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

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ABSTRACT – The land snail genus *Bothriembryon* Pilsbry, 1894, endemic to southern Australia, contains seven fossil and 39 extant species, and forms part of the Gondwanan family Bothriembryontidae. Little published data on the geographical distribution of fossil *Bothriembryon* exists. In this study, fossil and modern data of *Bothriembryon* from nine 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. 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. Cave environments proved an excellent source of fossil *Bothriembryon* material, where shells often showed signs of predation. The dataset from this study provided insights into the origin and radiation of *Bothriembryon*, and will enable future phylogenetic dating.

KEYWORDS: Gondwana, Orthalicoidea, aridification, extinction, Western Australia

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). But 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). 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 palaeoecological studies is on the rise, taxonomy has become less recognised, despite being inextricably intertwined with it (Forey et al. 2004).

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 high erosion via physical, chemical and particularly biological processes (Behrensmeyer et al. 1992). Environmental conditions in inland 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 a preservational bias rather than 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 39 extant species (Breure and Ablett 2012; Breure and Whisson 2012; Schneider and Morrison 2018; Stanisic et al. 2018).

TAXONOMIC HISTORY OF FOSSIL *BOTHRIEMBRYON* PILSBRY, 1894 SPECIES

The first described fossil species of *Bothriembryon* Pilsbry, 1894 was *Bulinus gunnii* Sowerby 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 additional species described from the fossil record in over 170 years since *Bothriembryon gunnii* was first discovered in Tasmania. Five of these species were from south-western Western Australia (SWWA): *B. consors* Kendrick, 1978 and *B. gardneri* Kendrick, 1978 from Windy Harbour; *B. douglasi* Kendrick, 1978 and *B. ridei* Kendrick, 1978 from Shark Bay; *B. kremnobates* Kendrick, 2005 from the Roe Plains. The remaining species, *B. praecursor* McMichael, 1968 was described from central Australia, being later revised by Ludbrook (1980). McNamara et al. (1991) listed Western Australian Museum type material and Richardson (1995) treated described fossil species. Later Breure and Whisson (2012) illustrated all fossil species, some for the first time, and listed type material.

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* (Kershaw 1981). 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.

FOSSIL DISTRIBUTION

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 geographical distribution. 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 *B. costulatus* (Lamarck, 1822) from the mainland as well as insular Shark Bay, with *B. 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 *B. whitleyi* Iredale, 1939 from the Geraldton area.

In south-east WA and eastward, fossil *B. 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 *B. rhodostomus* (Gray, 1834) (tentative identification) were recorded from near Esperance, apparently exposed in large numbers (Cram 2010). Kendrick and Wilson (1975) recorded *B. melo* (Quoy and Gaimard, 1832) at Bremer Bay and Limestone Head. On the Leeuwin-Naturaliste Ridge, unidentified fossils were noted from soil pockets at Hamelin Bay (Fairbridge 1967), and *B. 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 c. 145 km north of Rawlinna, on the southern edge of the Great Victoria Desert.

In this study we aimed 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).

We also assess the distribution of fossil and modern *Bothriembryon* in Australia, providing some insights into its origin and radiation.

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 (c. 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 (Geoscience Australia 2019). 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 examined for identification (or confirmation) using shell morphological characters under a Leica M80 dissecting microscope, and compared with available literature and type specimens. Shell measurements i.e. maximum shell height (H) and maximum shell diameter (D) were taken from intact adult shells using digital callipers to 0.01 mm and followed the methods figured by Breure (1974: fig. 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).

To assist with identification, a silicone cast of *Bothriembryon* from a mould found in pisolitic 'kankar' c. 145 km north of Rawlinna (WAM 70.158) was produced. 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; FMNH, Field Museum of Chicago, Chicago; GA, Geoscience Australia, Canberra; GSSA, Geological Survey of South Australia, Adelaide; MAGNT, Museum and Art Gallery of Northern Territory, Darwin; MV, Museum of Victoria, Melbourne; NHMUK, Natural History Museum, London; QM, Queensland Museum, South Brisbane; SAM, South Australian Museum, Adelaide; TMAG Tasmanian Museum and Art Gallery, Hobart; WAM, Western Australian Museum, Perth.

