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# Defining biodiversity gaps for North West Shelf marine invertebrates

**LISA KIRKENDALE [1]*, ANDREW M. HOSIE [1, 3] & ZOE RICHARDS [1, 2]**

[1] *Western Australian Museum, Department of Aquatic Zoology, 49 Kew St, 6109 Welshpool, Western Australia, Australia*

[2] *Curtin University, School of Molecular and Life Sciences, Kent St, 6102 Bentley, Western Australia, Australia*

[3] *Curtin University, School of Pharmacy & Biomedical Sciences, Curtin Health Innovation Research Institute, Kent St, 6103 Bentley, Western Australia, Australia*

* *Corresponding Author: ✉ lisa.kirkendale@museum.wa.gov.au*

## Abstract

After almost six decades of fieldwork on the North West Shelf (NWS), contemporary partnered expeditions have begun to discover and document the diverse marine biota of this area. Recent historical syntheses from the Western Australian Museum's Kimberley Project indicate over 5500 species occur in an area that includes much of the northern NWS. This compendium of biodiversity provides a new and important baseline of marine knowledge for the region. However, when considered with other NWS studies, several long-standing research gaps are evident, particularly for marine invertebrate taxa. Here we highlight and discuss these gaps in knowledge that can be grouped into five major categories: geographic, faunal, ecological, methodological and engagement. By directing future research towards these gaps, we hope to build a more complete dataset for managers tasked with protecting the many significant marine ecosystems in this extensive region.

**Keywords: Barry Wilson, biodiversity, crustaceans, environmental factors, hard corals, hotspot, marine invertebrates, molluscs, North West Shelf, research gaps**

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## INTRODUCTION

Part of the larger Australian continental margin, the North West Shelf (NWS) is a complex and extensive marine region (Wilson 2013). The area constitutes more than half of the Western Australian coastline, and is many times larger than most European countries. It is up to two km deep and extends 2500 km along its northwest–southeast axis. Whereas other definitions of this region exist—for example, Integrated Marine and Coastal Regionalisation of Australia (IMCRA) bioregions, Thackway & Cresswell 1998)—we follow the usage of Wilson (2013), who in turn followed Fairbridge (1953). They recognized that the NWS consists of the south-western Rowley Shelf and north-eastern Sahul Shelf, the marginal terraces (Rowley and Ashmore) and the marginal plateaux (Exmouth and Scott; Figure 1; Wilson 2013, Figure 1.1). Together this area incorporates 11 IMCRA bioregions. The Kimberley, and especially the Eastern Kimberley, remains one of the least explored areas of the shelf.

The reef ecosystems of the NWS are among the most pristine in the world due to the low human population (Halpern *et al.* 2008). The region features a multitude of habitat types (Wilson *et al.* 2011) and is increasingly recognised as a cache of diversity and endemism (Richards *et al.* 2015a; ter Poorten *et al.* 2017). Western Australia is well known as a resource rich state and exploitation of these resources on land and sea have supported many industrial projects of which some predate the requirement by the Environmental Protection Agency (EPA) for Environmental Impact Assessments (EIAs). Although now routine, basic biodiversity data along the NWS was not initially collected through these means leaving a pronounced gap in our knowledge of the State's marine fauna.

The Western Australian Museum (WAM) has compiled marine invertebrate macrofaunal inventories along the NWS since the 1960s (Table 1). Although each expedition incrementally improved our understanding of the diversity and distribution of marine invertebrates in the region, it has been rare for that data, often available only in the grey literature, to be consolidated in one place. Over the last 20 years the WAM with the support of Woodside Energy and the Net Conservation Benefits (NCB) fund have focussed not only on consolidating that data but on continuing to describe the regional biodiversity and international significance of the NWS.

To date the Woodside Collection project has accumulated more than 55 000 specimens from which over 1000 new species have been discovered. Other state and federal government agencies have also recognized the importance of this region and have contributed significant investment into research undertaken as part of projects led by the Western Australian Marine Science Institution (WAMSI, https://www.wamsi.org.au), the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Australian Institute of Marine Science (AIMS). Collectively, the extent of knowledge available on habitats, biodiversity, ecological processes and their influence on marine taxa across the NWS has rapidly increased.

One of the most challenging parts of the NWS to survey has been along the Kimberley, the north-westerly shoulder of the continent where a network of 2500 islands is spread across a dynamic oceanographic setting that includes tides of up to 11 m, strong currents and turbid water (Wilson *et al.* 2011). In recognition of

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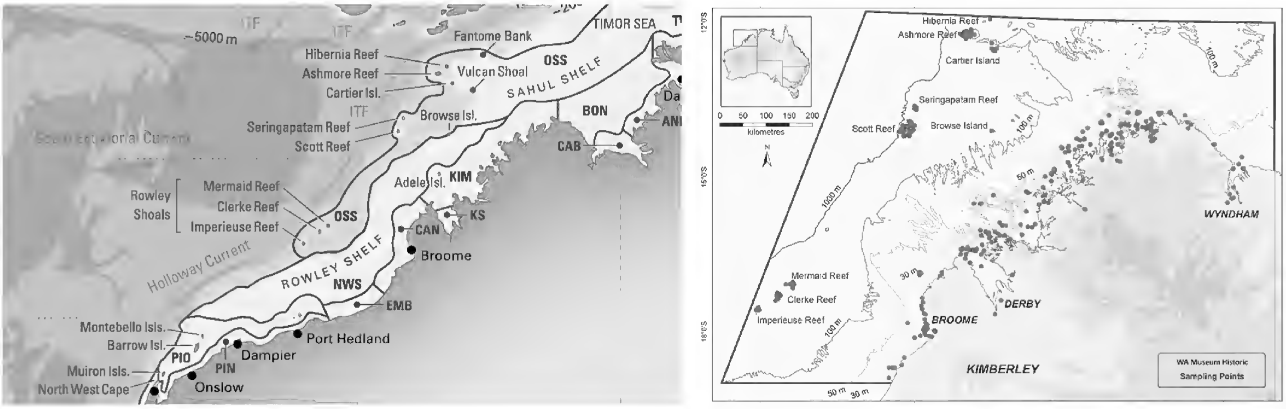

**Figure 1.** Left. The North West Shelf with prevailing currents and IMCRA bioregions (after ter Poorten *et al.* 2017). Right. Map of the Kimberley Project Area with Westen Australian Museum historic sampling points in green (after Sampey *et al.* 2014).

the biogeographic importance of this region, in 2009 the WAM, in partnership with Woodside Energy and collaborating institutions (Australian Museum, WA Herbarium, Queensland Museum) embarked on an ambitious project to firstly summarize all historical biodiversity records from the Kimberley (Jones *et al.* 2014–2017) and secondly, to undertake new contemporary surveys (2009–2014). Here we briefly review the combined WAM Kimberley historical dataset for eight marine invertebrate groups (hard corals, soft corals, sponges, molluscs, crustaceans, echinoderms, polychaetes and other marine invertebrates), and highlight pervasive taxonomic research gaps and emerging patterns to provide a framework for future marine biodiversity research in the region.

### Marine Invertebrate Biodiversity in the Kimberley (1880s–2009)

The Kimberley Historical project assimilated verified records (excluding poorly identified material) from voucher specimens lodged in Australian natural science collections from Cape Jaubert (south of Broome) to the WA/Northern Territory border and westward to the continental shelf atolls (specifically Hibernia Reef to Imperieuse Reef; Sampey *et al.* 2014). This compendium incorporated collections from 217 locations and details over 20 000 records from shallow waters (Jones *et al.* 2014–2017; Table 2 and Figure 2).

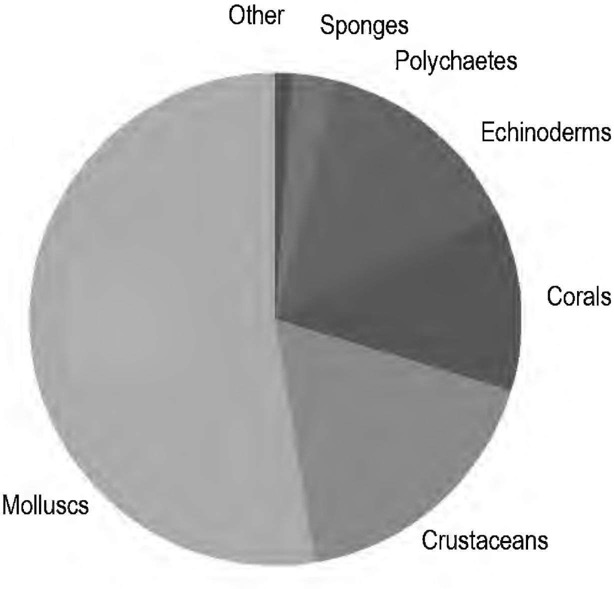

**Figure 2.** Visual breakdown of shallow water marine invertebrate records from the Kimberley Project Area (corals refer to soft and hard corals).

## PERVASIVE GAPS

One of the most obvious trends among historical Kimberley publications is the mention of gaps by different faunal experts and the similarity of these gaps, irrespective of group. By consolidating the data collected across the eight marine invertebrate groups, we identified data gaps that are summarized under five major categories: geographic, faunal, ecological, methodological and engagement. Here we summarize these knowledge gaps and highlight emerging areas in need of further research.

### Geographic Gaps

Despite ongoing work by numerous agencies, our knowledge of biodiversity and its distribution across the NWS is incomplete. We anticipate additional surveying of this region will continue to increase the number of species recorded. The regularity in discovery of new species from the region suggests that our knowledge of diversity is not saturated across taxonomic groups. For example, some of the newly described species from the NWS include bivalves (*Acrosterigma extremattenuatum* ter Poorten & Kirkendale 2017, *Ctenocardia pilbaraensis* ter Poorten & Kirkendale 2017); a nudibranch (*Moridilla fifo* Carmona & Wilson 2018); a spider crab (*Paranaxia keesingi* Hosie & Hara 2016); box jellyfish (*Malo bella* Gershwin 2014 and *Keesingia gigas* Gershwin 2014); and an octocoral, *Heliopora hiberniana* (Richards *et al.* 2018b). Many more new species are currently being described by scientists L. Kirkendale, A. Hosie, Z. Richards and J. Fromont and others at WAM.

