broad aim of this study was to provide an integrated data set that improves understanding of the genus *Bothriembryon* Pilsbry, 1894 and enhances conservation of the group. The results of this study have demonstrated the importance of a sound taxonomy to underpin conservation assessment, and therefore the conservation of biodiversity. It has also shown the importance of museum records in this process. This is especially important given the foundational role that taxonomy and systematics play in the development of sound conservation policy, especially in poorly studied areas (Cameron *et al*. 2005).

Chapter 2 involved curation of the large WAM modern *Bothriembryon* collection to current taxonomy. Fieldwork was also undertaken with emphasis given to the seven nominally threatened SWWA *Bothriembryon* species. The results of the study almost doubled the number of known records for the seven threatened species and provided new morphological, biogeographical and ecological data. This will lead to an updated assessment of the IUCN status of the seven threatened species. Similarly in Chapter 5 the WAM fossil *Bothriembryon* collection was curated to current taxonomy. The results revealed geological ages of *Bothriembryon* species for the first time and provided biogeographical information for fossil (and modern) *Bothriembryon*. The results generated in Chapters 2 and 5 have demonstrated the value of data in museum collections, especially when paired with taxonomic expertise, as suggested by Reigner *et al.* (2015).

Chapter 3 outlined a submission to the ICZN to conserve the current usage of the genus *Bothrienmbryon*. The results demonstrated the implications of incorrect nomenclatural process (detected in Chapter 2), which would have serious consequences for the conservation management of *Bothriembryon*.

Chapter 4 documents the formal description of a new species of *Bothriembryon*, detected during Chapter 2. The study incorporated museum records to define the biogeography of the species which will inform conservation management.

The study has highlighted the value of an integrated approach to conservation management, in particular the role of taxonomy and the value of using museum collections. Although the study has generated important data and clarified some taxonomic issues, a more in-depth molecular study will be required to resolve species complexes such as the *B. kingii* group. It will also help identify cryptic species within *Bothriembryon*, as discovered by electrophoretic work on *Bothriembryon bulla* (Menke, 1843) (Hill *et al.* 1983) and in the mitochondrial DNA results for the closely related bothriembryontid *Prestonella* in South Africa (Fearon 2011; Barker *et al.* 2013). Cryptic species are often an early indicator of short range endemism in a genus, important to consider for conservation (Jay *et al*. 2016). To answer these questions the molecular phylogeny of *Bothriembryon* will require sequencing of described species from their type localities, in conjunction with positive identification from type material.

An additional goal of this thesis (Chapter 2) was to flag material of described *Bothriembryon* species that were suitable for DNA extraction, particularly those found at or near type localities. This material will contribute to the first molecular phylogenetic framework of the genus *Bothriembryon* that will underpin taxonomic revision. Divergence timing can also be estimated using data generated from Chapter 5.

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Appendices

Appendix A Whisson, C.S., Kirkendale, L. and Siversson, M. (2017) The presumed extinct *Bothriembryon whitleyi* Iredale, 1939 remains elusive. *Malacological Society of Australiasia* Newsletter **163**, 1-6.

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The presumed extinct *Bothriembryon whitleyi* Iredale, 1939 remains elusive

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Land snails are a critical component of ecosystem food webs, performing a variety of environmental functions from contributing to the decomposition process, herbivorous and carnivorous feeding, calcium recycling, nutrification of soils and providing a food source for predators. Many land snails are endemic to Australia and occupy very small ranges, thus making them susceptible to environmental change. As such they are considered excellent bio-indicators (Stanisic, *et al.* 2010).

In Western Australia, the Environmental Protection Authority (EPA) recognized the importance of land snails in the Environmental Impact Assessment (EIA) process, specifically those taxa exhibiting short ranges, coined Short Range Endemics (SRE). This largely encompasses surveying for the families Camaenidae and Bothriembryontidae. The genus ***Bothriembryon*** (Bothriembryontidae) is largely confined to the mesic south-west corner of Western Australia (referred to as the SWWA region), where a number of species are listed as threatened.

In recent years the Western Australian Museum (WAM) and the Netherlands Centre for Biodiversity Naturalis (Leiden) have undertaken a large-scale project to better understand the relationships in the genus ***Bothriembryon***. This work is especially important given the foundational role that taxonomy and systematics play in the development of sound conservation policy, especially in poorly studied areas (Cameron, *et al.* 2005). During this work, the importance of updating the status and/or ongoing monitoring of threatened species from key sites in WA was revealed. **(continued on page 5)**