RESULTS

FOSSIL TAXONOMY

Fossil *Bothriembryon* were represented by 631 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 material was included from the NHMUK (1 lot).

Seven described fossil species and 22 described extant species were identified from fossil material during this study (Table 1). Of the 22 extant species, 15 have a fossil record published for the first time here: *B. bulla* (Menke, 1843); *B. dux* (Pfeiffer, 1861); *B. esperantia* Iredale, 1939; *B. fuscus* Thiele, 1930; *B. gratwicki* (Cox, 1899); *B. indutus* (Menke, 1843); *B. irvineanus* Iredale, 1939; *B. jacksoni* Iredale, 1939; *B. kendricki* Hill, Johnson and Merrifield, 1983; *B. leeuwinensis* (Smith, 1894); *B. mastersi* (Cox, 1867); *B. naturalistarum* Kobelt, 1901; *B. notatus* Iredale, 1939 (treated here as a distinct species from *B. kingii*); *B. perobesus* Iredale, 1939; *B. sayi*.

Sixteen extant species did not have a fossil record: *B. angasianus* (Pfeiffer, 1864); *B. balteolus* Iredale, 1939; *B. bradshawi* Iredale, 1939; *B. brazieri* (Angas, 1871); *B. decresensis*, Cotton 1940; *B. distinctus* Iredale, 1939; *B. glauerti* Iredale, 1939; *B. kingii* (Gray, 1825); *B. perditus* Iredale, 1939; *B. praecelsus* Iredale, 1939; *B. revectus* Iredale, 1939; *B. richeanus* Iredale, 1939; *B. sedgwicki* Iredale, 1939; *B. serpentinus* Iredale, 1939; *B. sophiarum* Whisson and Breure, 2016; *B. 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 and await description.

GEOGRAPHICAL DISTRIBUTION

Fossils

Based on available registered specimens, the geographical distribution of fossil *Bothriembryon* species is largely restricted to coastal areas within SWWA (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 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 (c. 165 km) south to the Busselton area. They are then recorded from Cape Naturaliste to Cape Leeuwin, and after a small gap (c. 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.
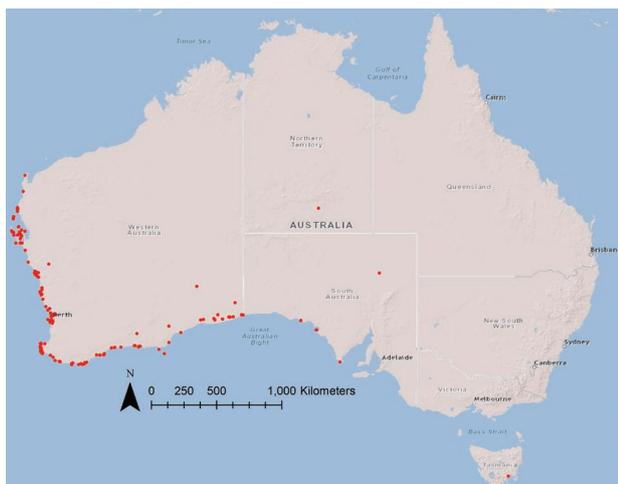
FIGURE 1 Fossil records of *Bothriembryon* species in Australian museums and institutes (c. 631 lots as of 3 April 2019).
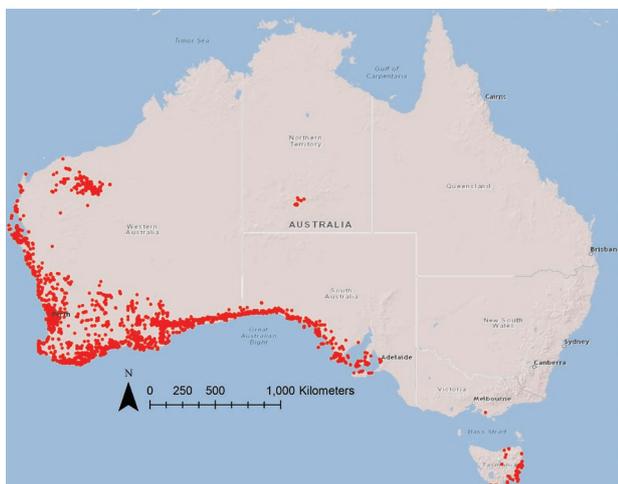

FIGURE 2 Modern records of *Bothriembryon* species in Australian museums and institutes (c. 7,436 lots as of 3 April 2019).