Generally, the eastern Kimberley has been less well surveyed compared to the western areas. The 2013 survey of the King George River was the only recent

**Table 1**
Contemporary marine invertebrate biodiversity surveys on the North West Shelf (most recent first) resulting in significant collections (>100 WAM records). AIMS, Australian Institute of Marine Science; CSIRO, Commonwealth Scientific and Industrial Research Organisation; WAM, Western Australian Museum; CReefs, Coral Reefs survey, aspect of Census of Marine Life; ARMS, Autonomous Reef Monitoring System.

| Project | Date(s) | Locality | Depth | Methods | Outcome |
|---|---|---|---|---|---|
| WAMSI 1.1.1 & WAMSI 1.1.3 Kimberley (WAM, CSIRO, AIMS) | 2015–2020 | Kimberley | 0 m & 30–40 m | trawl, some intertidal, genetic sampling conducted | Collections of marine fauna across groups (e.g. Berry *et al.* 2017a, b) |
| Conservation Systematics of Pilbara fauna (WAM) | 2014–2019 | Ningaloo to Broome | 0–15 m | hand collecting, intertidal and scuba, small hand held dredge, genetic sampling conducted | collections of marine fauna across groups suitable for genetic study, ongoing |
| Investigator "North West Shelf" | 2017 | Offshore Barrow Island | 30–40 m | trawl, genetic sampling conducted | Collections of marine fauna across groups, ongoing |
| NCB Pilbara Expeditions | 2014–2017 | Montebello Islands, Exmouth Gulf, Dampier Archipelago | 0–30 m | hand collecting and scuba, genetic sampling conducted | Collections of marine fauna across groups, ongoing |
| WAM–NCB Bonaparte Expedition | 2016 | Coral reefs in the Bonaparte Archipelago | Intertidal and subtidal > 15 m | hand collecting and scuba, genetic sampling conducted | Collections of marine fauna across groups, bleaching assessment (Richards *et al.* 2018a) |
| Pilbara Marine Conservation Partnership (CSIRO, WAM et al.) | 2013–2017 | Ningaloo to Dampier | 10–50 m | trawl, dredge, genetic sampling conducted | collections of marine fauna across groups (e.g. Pitcher *et al.* 2016) |
| Royal Netherlands Institute for Sea Research Migratory shorebird study | from 2000, with return in 2017 | mudflats of Roebuck Bay and Eighty mile Beach | intertidal | hand collecting to asses marine invertebrate taxa targeted by migratory shorebirds | coastal invertebrate fauna (published literature summarized in Wilson 2014) |
| Woodside Collection project (Kimberley) | 2009–2014 | Kimberley, Ashmore, Rowley Shoals | 0–15 m | hand collecting, intertidal and scuba, small hand held dredge, genetic sampling conducted | collections of marine fauna across groups focused on coral reef habitats (Jones *et al.* 2014–2017) |
| King George River project (WAM–CSIRO partnership) | 2013 | Far north-eastern Kimberley | 0–73 m | limited snorkelling, intertidal walks, epibenthic sled (small and large), traps, genetic sampling conducted | collections of marine fauna across groups across range of habitats (Keesing 2014) |
| INPEX Browse Survey | 2006–2007 | Bonaparte Archipelago | 0–20 m | hand, scuba | collections of marine fauna across groups (published literature summarized in Wilson 2014; see also Richards *et al.* 2015) |
| Ningaloo CREEFs (AIMS, WAM, many others) | 2008–2010 | Ningaloo Reef | 0–30 m | ARMS, scuba, etc, genetic sampling conducted | crabs and other crustaceans, invertebrate marine animals, shrimp, barnacles, worms, parasites, algae, soft corals and zoanthids |
| Woodside Collection Project (offshore atolls) | 2006 | Rowley Shoals, Scott and Seringapatam Reefs | 0–30 m | scuba | collections of marine fauna across groups (published literature summarized in Wilson 2014) |

| **Project** | **Date(s)** | **Locality** | **Depth** | **Methods** | **Outcome** |
|---|---|---|---|---|---|
| R.V. Southern Surveyor "Voyage of Discovery" Project | 2005–2007 | Dampier to Ashmore reef | 100–1000 m | trawl, dredge, some genetic sampling conducted | McEnnulty *et al*. (2011) |
| Woodside Collection Project (Dampier) | 1999–2002 | Dampier Archipelago | 0–45 m | scuba, dredging | collections of marine fauna across groups (published literature summarized in Wilson 2014) |
| Canning Bioregion survey | 1997 | Beagle Bay | 10 m | hand, scuba | for molluscs, sponges in 'garden bottom' (published literature summarized in Wilson 2014) |
| CRIMP Port Hedland Survey | 1998 | Port Hedland | 0–10 m | hand, scuba, dredge | Collections not full identified, mostly deposited at WAM |
| WAM Central Kimberley Coast Survey 1996 | 1996 | Kimberley | 0–30 m | hand, scuba, dredge | unpublished reports (summarized in Wilson 2014) |
| WAM Eastern Kimberley Survey 1995 | 1995 | Kimberley | 0–30 m | hand, scuba, dredge | unpublished reports (summarized in Wilson 2014) |
| WAM Southern Kimberley Islands Survey 1994 | 1994 | Kimberley | 0–30 m | hand, scuba, dredge | unpublished reports (summarized in Wilson *et al*. 2014) |
| WAM Kimberley Islands & Reefs Survey 1991 | 1991 | Kimberley | 0–30 m | hand, scuba, dredge | plant, invertebrate, fish collections (published literature summarized in Wilson *et al*. 2014) |
| WAM Kimberley Islands Survey 1988 | 1988 | Kimberley | 0–30 m | hand, scuba, dredge | collections of marine fauna across groups (published literature summarized in Wilson 2014) |
| Ashmore and Hibernia Reefs & Cartier Island surveys | 1988 | Ashmore and Hibernia Reefs & Cartier Island | 0–30 m | hand, scuba | collections of marine fauna across groups (published literature summarized in Wilson 2014) |
| Kimberley Mollusc Surveys | Oct–Nov. 1976, 1988 | Institut Islands, Cape Voltaire and Admiralty Gulf as well as other islands in Kimberley bioregion | 0–30 m | hand, scuba | Mollusc lists (published literature summarized in Wilson 2014) |
| Crown of Thorns Expedition | 1972–1974 | Dampier Archipelago | 0–30 m | hand, scuba, dredge | Incidental collecting, main aim was to survey crown of thorn seastar numbers |
| CSIRO scampi surveys | 1984 | Broome and Augustus Island | 200–600 m | engel trawls | benthic invertebrates |

| Project | Date(s) | Locality | Depth | Methods | Outcome |
|---|---|---|---|---|---|
| Browse Island marine ecology | 2005–2008 | Browse Island | 0–30 m | intertidal (hand) and subtidal (scuba, video, ROV) surveys | Coral and mollusc ecological surveys (Comrie-Greig & Abdo 2014) |
| Rowley Shoals, Scott & Seringapatam Reef surveys | 1982–1984 | Rowley Shoals, Scott &, Seringapatam Reefs | 0–50 m | hand, scuba | collections of marine fauna across groups (published literature summarized in Wilson 2014) |
| CSIRO scampi surveys | 1979, 1982 | Rowley Shoals | 276–520 m | engel trawls | benthic invertebrates |
| Umitaka Maru surveys | 1969 | 17 stations from Joseph Bonaparte Gulf to Rowley Shoals | 29–260 m | dredged | molluscs deposited to WAM |
| Dorothea Expedition | 1962 | Kimberley coast | 22–90 m | dredged | benthic invertebrates |

study that ventured east of Cape Londonderry. This study documented 736 marine invertebrate species from a variety of habitats across 150 stations using diverse methods (Keesing 2014, Table 1). However, species accumulation curve predictions indicate the true species richness of marine invertebrates is likely to double with further sampling (Keesing 2014). Future surveys in the vicinity of Admiralty Gulf and Cape Bouganville such as the Sir Graham Moore Islands, Troughton Island, Eclipse Islands and Holothuria Banks are warranted along with the Berkeley River to Cambridge Gulf region. Furthermore, some areas in the western Kimberley are still data poor including the Lacepede islands, the entire western edge of Dampier Peninsula, King Sound and the Buccaneer Archipelago.

Robust biodiversity datasets are available for offshore atolls (see Wilson 2014 for a summary). However, invertebrate biodiversity at many of the submerged banks and shoals is largely unknown. For example, Fantome Bank and nearby Vulcan Shoals are unsurveyed and lightly surveyed, respectively (ter Poorten *et al.* 2017). Preliminary ROV work has also revealed extensive coral communities near Browse Island (Andrew Heyward, pers comm, Sept. 2017). The WAMSI 1.1.1 project has highlighted that extensive inter-reefal soft-sediment benthic communities (most specifically sponge and soft coral gardens) exist across the shallow Sahul Shelf and further surveying of habitats below 30 m is likely to reveal additional biodiversity (Table 2).

**Table 2**
Summary of shallow water (>20m depth) marine invertebrate biota from the Kimberley Project Area (after Sampey *et al.* 2014).

| Group | Shallow water records | Excluded records (deep water/ incomplete identification) | Shallow water species |
|---|---|---|---|
| Sponges | 665 | 236/406 | 342 |
| Hard Corals | 2423 | 69/243 | 338 |
| Soft Corals | 140 | 9/505 | 63 |
| Echinoderms | 2014 | 74/325 | 382 |
| Polychaetes | 1046 | 0/812 | 261 |
| Crustaceans | 3893 | 840/4700 | 882 |
| Molluscs | 11551 | 3347/5383 | 1784 |
| Other marine invertebrates | 229 | 7/364 | 121 |
| Total | 21961 | 4582/12 738 | 4173 |

## Faunal Gaps

Organism bias is prevalent in biodiversity research and can depend on the perceived value, including commercial, of particular taxa, as well as available taxonomic expertise. This is seen at high taxonomic levels for groups such as sponges, non-scleractinian Cnidaria and Bryozoa that historically were underrepresented. Moreover, more than 80% of records in the Kimberley Historical project relate to molluscs, crustaceans and scleractinians (Figure 2). Within groups this bias is also apparent, for example, the order Decapoda represents only 31% of total crustacean species recorded from Australia, but makes up 85% of the WAM crustacean dataset (ABRS 2009; Hosie *et al.* 2015). The diverse morphology in Crustacea is such that specific orders often require experts thereby focussing resources to the exclusion of other crustacean taxa. A compounding factor is size, as it is generally more difficult to identify smaller than larger species across different taxonomic groups. This is largely a function of handling time associated with sorting, requirement of microscopy and utility of photography (Middelfart *et al.* 2016). Although, crustacean infauna (e.g. benthic copepods, ostracods) were collected during recent Kimberley biodiversity surveys, sampling was not comprehensive and there was a lack of resources (funds, expertise) to fully curate these collections.