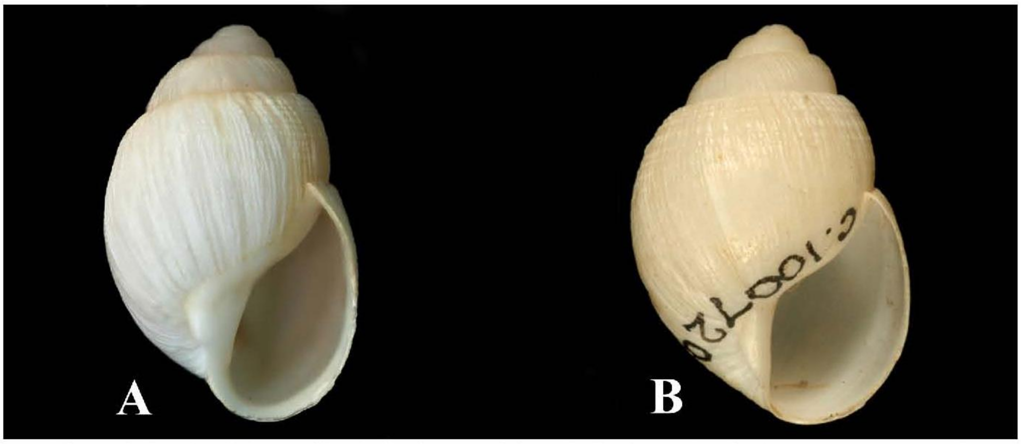

Figure 1. Apertural views of *Bothriembryon whitleyi* shells. A, shell collected by environmental consultants in 2009 (height 17.3mm); B, Syntype AM C.100729 (height 14.4mm).

The presumed extinct *Bothriembryon whitleyi* Iredale, 1939 remains elusive (continued from page 1)

***Bothriembryon whitleyi* Iredale, 1939**

A series of shells was collected by Mr G.P. Whitley from the Geraldton area in Western Australia, and later (1939) described as ***Bothriembryon whitleyi*** by Tom Iredale at the Australian Museum. Syntypes were deposited with the Australian Museum (Figure 1B) and the Western Australian Museum (Breure & Whisson, 2012). Additional locality data have now come to light which may restrict the type locality, but need confirmation. The original labels written in handwriting by Mr G.P. Whitley were found with two Australian Museum syntype lots (AM C.127615 and AM C.127713) and give the type locality as "Sand Dunes, Bluff Point near Geraldton" (Michael Shea pers. comm.). The Bluff Point Lighthouse cottage and tower are situated a few kilometers north of Geraldton, and nearby lie the remains of the Bluff Point Lighthouse beach tower. Both were constructed in 1876 with the beach tower removed in the early 1950s due to fire. Further north is another locality termed Bluff Point (ca. 100 km north of Geraldton) but Iredale (1939) specifically mentions Geraldton. (There seems to be a lot of 'Bluffing' around Geraldton!)

Listed as Presumed Extinct with the IUCN in 1996, efforts to attempt to collect live specimens since this time have been low. The only confirmed fieldwork in over 20 years has been in response to threatening processes to bushland (e.g. industrial development), which prompted a survey as stipulated by the EPA. To meet governmental regulations, environmental consultants surveyed target sites in 2009 and recovered several shells of ***B. whitleyi*** (Figure 1A). WAM staff undertook a fieldtrip to Geraldton in late August to begin a search for live *B. whitleyi*, targeting the sites that yielded ***B. whitleyi*** during the 2009 survey.

Several sites were visited near the Geraldton townsite including Bluff Point and Point Moore Lighthouse. In these areas, no specimens of ***B. whitleyi*** were found, dead or alive. These areas are bordered by dense residential development and although pockets of remnant coastal vegetation exist, introduced plants and land snails were observed, specifically ***Theba pisana*** and ***Cochlicella acuta***, which at times were so dense that the ground resembled snow!

We also searched further south and north of the Geraldton townsite and encountered many shells of ***Bothriembryon whitleyi*** across two sites! The shells were found on white sands among coastal dunes that consisted of native wattle and low shrub vegetation (Figure 2). Non-native flora or fauna was generally absent or sparse at these sites. The shells were solid and consistently bleached white. Nearby to the shells at both sites we noted a narrow limestone outcrop running parallel to the coast and on one of these outcrops we observed a ***B. whitleyi*** shell partly insitu and a ***Succinea*** shell (Figure 3).

Figure 2. Holocene dune sands where numerous *B. whitleyi* shells were found, with outcropping Tamala Pleistocene limestone just visible in background. Senior author recording data.

Figure 3. *Bothriembryon whitleyi* shell partly embedded in Tamala Pleistocene limestone

Upon return to the WA Museum we consulted our WAM Palaeontology Curator Dr. Mikael Siversson and also examined the Palaeontology ***Bothriembryon*** collection. It would seem the shells we collected were rather recent, likely of Holocene age, and were associated with the Pleistocene Tamala Limestone. The latter unit comprises lithified wind-blown dunes, beach deposits and offshore reefs (Kendrick et al., 1991). The Tamala Limestone runs almost the entire length of the SWWA coast. Examination of the WAM Palaeontology collection revealed subfossil ***B. whitleyi*** from the Geraldton region, but also a somewhat larger, strongly lithified shell that is possibly ***B. whitleyi***, noted as tentatively Pleistocene age.