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.

Modern

Modern records of *Bothriembryon* were mapped for the first time. This included a total of 7,436 lots from the following Australian museums: WAM (5,709 lots); AM (463 lots); MV (326 lots); SAM (513 lots); FMNH (279 lots); TMAG (76 lots); QM (48 lots) and MAGNT (22 lots).

The geographical distribution of modern *Bothriembryon* largely mirrors the fossil distribution,

having a range from Exmouth in Western Australia, southward to eastern South Australia, with isolated occurrences in lower Northern Territory and eastern Tasmania (Figure 2). A potentially significant specimen has been found from lower Victoria, but label data needs confirmation.

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.

GEOLOGICAL AGE

The geological age of *Bothriembryon* spans from a minimum Late Oligocene ($\geq$25.7 MYA), based on the stratigraphy of the extinct Tasmanian *B. gunnii* (Kershaw 1981), 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 (25.7–12.5 MYA) (Table 1).

All extant, endemic Western Australian species have a Pleistocene age (2.58 MYA–11.7 KYA). Similarly all extinct, endemic Western Australian species terminate in the Pleistocene. Some extant species, which occur across the Nullarbor into South Australia (*B. barretti*, *B. indictus* Iredale, 1939) were recorded as older, being dated as Late Pliocene to Early Pleistocene (2.6–1.8 MYA) from the Roe Calcarenite formation. The extinct Nullarbor species *B. kremnobates* can be traced back to the late Pliocene. A specimen from c. 145 km north of Rawlinna (WAM 70.158, Figure 3 and 4) identified as *B.* cf. *praecursor* during this study, was tentatively dated as Pliocene to Pleistocene (5.33 MYA–11.7 KYA) (Lowry 1970).

SHELL SIZE

The adult internal cast from Rawlinna (WAM 70.159) measured 21.83 mm H, 12.80 mm W and 1.705 H/W (Figure 3F–H). 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 3D–E).

SHELL PRAEDICHNIA

Fossil shells of several extant species showed signs of extensive predation, typically having the shell spires removed. This was most common for the species *B. leeuwinensis* in cave deposits along the Cape Leeuwin-Cape Naturaliste Ridge (Figure 5). 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*.

DATA SET

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

TABLE 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] Geoscience Australia and Australian Stratigraphy Commission 2018; [4] Shackleton et al. 2003; [5] Playford et al. 2013; [6] Cohen et al. 2003).

Species	Stratigraphy	Epoch/Stage	Approximate 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 KYA to 11.7 KYA[3]	60.425	Groyne
B. consors Kendrick, 1978+	Calcarenite[1]	Probably Pleistocene[1]	2.58 MYA to 11.7 KYA[6]	00.562	
B. costulatus (Lamarck, 1822)	Peron Sandstone[5]	Probably Middle to Late Pleistocene[5]	133 KYA to 11.7 KYA[3]	79.3121	GSWA Locality 1660
B. douglasi Kendrick, 1978+	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	96.410	
B. dux (Pfeiffer, 1861)		Post Eemian[1] (= Late Pleistocene to Holocene[4])	106 KYA to present[4]	72.216	Lake floor
B. esperantia Iredale, 1939		Early to Middle Pleistocene[1]	2.58 MYA to 781 KYA[6]	96.360	In bore, 19.5–22.0 m depth
B. fuscus Thiele, 1930	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	70.1870	Base of cliffs
B. gardneri Kendrick, 1978+	Calcarenite[1]	Probably Pleistocene[1]	2.58 MYA to 11.7 KYA[6]	70.1603	Excavation
B. gratwicki (Cox, 1899)		Probably Holocene[1]	11.7 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 Pliocene to Early Pleistocene[3]	2.6 MYA to 1.8 MYA[3]	70.2161	Excavation
B. indutus (Menke, 1843)		Holocene[1]	11.7 KYA to present[6]	86.1211	Road excavation