Similarly, preliminary investigations of micromollusc fauna indicate an astonishing diversity (Middlefart *et al.* pers. comm. Jan. 2019); however a lack of funding has constrained work to the morphospecies identification level only. Other sessile marine invertebrate taxa such as sea pens, ascidians, zooanthids, hydrozoans and anemones also require further study. In addition, little is known about the sea jellies including stingers that inhabit the region. Specimens from some of these groups housed at the WA Museum are available for examination by relevant experts. Further investment into taxonomic studies is warranted across a broad range of marine invertebrate taxa given the strong likelihood that many new species will be revealed.

### Ecological Gaps

Although much of the world's seafloor habitat is soft sediment (mud, clay, sand), studies of the marine invertebrate fauna in soft sediment are notably sparse in WA, and the NWS is no exception. Eighty Mile Beach, for example, incorporates expansive sand and mudflats, recognized as a Ramsar wetland of international significance and recently gazetted as a marine park, at present better sampled by international groups (Dutch-led) rather than State or Federal agencies. Whereas the importance of coral reef habitats is undeniable, other habitats are important too, playing a role as sources of evolutionary novelty and underpinning the productivity and integrity of the wider marine ecosystem and food webs. Mangroves, for example, can be challenging to access but are well recognized as nursery habitats for many marine groups and are expected to have specialized invertebrates that await documentation. Similarly, sandflats, and particularly the marine invertebrate infauna of these systems, provide abundant food for many migratory seabirds that find refuge in the Kimberley along with other taxa of biological and cultural significance such as sawfish (Department of Fisheries 2018).

Even in well-studied taxa, such as molluscs from relatively well-examined habitats such as coral reefs, we know little about seasonal faunal shifts and nocturnal transitions (Richards *et al.* 2018a). For motile fauna, including molluscs and crustaceans, reefal biodiversity is best captured during nocturnal surveys; however, this is rarely feasible given current dive-safety restrictions.

Shallow-water habitats are better sampled than deeper ones. This is well illustrated by the Kimberley Historical project, in which only 16.5% and 9% of mollusc and crustacean WAM records, respectively, were collected from depths below 30 m. Recent projects have begun to fill some knowledge gaps. For example, Poore *et al.* (2015) collected specimens to depths of 1100 m and sampled over 1100 crustacean and 359 mollusc specimen lots respectively from 30–100 m during the recent WAMSI 1.1.1. Project. Future collaborative projects between the WAM, AIMS and Curtin University aim to address this imbalance (e.g. Schmidt Ocean Institute Expeditions planned for 2020), and are likely to reveal entirely new fauna and communities and address longstanding questions regarding the importance of submerged coastline habitats along the NWS.

Although new work is proposed, the petroleum industry has logged many more hours in WA's deep sea than have other groups. This represents a clear opportunity, given the experience and capacity of the industry, to work together to better document our deep-sea biota. As well, there is considerable data in unpublished work that is held as commercial in confidence. More use could be made of these data if unpublished reports were shared and voucher specimens were deposited with the WAM.

### Methodological gaps

Describing new species and assessing phylogenetic relationships across major branches of the tree of life can be a daunting task for which genetic methods are critical (Wilson & Kirkendale 2016). The importance of genetic methods in screening diversity broadly is perhaps best highlighted by the discovery in 2013 of a new lineage of giant clam based entirely on sequence data (Huelsken *et al.* 2013). However, genetic data alone can be insufficient to make robust interpretations about phylogenetic relationships; hence an integrated approach (see Richards *et al.* 2018b for an example) utilizing all evidence is the best-practice for modern taxonomy and systematics.

Many research expeditions have begun to focus on the collection of ambient and ultra-freeze tissue specimens for genetic analysis along the NWS (Table 1). Whereas sampling specimens appropriate for future genetic analysis is routine, unfortunately little funding exists for downstream application. Moreover, the time and funds required for analysis, storage and publication of genetic data is usually minimal and more funding needs to be made available for post-collection analyses in biodiversity discovery projects. One major collections-based project across faunal groups is underway at the WAM via the Net Conservation Benefits project. The goal of this long-term project has been to build phylogenetic trees to better understand systematic relationships among sensitive taxa in the greater Pilbara area (from Shark Bay in the south to the southern Kimberley in the north, representing a significant part of the NWS). Whereas this project is an important start, many marine invertebrate taxa are beyond its scope indicating much more work remains to be done.

Emerging technologies such as environmental DNA (eDNA) also offer alternative and complementary ways to detect biodiversity. While eDNA surveys have the potential to identify biodiversity hotspots that could be worthy of closer scrutiny, the accuracy of eDNA audits relies on the availability of genetic reference material, even when analysed at the level of operational taxonomic units (OTU's).

### Engagement gaps

The protocols for undertaking marine science in Western Australia have advanced considerably over the last decade. Today 'right way science' focussing on traditional owner engagement and collaboration is firmly established as the model for future research on the NWS, and protocols are available to guide that process (Austin *et al.* 2017, see also: https://www.klc.org.au/research-facilitation). Further work is needed to integrate traditional ecological knowledge and management practices into Kimberley marine conservation and

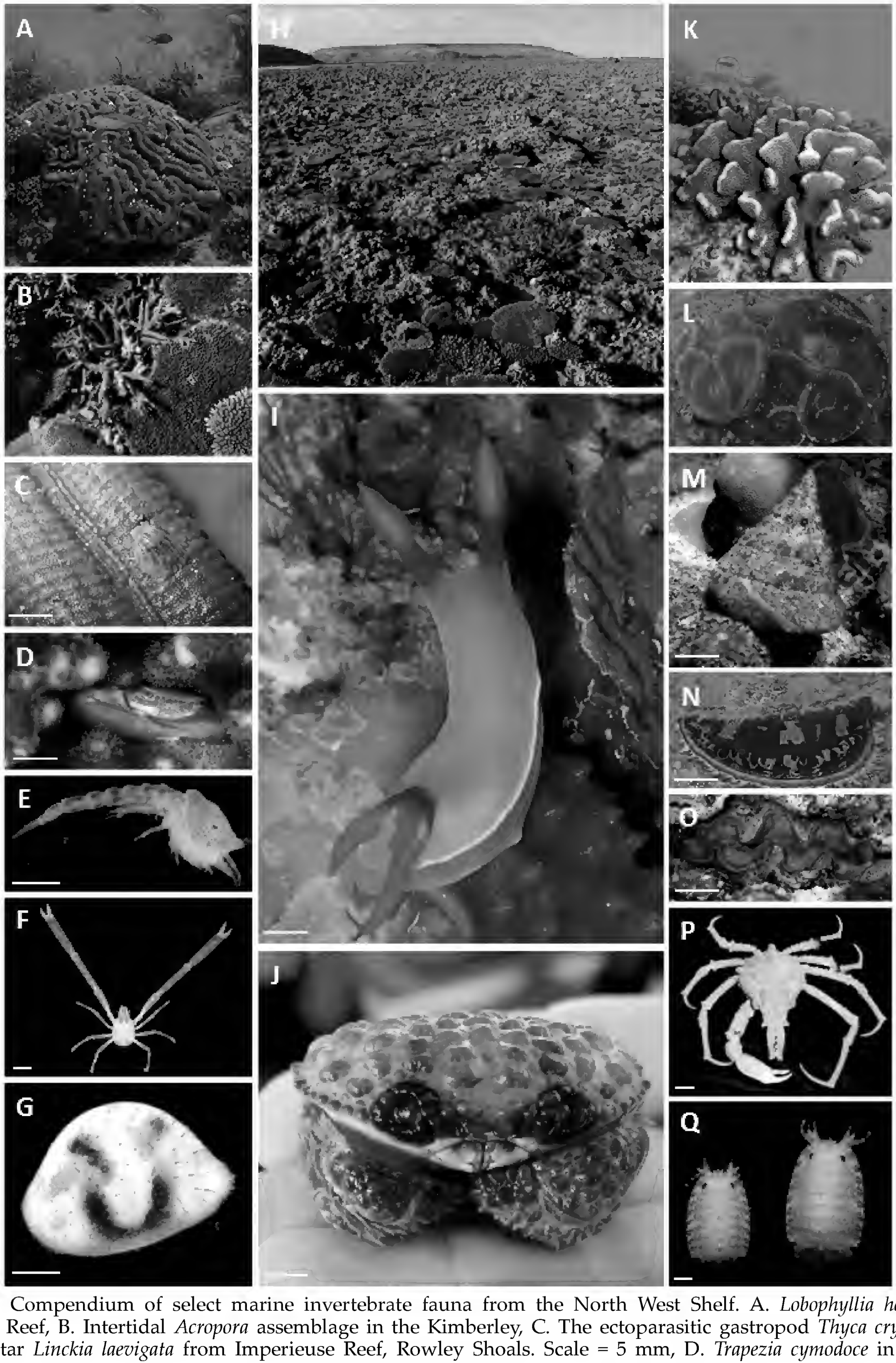

**Figure 3.** Compendium of select marine invertebrate fauna from the North West Shelf. A. *Lobophyllia hemprichi* at Ashmore Reef, B. Intertidal *Acropora* assemblage in the Kimberley, C. The ectoparasitic gastropod *Thyca crystallina* on blue seastar *Linckia laevigata* from Imperieuse Reef, Rowley Shoals. Scale = 5 mm, D. *Trapezia cymodoce* in *Stylophora pistillata* at the Montebello Islands. Scale = 10 mm, E. An interstitial cumacean from Montgomery Reef. Scale = 1 mm, F. *Uroptychus* sp. nov. from Rob Roy Reef. Scale = 10 mm, G. A benthic ostracod from Montgomery Reef. Scale = 1 mm, H. A diverse intertidal coral community at Patricia Island, Bonaparte Archipelago, Kimberley, I. *Hypselodoris* nudibranch from Imperieuse Reef, Rowley Shoals. Scale = 4 mm, J. *Daira perlata* from the Kimberley. Scale = 5 mm, K. *Pocillopora grandis* at Browse Island, L. *Moseleya latistellata* in the soft sediment at Dampier Archipelago, M. *Rochia nilotica* from Scott Reef. Scale = 30 mm, N. *Spondylus* clam from Imperieuse Reef, Rowley Shoals. Scale = 50 mm, O. *Tridacna* from Mermaid Reef, Rowley Shoals. Scale = 50 mm, P. *Paranaxia keesingi* a newly described species from NW WA. Scale = 30 mm, Q. *Agostodina munta* from the Montebello Islands. Scale = 5 mm.

management and to enhance mutually beneficial collaborations between indigenous peoples and non-indigenous partners that are focussed on research in 'saltwater country'.