In summary, whilst the specimens we collected during fieldwork (plus additional information from the WAM Palaeontology collection) suggest a mixture of recent (Holocene) and older (late Pleistocene) populations of ***B. whitleyi***, an extant population cannot be dismissed. Some shells of ***B. whitleyi*** in the WA Museum Mollusc Collection, collected between 1950 and 1970, appear freshly dead. A good ontogenetic series is present; shells are thin (likely would not persist long) and some shells show faint coloration. These key localities require further targeted collecting for the elusive ***Bothriembryon whitleyi*** and we encourage enthusiastic naturalists to continue the hunt! Our fieldwork was in late winter and because ***Bothriembryon*** are most active during the middle of winter, when conditions are moist and temperatures low, we will need to head north earlier in the season for another search.

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2018 MSA Conference to be held New Zealand

A reminder that the MSA conference will be held in New Zealand in late 2018 (likely over the last week of November and first week of December).

Further details on location, programme, call for abstracts, accommodation and application details will be posted in the near future on the MSA website.

Please block-off this time period in your diaries!

2017 MSA Annual General Meeting (AGM)

The Annual General meeting will be held on Thursday 30 November, 2017, 12.00 noon to 2.00 pm, Australian Eastern Standard Time.

Members can access the meeting by dialling 07 5678 2305.

An agenda and further information will be emailed to members in advance.

Appendix B Kirkendale, L. and Whisson, C.S. (2018) Wheatbelt *Bothriembryon*. *Landscope* **34**: 37.

Discovered by Lisa Kirkendale and Corey Whisson

Wheatbelt *Bothriembryon*

Western Australia's Wheatbelt region is a vast area, well known for its geological structures and diverse floral assemblages. This year's winter rains led to strong spring floral growth, which is expected to continue into summer. However, the Wheatbelt's terrestrial diversity has been impacted by long-term agriculture. While nature reserves are caches of native and endemic terrestrial biota, the area surrounding the reserve islands is usually highly modified. This presents a challenge for animals that evolved in a markedly different habitat – with larger trees and denser understorey – that would have existed before mass agriculture. Native land snails are one such group of invertebrates that have been adversely affected.

Bothriembryon is a genus of large-bodied (up to five centimetres) native terrestrial snails found in the southern half of mainland Australia. The majority of the 37 currently recognised species are limited to the wetter areas of south-west WA. Members of the genus are commonly found near the coast but can also be found inland among woodlands or on rocky areas. They also persist deep into the Wheatbelt, where they inhabit numerous reserves. Five described species are currently known from the Wheatbelt region (*Bothriembryon bulla, B. kendricki, B. perobesus, B. praecelsus* and *B. sedgwicki*). The latter three species are now largely relegated to a patchwork of nature reserves, some of which have also been grazed or were disturbed prior to being gazetted.

A team of scientists at the WA Museum, in concert with international partners, has been working to understand the relationship among species of *Bothriembryon* using a molecular phylogenetic approach. This work is necessary to help to identify the true number of distinct lineages in the genus. To construct this phylogeny we have relied on existing collections in the WA Museum. However, not all species had appropriate vouchers for this work, so new fieldwork was necessary to recollect key species.

Unsurprisingly, some of the species that were the most difficult to find, were rare and endangered. Of those species known to occur in the Wheatbelt, two species (*B. perobesus* and *B. praecelsus*) are of special conservation significance.

During our searches in the Wheatbelt over the past five years, we were fortunate to locate a number of juvenile specimens that could be *B. praecelsus*. This species is listed as presumed extinct and has never been observed live, so it could be an incredibly significant find. Unfortunately, adults are required for conclusive identification, so we are still on the lookout for mature specimens. During the course of our sampling, we visited some new sites across the Wheatbelt. One of these sites was among the giant granite outcrops south of Kellerberrin. Although we did not find *B. praecelsus* there, it seems that we may have discovered something new. While these early results are promising, all of these discoveries require careful study, proper comparisons and a lot of consideration before a new species can be described or a conservation listing updated. However, time may be running out, especially given that on our most recent trip to Kellerberrin and surrounds we came up empty handed – even after good rains! This complete absence of *Bothriembryon*, with no sign of even long-dead shells, is concerning.

So while the Wheatbelt region continues to display spectacular wildflowers each year, it also comprises vast areas of highly modified landscape and this presents challenges when we're trying to protect our native biota. But we can all play a role, and we ask everyone to keep a look out for *Bothriembryon* land snails, dead (shells) or alive (crawling)! You never know whether your find might help with a much-needed identification or even provide a species new to science.

Above *Granite outcrop snail from a reserve in the Wheatbelt.*
Photo – Lisa Kirkendale

For more information or to report possible sightings, please email lisa.kirkendale@museum.wa.gov.au or corey.whisson@museum.wa.gov.au