| Species	Stratigraphy	Epoch/Stage	Approximate Age	WAM No.	Remarks
B. irvineanus Iredale, 1939		Middle Pleistocene[1]	781 KYA to 126 KYA[6]	94.784	Dam excavation, 3.1–3.7 m depth
B. jacksoni Iredale, 1939	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	04.242	
B. kendricki Hill et al., 1983		Quaternary[1]	2.58 MYA to present[6]	66.689	Cave
B. krennobates 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 KYA to 126 KYA[6]	03.86	
B. mastersi (Cox, 1867)		Post 5e[1] (= Late Pleistocene to Holoecene[4])	11.7 KYA to present[6]	03.294	Dune system
B. melo (Quoy and Gaimard, 1832)	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	70.106	
B. naturalistarum Kobelt, 1901	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	65.1178	
B. notattus Iredale, 1939	Below Calcarenite[1]	Holocene[1]	11.7 KYA to present[6]	86.1503	
B. onslowi (Cox, 1864)	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	03.76	
B. perobesus Iredale, 1939		Holocene[1]	11.7 KYA to present[6]	77.2770	Cave, 2.01–2.10 m 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 KYA to 126 KYA[6]	05.316	
B. ridei Kendrick, 1978+	Tamala Limestone[1]	Middle to Late Pleistocene[3]	133 KYA to 11.7 KYA[3]	05.262	
B. sayi (Pfeiffer, 1847)		Holocene[1]	11.7 KYA to present[6]	04.29	Excavation
B. whitleyi Iredale, 1939		Pleistocene[1]	2.58 MYA to 11.7 KYA[6]	96.619	
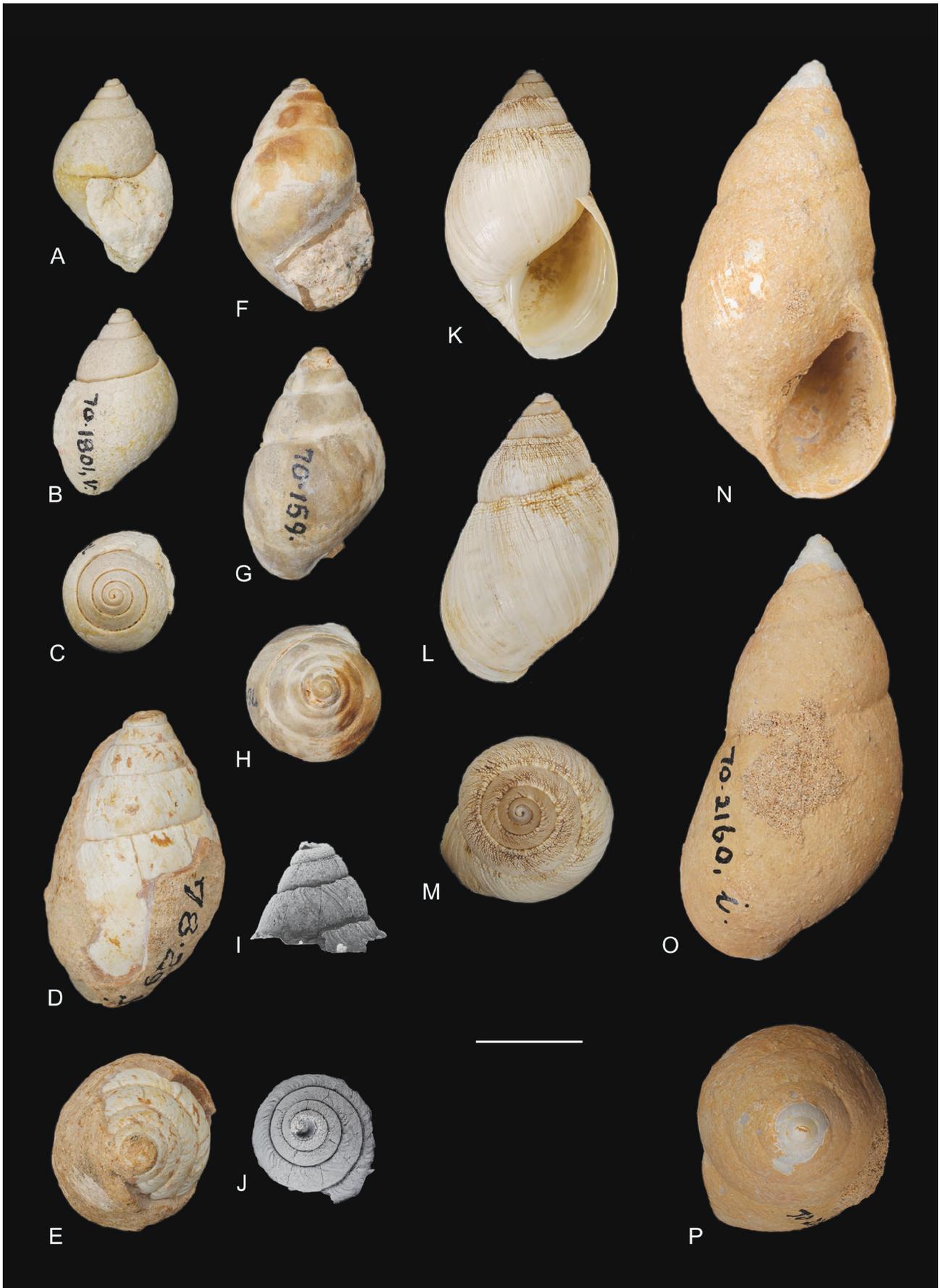
FIGURE 3   Plate of fossil and modern *Bothriembryon* species from the Nullarbor region and north-east South Australia. A–C, *B. praecursor*: WAM 70.1801v; D–J, *B.* cf. *praecursor*, D–E: WAM 78.297; F–H: WAM 70.159; I–J: WAM 70.158g (cast); K–M, *B. barretti*, WAM S1635; N–P, *B. indictus*: WAM 70.2160i. Scale bar = 10 mm.