Partnerships with industry also form a unique component of research facilitation in Western Australia—they will be important to continue to build and foster relationships and conduct demand-driven research (e.g. deep sea and decommissioning) to achieve multiple outcomes. Another important gap that requires renewed and ongoing investment is the ability to attract, train and retain the next generation of WA marine invertebrate taxonomists. There are five universities in the Perth area but few undergraduate programs develop student taxonomic capacity in invertebrates. Although this is certainly a worldwide trend, this is in spite of ongoing work that reveals many unsurveyed areas, likely with many species yet to be discovered, and many threats jeopardizing this diversity in WA. This is a significant gap requiring strategic focus.

## SUMMARY

The issues facing marine invertebrate taxonomy in Western Australia are not endemic to the State and require a synthetic, broad-based approach for improving biodiversity research nationally. Many of these issues are highlighted in the newly released *Discovering Biodiversity: A decadal plan for taxonomy and biosystematics in Australia and New Zealand 2018–2027* (Taxonomy decadal plan working group 2018). Please also refer to https://www.taxonomyaustralia.org.au/.

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There have been several fitting tributes to the prolific career of Barry Wilson, who passed away on 12 June 2017 at the age of 82. One of the most recent has been the dedication of *Marine Biodiversity of the Kimberley 1880s–2009* by WAM given his body of research in this area. The span of work completed by Barry was as immense as his intellect; he touched on many disciplines including molluscan taxonomy, invertebrate biodiversity and biogeography and marine conservation, and many lives as a result. We are grateful for the foundation he has laid at the WAM, and in Western Australia and we dedicate this paper to him.

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# Western wonders under the microscope: building a micromorphology reference collection for northwest Australia

INGRID WARD[1]*, DORCAS VANNIEUWENHUYSE[2], KANE DITCHFIELD[1]
& JILLIAN BARTEAUX[1]

[1] *School of Social and Cultural Studies, University of Western Australia, 35 Stirling Highway, Crawley, WA 6009, Australia*

[2] *Artefact Heritage Pty Ltd, Pyrmont, NSW 2009, Australia*

* *Corresponding author:* ✉ *ingrid.ward@uwa.edu.au*

## Abstract

Micromorphology is an effective and useful tool for documenting and differentiating cultural and non-cultural (including post-depositional) contextual features within archaeological matrices. Archaeological micromorphology is still a nascent field in Australia and, more generally, in arid and semi-arid environments, and as such would benefit from a reference collection to help identify cultural and non-cultural remains and features in this region. Here we introduce the beginnings of an archaeological micromorphological reference collection themed around material from northwest Australia. Reference material includes lithogenic and biogenic components such as stone artefacts, shells, plants and scats from native fauna and sedimentary contextual features from archaeological sites in the Kimberley and coastal Pilbara regions. This reference collection is useful for teaching and research, including regional Quaternary studies, and we encourage the development of similar regional micromorphological datasets for other parts of the continent and dryland environments more generally.

**Keywords: Micromorphology, reference, archaeology, northwest Australia**

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## INTRODUCTION

Micromorphology is the microscopic study of oriented, undisturbed (relative to bulk samples) sediment samples to describe, measure and interpret the spatial relationship of the constituent materials. It is increasingly used in geoarchaeological studies to aid palaeoenvironmental reconstruction and help unravel lithogenic and anthropogenic inputs and formation processes in archaeological sites (Goldberg & Aldeias 2018). A key aspect of this is understanding the contribution of people not just with lithics, bones or plants but also on the original sedimentary signal (Stein 1985) and role of sediments themselves as 'artefacts' (Goldberg & Berna 2010). Both soil micromorphology and archaeological micromorphology are well used and developed in cold or temperate contexts in Northern Hemisphere (Sageidet 2000; van der Meer & Menzies 2011; Nicosia & Stoops 2017).

Despite the foundational work of Brewer (1964) on soil micromorphology in Australia, micromorphology remains a nascent but growing field here. Emerging post-graduate studies highlight the potential of this technique for understanding and interpreting the archaeological sediments and the objects they enclose (e.g. Venn 2008; Murszewski 2013; Murszewski *et al.* 2014; Jankowski 2014, Jankowski *et al.* 2015; Lin 2016; Lowe *et al.* 2016; Vannieuwenhuyse 2016; Vannieuwenhuyse *et al.* 2017). In semi-arid environments, soil micromorphological studies are helpful to determine palaeoenvironments, palaeoclimate (e.g. Courty & Fédoroff 1985; Singhvi & Derbyshire 1999) and past cultivation[1] (Presley *et al.* 2014; Verba *et al.* 1995). Less foundational work has been done on archaeological micromorphology in humid tropical regions (though see Friesem *et al.* 2016; Morley & Goldberg 2017 and references therein) and arguably even less in hot dryland contexts where processes are greatly influenced by eolian deposition where natural and cultural contributions are primarily inorganic in nature.

One way to help advance and teach this technique is to create a micromorphological reference collection of archaeological (including stone artefacts, shell, bone, charcoal remains), and associated environmental material that may be found in different sites and contexts around Australia. Also useful are reference slides of microstructures and features that relate to a particular sedimentary context, building on what is already known from soil micromorphology (e.g. Courty & Fedoroff 1985; Stoops *et al.* 1993; Amit & Yaalon 1996). In effect this constitutes a drylands-focused response to Courty's (1991) call to progress archaeological micromorphology by building and publishing reference systems that are accessible to all archaeologists.

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[1] Of interest is a recent application of soil micromorphology to look at historic evidence of water and soil management in a semi-arid part of Tanzania. See https://www.ramsar.org/archaeological-evidence-for-shifting-irrigation-and-cultivation-practices-at-engaruka-tanzania

## Building a northwest Australian micromorphological reference collection

Northwest Australia covers a large diversity of landscapes and climatic zones from arid coastlines of the Pilbara, through inland deserts to the semi-arid tropics of the Kimberley. These environments also comprise a wide array of rocks ranging from the Archaean sedimentary and volcanic formations of the Pilbara to the Phanerozoic sedimentary rocks of the Kimberley (Figure 1). These broad rock units not only provide sites for caves and rockshelters but also the material from which stone artefacts are manufactured.

This paper presents an overview of lithogenic (stone artefacts) and biogenic reference material (shells, scats, botanical samples) from the Pilbara and the Kimberley. As no micromorphological reference collection currently exists for Australia, the applied aspect of such a reference collection is largely synthetic and here based on previous and current micromorphological studies in the Devonian Ranges of the Kimberley – Carpenters Gap 1, Riwi and Mount Behn (Vannieuwenhuyse 2016), Boodie Cave (Ward *et al.* 2017), and Dampier Archipelago in the Pilbara (Figure 2). The objectives of archaeological micromorphology are contextual: to consider human activities through time and through space by analysing spatio-temporal relationships between the sedimentary matrix and its artefactual content (Courty 1991). Hence, we also incorporate 'contextual' slides relating to midden deposits, hearth/ash features, wall spall containing pigment, post-depositional structures, and sediments containing stone artefacts and plant fragments from the study areas into the reference collection. This preliminary work is intended to highlight the value in further developing micromorphological reference collections for the northwest and also in other parts of Australia.

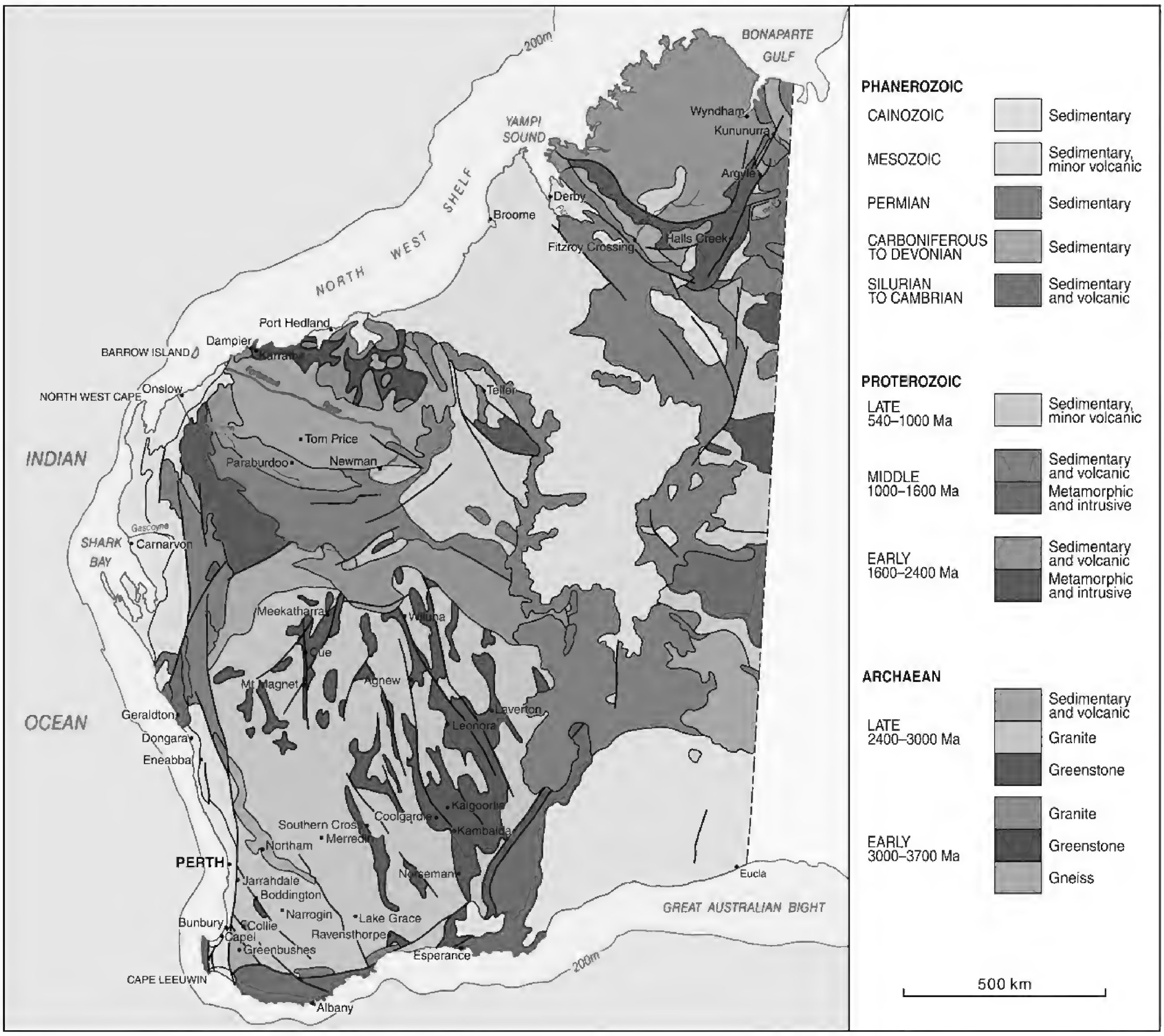

**Figure 1**. Simplified geology of Western Australia (from Martin *et al.* 2015).

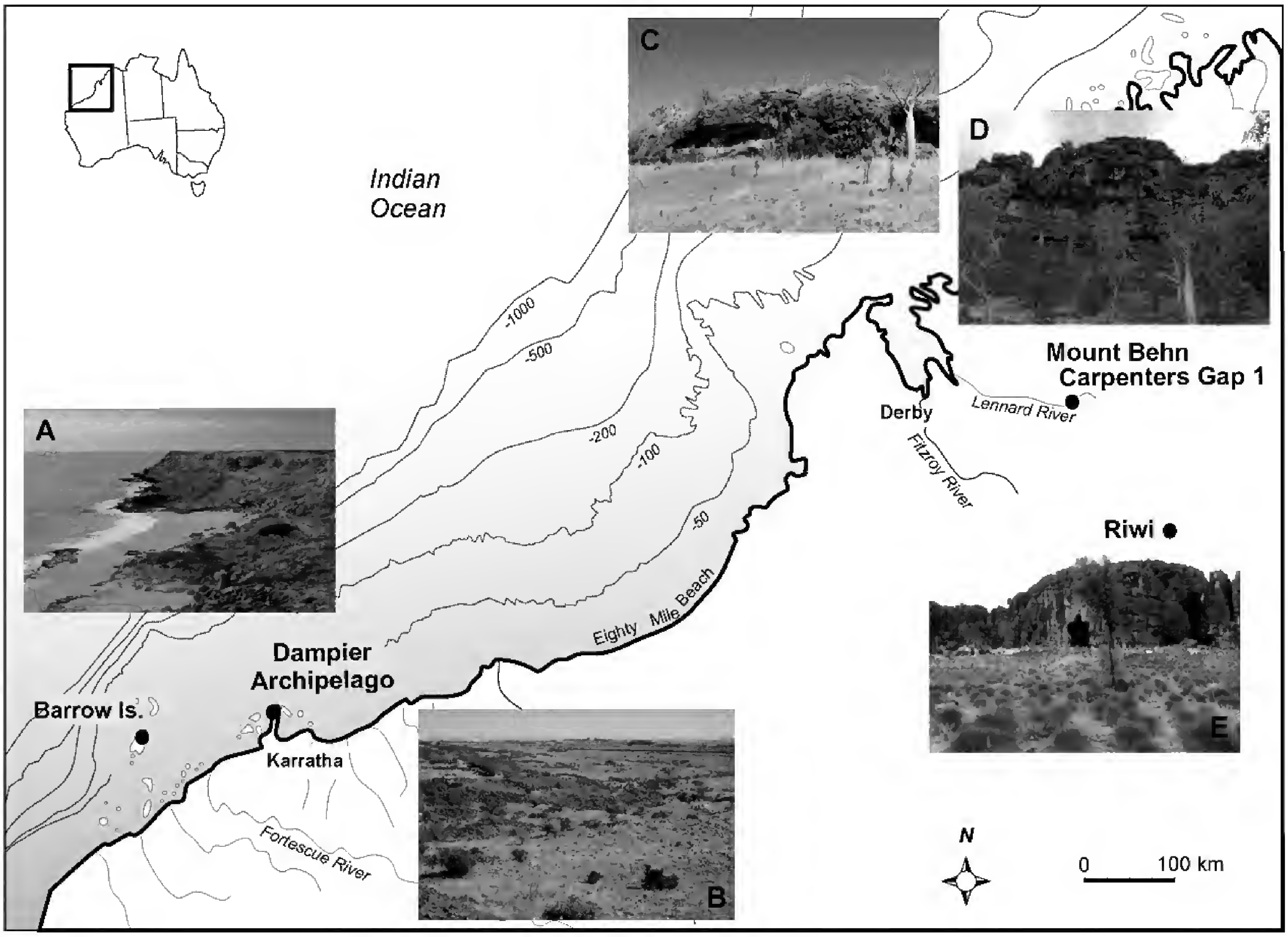

**Figure 2**. Map of northwest Australia showing sites mentioned in text including: A, Boodie Cave; B, Burrup Peninsula (Dampier Archipelago); C, Mount Behn; D, Carpenters Gap 1; E, Riwi.

## METHODS

Lithologic (stone artefacts, spalled rock) and biogenic reference material (shells, scats, botanical samples) were obtained from field collection or archaeological surveys and excavations. Mollusc shell samples were largely obtained from samples collected by University of Western Australia (UWA) archaeology staff, and supplemented where necessary with modern samples. Species include the baler shell (*Melo* sp.), *Nerita lineata*, mangrove whelk (*Terebralia palustris*) and landsnail (*Rhagada ballarensis*) among the Gastropoda; oysters (Ostredidea) and pearl shells (Pinctada) among the Bivalvia; and limpet shells (Patelloida). In addition, there is also eggshell from marine turtles (Chelonioidea) and birds (Cacatuidae).

Scats from native fauna that occupy caves and rockshelters on Barrow Island were especially collected by the Western Australian Department of Parks and Wildlife for this study. Barrow Island is a Class A reserve hence collections from this island ensure that any decomposed material within the scats represents native rather than introduced vegetation. Seven species are represented including the herbivorous euro (*Macropus robustus isabellinus*), black-flanked rock wallaby (*Petrogale lateralis lateralis*), northern brushtail possum (*Trichosurus vulpecula arnhemensis*), and the omnivorous golden bandicoot (*Isoodon auratus barrowensis*), burrowing boodie (*Bettongia leseur*), the insectivorous Finlayson's Cave bat (*Vespadelus finlaysoni*) and the carnivorous perentie (*Varanus giganteus*).

Stone artefact, shell and scat samples were prepared for thin sectioning by resin impregnation (using a 7:3 mix of polyester resin with styrene) of discrete samples in ice-cube trays, which were then made into 2.5 x 5 cm polished thin sections. Stone artefact samples were obtained from field collections and include (siliceous-) sedimentary, igneous, metamorphic and meta-sedimentary rocks. Where possible comparisons are made with 'contextual' thin sections from previous micromorphological studies undertaken in the Kimberley (Vannieuwenhuyse 2016) and Pilbara (Ward *et al.* 2017). These larger (5 x 7 cm) contextual thin sections were made by Spectrum Petrographics in the USA from resin-impregnated coherent sediment blocks taken from archaeological excavation profiles, and are more suitable to document depositional and post-depositional features.

Slides were scrutinised using a polarising petrographic microscope available at UWA under plane polarised light (PPL) and crossed-polarised light (XPL) using different magnifications (10x, 25x, 50x, 100x, 500x). The terminology used follows Stoops (2003), Stoops *et al.* (2010), and Nicosia & Stoops (2017).

## RESULTS

### Lithogenic Fraction

STONE ARTEFACTS

One of the primary criteria for distinguishing stone artefacts in micromorphological sections is their raw material. Past people often selected materials for stone artefact manufacture based on specific attributes such as their size, shape and quality (e.g. Braun et al. 2009; Harmand 2009; Ditchfield 2016). This can make stone artefacts easy to distinguish in micromorphological sections when the raw materials are different to the sediments in which they were discarded (Figure 3) but much less so when they are manufactured from a similar (local) lithology (e.g. Ward *et al.* 2017). Most stone artefact assemblages in Western Australian archaeological sites are characterised by an extraordinary range of lithologies, particularly in the geologically diverse Pilbara region (Hickman 1983). These include a wide range of igneous (e.g. granite, basalt, dolerite), sedimentary (e.g. chert, limestone, silcrete, banded iron formation), metasedimentary (e.g. slate) and metamorphic (e.g. mylonite) rock types (Figure 1). Hence, we know very little about geological source locations beyond broad inferences of 'non-local' versus 'local' availability. This is further complicated by limited petrographic data, incomplete detailed geological mapping (with many geological units exceeding several hundred kilometres), unknown potential quarry locations and also limited stratigraphic information with which to assess changes in lithology and their sources (Martin 1982). This situation is improving with updated geological maps (e.g. Martin *et al.* 2015) and localized studies (by government agencies, university researchers, and industry) within these broader regions.

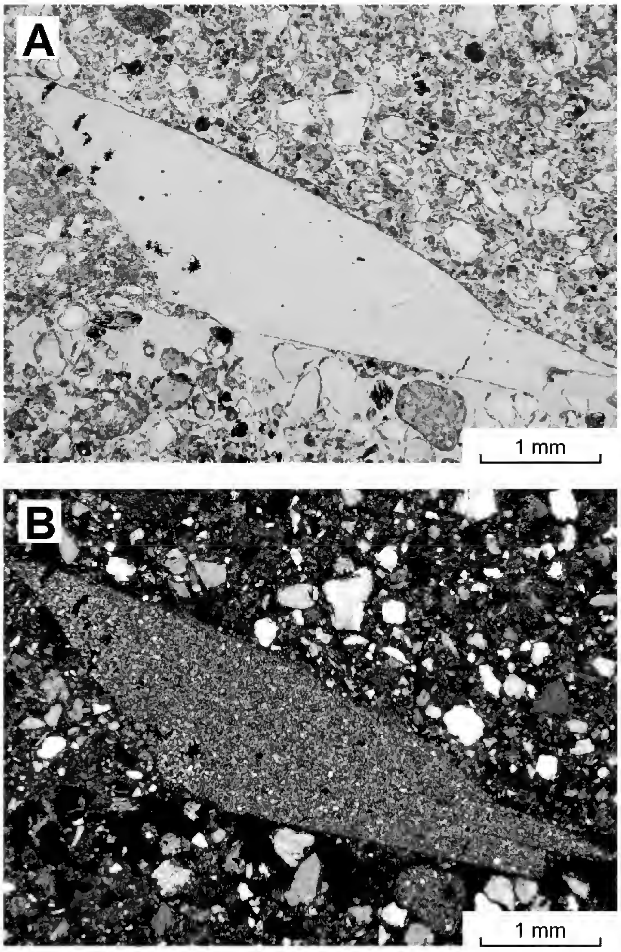

**Figure 3**. Example of lithic artefact from Mount Behn sequence, Kimberley (sourced from Vannieuwenhuyse 2016). Note the sharp edges and the cryptocrystalline siliceous nature (probably chert) of the artefact, which contrasts with the quartz dominated surrounding sandy matrix (A, PPL; B, XPL).