FIGURE 4 SEM image of protoconch and early teleoconch whorls of silicon cast of *Bothriembryon* cf. *praecursor* fossil from c. 145 km north of Rawlinna, WA (WAM 70.158g), 40x magnification.

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). 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 geographical distribution 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. 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 the SWWA is regarded as limited, but inclusion of fossil material enables phylogenetic dating and may generate new insight into 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 Western Australian 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, c. 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 contraction may be the case for some *Bothriembryon* taxa (e.g. *B. kingii* group, *B. fuscus*), it could have been an opportunity for expansion of 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 the opinion of the senior author 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 3), based primarily on shell shape. However, Kendrick (2005) did not include the latter species. Given the slightly older geological age of these Nullarbor species i.e. Pliocene, as opposed to younger Pleistocene SWWA species (Table 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 c. 145 km north of Rawlinna and tentatively aged as Pliocene (Lowry 1970) may further support this hypothesis. Lowry (1970)
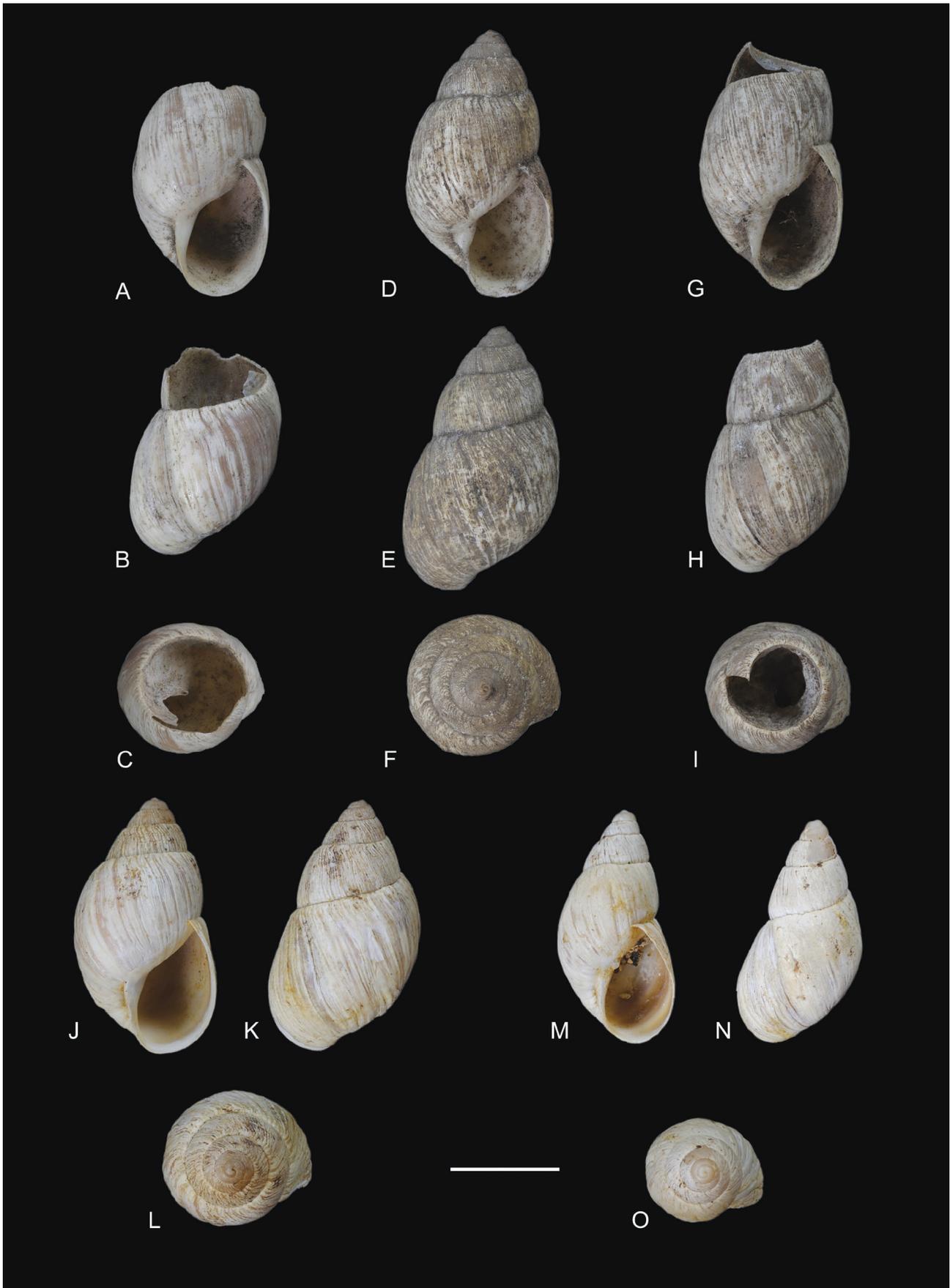
FIGURE 5 Plate of fossil and modern *Bothriembryon* from along the Cape Naturaliste–Cape Leeuwin Ridge. A–I, *B. leeuwinensis* cave subfossils: A–C, predated shell, WAM 04.25a; D–F, intact adult shell, WAM 04.25b; G–I, predated shell, WAM 04.25c; J–O, *B. leeuwinensis* mixed syntype lot: WAM S15124, J–L, *B. leeuwinensis* adult shell, M–O, *B. sayi* adult shell. Scale bar = 10 mm.

suggested this fossil resembled the Nullarbor species *B. barretti*, but based on morphology and size of the adult internal cast (WAM 70.159, Figure 3F–H), and part silicone external cast (Figure 3I–J and 4) 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 (c. 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 3D–E), 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 Western Australia. 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 they are broadly sympatric, suggesting a similar biogeographic history (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 Australian species and also has a shell morphology (shape) with closer affinity to South American or African bothriembryontids *Prestonella* and *Plectostylus*. Other workers have argued 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. gunnii* 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 species were not preserved in the fossil record and many areas in SWWA lack *Bothriembryon* fossils. Whilst this might reflect poor fossil record preservation caused by geological activity, it could also offer insight into the origin and radiation of *Bothriembryon*. In WA a large number of fossils have been found in the Shark Bay area, along the Cape Leeuwin to Cape Naturaliste Ridge (Figure 5), particularly in cave deposits (e.g. Skull Cave) and along the Nullarbor. 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 c. 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 (c. 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.

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.

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 aridification, 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).

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