Where stone artefacts are manufactured from material similar to that in their geological and/or sedimentary environment, other attributes can be used. Stone artefacts are largely made from amorphous or fine-grained rocks, with an aim towards angular sharp edges (e.g. Figure 4) that may contrast with naturally-deposited rounded or sub-angular stone or coarse sediments. Another attribute that can sometimes be helpful in distinguishing stone artefacts micromorphologically is their minimal weathering compared to other lithic material in the same depositional setting. As stone artefacts are often manufactured from siliceous material, they tend to weather more slowly than other non-siliceous stone. All of these attributes accord with the main micromorphological features of stone artefacts as outlined by Angelucci (2010, 2017; Table 1).

Another potential attribute is the effect of heat treatment, which is a common technique to improve the quality of some flakes and tools (Domanski *et al.* 1994). This involves heating a stone to temperatures of 250–400°C for cryptocrystalline rocks (e.g. chert) and 500°C or above for macrocrystalline rocks (e.g. silcrete, quartzite). Effects of heat treatment include 'crazing' (fine internal cracks), chromatic variation and microstructural changes related to recrystallization of quartz (Angelucci 2017). The latter are best detected by comparing burnt

**Table 1**
Main micromorphological features of knapped lithic artefacts (from Angelucci 2010, 2017).

| Characteristic | Description |
|---|---|
| Grain size | < 300 μm and often anomalous in respect to grain size of embedding matrix |
| Alteration | Absent or minimal |
| Shape and roundness | Tabular or platy, and angular to very angular |
| Surface roughness | Regular, smooth |
| Boundary | Sharp, straight to regularly curved |

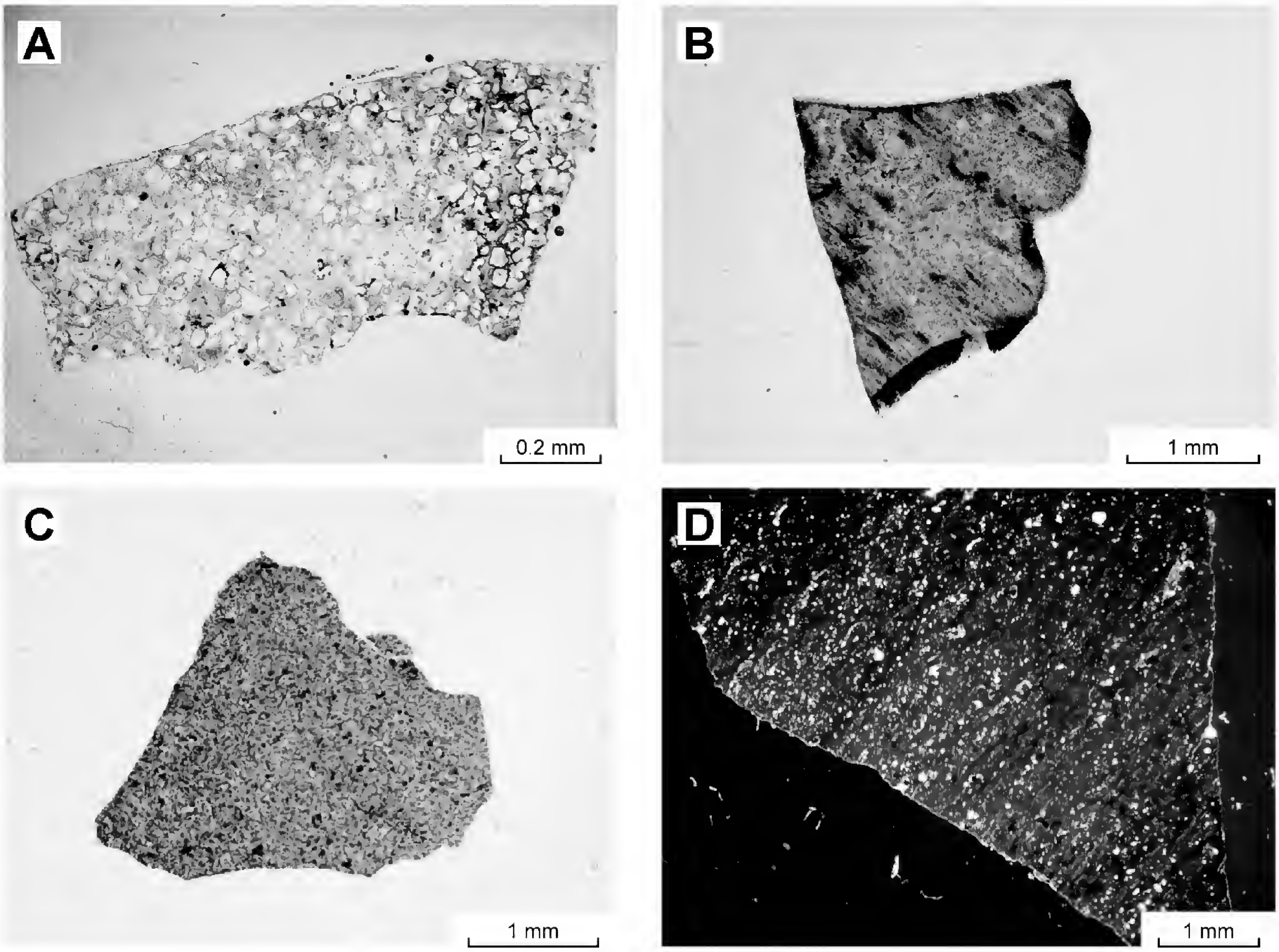

**Figure 4**. Examples of sharp edges lithic artefacts from Boodie Cave, Barrow Island, Pilbara, including: A, siltstone; B, mudstone; C, basic volcanic; D, ferruginised limestone or 'calcrete'. All images except are PPL except D, which is XPL.

and unburnt artefacts from the same material. Whilst there are no heat-treated artefacts in the current reference collection, this does not mean heat treatment was not used.

Whilst a classification scheme that incorporates both macroscopic and microscopic data would be useful, Martin (1982) emphasized the greater contribution of microscopic characteristics to the identification of artefactual rock types. Figure 4 presents some thin section images of artefacts from Boodie Cave as a guide to their identification in micromorphological sections and, more generally, from basic petrological analyses. Examples include coarser limestone, sandstone and siltstone (Figure 4A) through to the finer grained volcanics (Figure 4C) and mudstones (Figure 4B). A comprehensive guide to the range of stone artefact petrology for Barrow Island can be found in Ditchfield (2016), with results from this work forming part of a larger stone artefact database that is being developed at UWA.

### SPALLED ROCK FRAGMENTS (ROCK ART PRODUCTION)

An unusual example of lithogenic material are spalled fragments of painted wall within the sedimentary deposits of Mount Behn rockshelter (Figure 5). These provide a unique insight into early art production techniques and weathering processes at the shelter, with the advantage of not damaging any of the wall paintings. The multilayered fragment reveals pigments of yellow to dark red ochrous minerals, black charcoal and white ash (Finch *et al.* 2013; Vannieuwenhuyse 2016). The identification and geochemical fingerprinting of these mineral pigments can be useful to determine the source of ochres using in rock art (e.g. Ward *et al.* 2001; Huntley *et al.* 2015; Wallis *et al.* 2016).

The micromorphological analysis of spalled rock fragments and surface crusts from rockshelter walls and ceilings can also provide proxy environmental information of changing microclimate and aid dating of underlying paintings and engravings (Watchman *et al.*

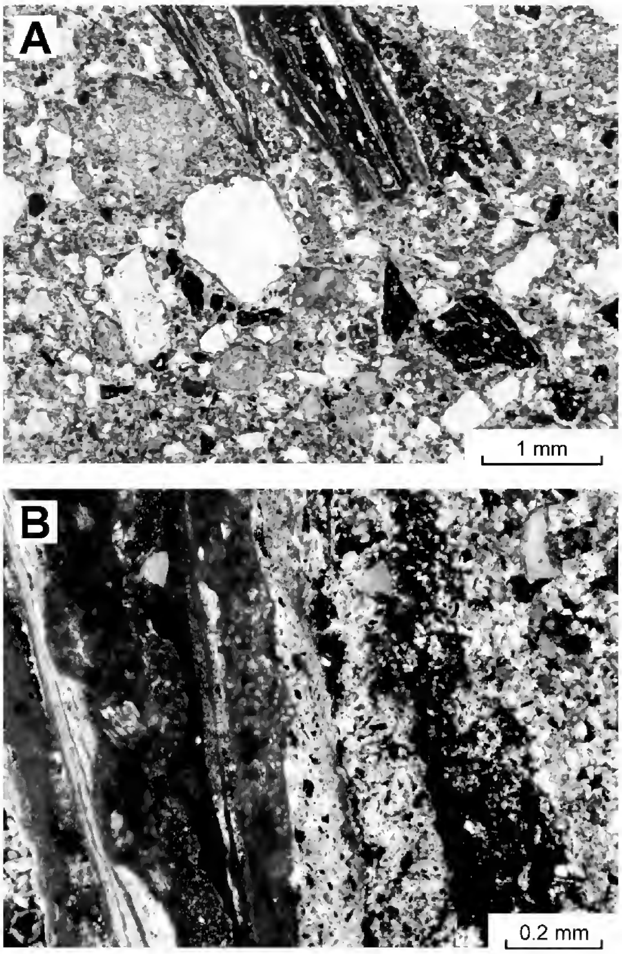

**Figure 5**. Example of painted wall spall from the Mount Behn sequence, Kimberley (sourced from Vannieuwenhuyse 2016): A, thin-section scan (PPL); B, microphotograph showing the multilayered composition of the fragment (XPL).

2001). Indeed, dedicated research on mineral coatings on the surfaces of sandstone rock shelters in Western Australia's Kimberley is currently underway to find datable materials to bracket ages of rock art motifs with which they are often spatially associated (Green *et al.* 2017).

## Biogenic fraction

### MOLLUSC SHELL

Molluscan microstructures are highly ordered aggregates of either calcite or aragonite crystals with varied morphologies and three-dimensional arrangements, which may be physically and/or biological determined (Brom & Szopa 2016; Checa 2018). In general bivalve and gastropod shells consist of a non-mineralized layer (the periostracum), with a homogeneous layer embedded between an outer and inner prismatic layer (composed of polymorphs of calcium carbonate) and the iridescent nacreous or porcelaneous layer (composed of tabular aragonite; Canti 2017b). The pigmented organic periostracum is rarely found on archaeological specimens and is not present in any of the reference material (which derive from excavated material). The nacreous shell layer is generally not a reliable discriminating feature (Debryne 2014), hence shell taxa are mainly identified at order or family level from their internal shell composition and arrangement of crystal layers – namely crossed-lamellar, foliate, prismatic and their sub-types (for further detail refer Kobayashi 1969; Claassen 1998; Allen 2017). The different fracture properties of prismatic and nacreous layers of shells are also relevant to the success of different shell-working techniques (Szabo 2008), such as in the ground-edge knives manufactured from baler shell (Akerman 1975), and presumably also to the differential preservation of these layers.

The baler shell (genus *Melo*) is an extremely hard shell (~5 on the Mohs scale) comprised of both sheets of foliated calcite and aragonite (Figure 6A). Indeed Akerman (1975, p. 19) suggested that the absence of ground-edge pearl shell tools on northwest Australian archaeological sites may be explained by the tendency of pearl shells to disintegrate rapidly compared to the much harder baler shell. The pearl shell (*Pinctata* sp.) also has a thin outer calcitic prismatic layer but the middle and inner layers consist of nacreous aragonite (Figure 6B; Taylor et al. 1969). In contrast, *Dentalia* (tusk shell) is entirely composed of aragonite, with a thick middle layer (crossed-lamellar ultrastructure) and two thin surface layers (homogeneous or finely prismatic; Smith & Spencer 2016). The latter were used for making personal ornaments and intentionally fractured segments have been found in archaeological deposits dated as early as 30 000 years ago (Balme & Morse 2006) as far inland as Riwi and Mount Behn (Balme 2000; Balme & O'Connor 2017; Maloney *et al.* 2017).

Crossed-lamellar aragonite also forms the shell for landsnails (Figure 6C), gastropods of genera *Haliotis*, *Nerita* (Figure 6D) and *Anadara* (Figure 6E), whilst layers of calcite and aragonite alternate in *Patella* limpets (Figure 6F; Claassen 1998). *Terebralia* (Potamididae) is similarly composed of both aragonite and calcite (Figure 6G). In oysters (Ostreadidea) the shell is almost entirely of foliated calcite, with a thin outer prismatic layer (Figure 6H). Mussels (Mytilacea) may be wholly aragonitic with nacreous and complex-lamellar structures, or may contain finely prismatic calcitic layers. For example, *Mytilus edulis* has crossed-lamellar (platy) layer over a layer of elongated crystals of calcite, with shells showing up as pink in thin section (see also Villagran *et al.* 2011). This genus is recorded more often in archaeological sites on the east coast and inland of Australia (e.g. Sullivan 1987; Wallis & Collins 2013) than in the west, although the freshwater river mussel (*Lortiella* sp.) has been recorded at Carpenters Gap 3 (O'Connor *et al.* 2014) and mud mussel (*Polymesoda coaxans*) is still collected in the Kimberley (Dilkes-Hall, pers. comm. 2018). More common in coastal archaeological sites are the turreted mangrove whelk *Terebralia palustris* and rocky shore cockle shell *Anadara granosa* (Figure 8F), with the latter stratigraphically overlying the former in several midden sites in northwest Australia (Bradshaw 1995; Clune & Harrison 2009). Whilst understanding past depositional settings may aid identification of economic (edible) shell species, many specimens may still be unidentifiable even with available reference material.

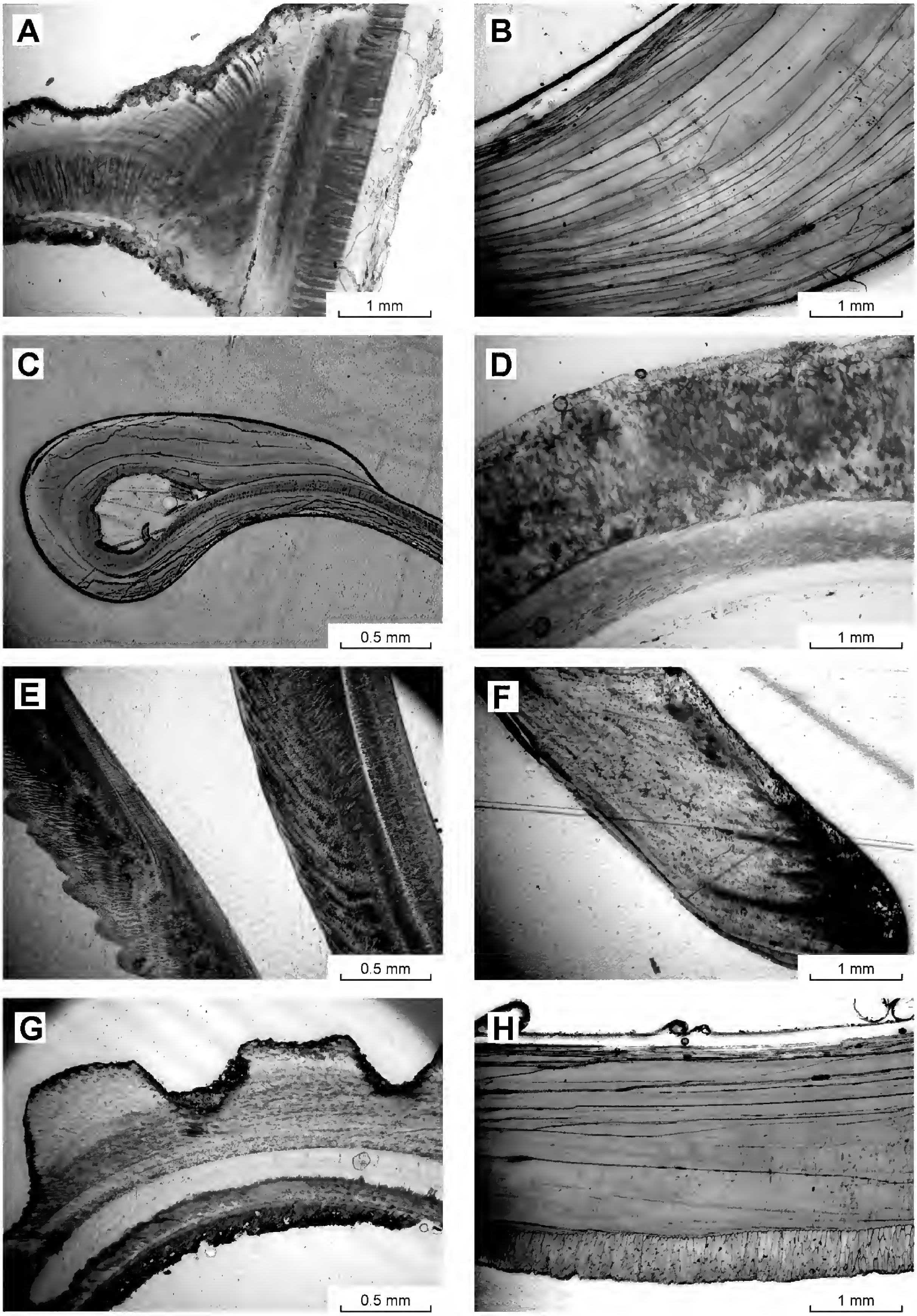

**Figure 6**. Thin section PPL images of various shells: A, baler shell, *Melo* sp.; B, pearl shell, *Pinctada* sp.; C, landsnail, *Rhagada ballarensis*; D, *Nerita lineata*; E, cockle, *Anadara* sp.; F, limpet, *Patelloida*; G. mangrove whelk, *Terebralia palustris*; H, oyster, Ostredidea.

### AVIAN AND REPTILIAN SHELL

Other shell types found in archaeological sites in northwest Australia include avian and reptilian eggshell (Figure 7). As in mollusc shells, eggshell structures are distinguished by the general arrangement of calcite crystals (or aragonite in turtle eggs) ranging from testudoid in Chelonioidea (turtles; Figure 7A), chrocodiloid in Chrocodylia (crocodile) to an ornithoid-ratite morphotype in Struthionidae (emu; Mikhailov *et al.* 1996). Whereas crocodilians and some turtles lay eggs with tough shells the soft, leathery nature of most reptilian eggs mean that do not preserve well in most archaeological sites. The presence of turtle bone in midden deposits, such as Boodie Cave (Veth *et al.* 2017), are evidence that they constituted part of the dietary assemblage of this region.

Under the microscope, avian eggshells (Figure 7B) typically reveal edge columnar crystals (the palisade/mammillary layer) whereas mollusc shells display interwoven fibrous crystals (Durand *et al.* 2018). When the thin section is viewed obliquely against a dark background, avian eggshell will also stand out as a white line in contrast to mollusc shell, which is more transparent (Canti 2017a). Avian eggshells, some of which is possibly burnt (Figure 8A, B), have been recovered from excavations in many sites in both the Pilbara (Ward *et al.* 2017) and Kimberley (Vannieuwenhuyse 2016; Vannieuwenhuyse *et al.* 2017).

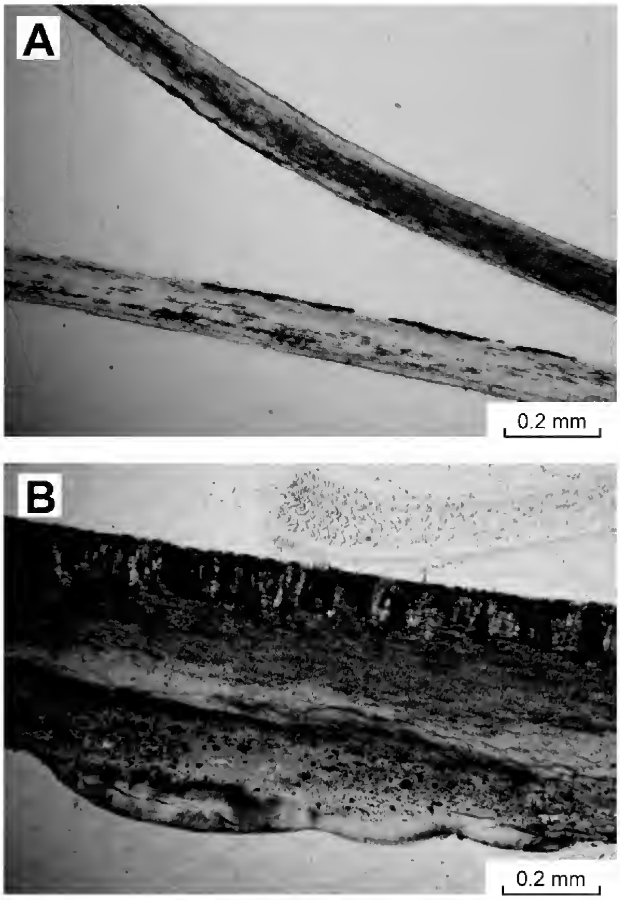

**Figure 7.** Thin section PPL views of: A, marine turtle, Barrow Island, Pilbara; B, modern emu eggshell.

In larger emu eggs, the mammillary layer can be up to one-third of the shell thickness with a radial, wedge-like arrangement of the columnar crystals, whilst the continuous inner layer has pronounced, horizontal growth lines (Long *et al.* 1998). In addition, the palisade layer tends to be less porous than for other avian species. Although not observed in Boodie Cave, emu eggshell was recorded at Cape Range, southwest of Barrow Island, alongside crab, sea urchin, fish and ochre in deposits dated before ~ 26 ky BP (Morse 1993a, 1993b).

### Contextual examples

Heated or burnt marine or other shell is not explicitly included in the shell reference material except within the context slides (see below). The two main types of alteration in burnt carbonates are scorching between 300–700°C and calcining at temperatures above ca. 800°C (Canti 2017c). The former produces progressive darkening (Figure 8B) whilst the latter produces isotropic calcium oxide that may reform to (cryptocrystalline) calcium carbonate under moist conditions. Darkened shell is more common in midden deposits of northwest Australia (Ward *et al.* 2017) and may indicate low temperature heating of shells in order to open rather than cook them.

It should be noted, however, that discolouration of mollusc, crustacean and echinoderm shell can also relate to residence time in the intertidal zone and/or sedimentary context (Kolbe *et al.* 2011; Powell *et al.*, 2011). In the case of the larger foraminifera *Alveolinella quoyi* (Figure 7C) the dark brown colour in thin section is typical of exceptionally well-preserved tests, which are white in reflected light. The test wall is composed of high-Mg calcite (very susceptible to corrosion) and is made of minute randomly oriented rod-like crystallites, which inhibit the passing of transmitted light.

The pigmented organic periostracum of molluscs can also be destroyed by heating above 300°C and/or from degradation from organic acid in the soil (Villagran *et al.* 2011; Villagran & Poch 2014), hence is unlikely to be encountered in most northwest Australian contexts, and was not observed in any of the archival material. Of the inorganic component, calcitic shell is generally harder, denser and less soluble than aragonitic shell, and thus more likely to survive (Claassen 1998). However, in Boodie Cave (Veth *et al.* 2017) shell remains of *Nerita* sp. can preserve relatively well for long periods (here dated to 40.3 – 42.5 ky BP, WK-42542) because they have a calcitic outer prismatic layer, which is less stable than aragonite found in the outer and inner layers of almost all other gastropod groups (Cox 1969). However, it is important to check recrystallization at the nanoscale to avoid any biased isotopic signatures (Weiner 2010). Also, well preserved in Boodie Cave are baler shell fragments (Figure 8D) and also intact serrated baler spoons or 'sporks' (Veth *et al.* 2017). In many coastal midden sites of northwest Australia, more deeply buried shell tends to be 'sacrificed' or degraded relative to the uppermost shell layers, despite the alkaline conditions provided by the carbonate (Clune 2002). This reflects a general decalcification of shell under more acidic conditions and hence is more apparent where middens have accumulated away from the immediate

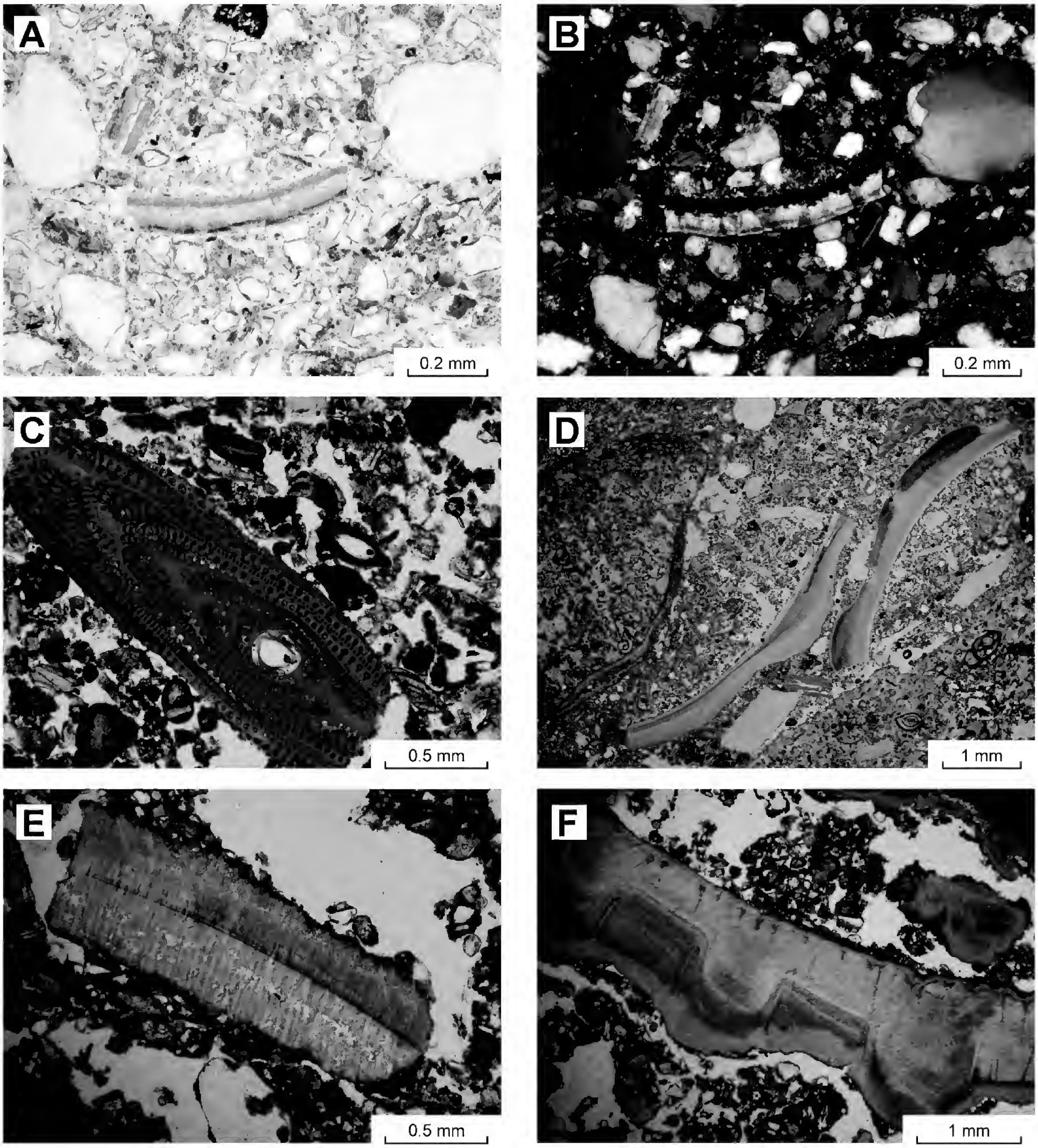

**Figure 8.** Examples of shells found in Kimberley and Pilbara archaeological sites: A & B, avian eggshell, possibly burnt (PPL & XPL, Riwi, sourced from Vannieuwenhuyse 2016); C, centred axial section of the foraminifera *Alveolinella quoyi* (not discoloured; Boodie Cave); D, baler shell fragments (Boodie Cave); E, decalcified cockle shell in a midden deposit (Dampier Archipelago); F, cockle (*Anadara* sp.) in ferruginous siliciclastic matrix (Dampier Archipelago). All images are PPL unless otherwise specified.

coast and over sediment derived from volcanic rock such as on the Burrup Peninsula (Figure 8E). Shell may also show increasing fragmentation due to reworking by cyclone or storm events in middens nearest the contemporary coast (Clune 2002). In this regard and more generally, micromorphological analysis of shell should be considered as an aid to macromorphological studies to provide some relationship with the deposits in which they occur and gain a more holistic view of site formation (Canti 2017b, p. 46).

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Dung is more common in archaeological sites than is perhaps realized, and in some cases may be the only evidence for the presence of species not represented among the bone remains (Linseele *et al.* 2013). Criteria for micromorphological identification are best achieved through a combination of morphometric features, associated content (e.g. plant remains, bone fragments) and again aided by reference collections (*ibid*). Fresh herbivore excrements are usually porous, loosely packed and consist mainly of poorly digested to undigested plant fragments, sometimes embedded in a brown to dark brown amorphous organic groundmass that becomes darker and/or redder with weathering due to humification or oxidation (Brönnimann *et al.* 2017a). Whilst carnivore coprolites typically contain bone fragments and optically isotopic matrix, their diet and feeding habits make them much more diverse (Brönnimann *et al.* 2017b).

The content of excrements from fauna on Barrow Island, a Class A reserve, are considered to reflect more pristine native environments than on the adjacent developed mainland coast. As in most Australian contexts, the scats of wallabies and kangaroos are small and round with a dry grassy matrix inside (Figure 9A, B). The dense outer rim of these scats mean they are less likely to disintegrate. Along with several other grasses, part of the diet for the euro on Barrow Island is thought to be the developing flower stalks and growth tips of spinifex (*Triodia* sp.), whilst the diet of the wallaby consists of grasses and some fruits, leaves of shrubs, and figs. The northern brushtail possums are omnivorous and nocturnal and hence do most of its foraging for leaves, flowers and fruits during the night but have been seen to feed on insects (Russell *et al.* 1989), as evidenced by the occasional chitin fragment in thin section (Figure 9C). The scats of large possums, such as brushtails (*Trichosurus* sp.) and scaly tails (Wyulda), produce generally dark, cylinder-shaped scats, whereas smaller possums, such as the pygmy (*Burramys* sp. and *Cercartetus* sp.), leave rat-sized pellets.

Bandicoots are omnivorous: their diet includes ants, termites, moths, turtle eggs and hatchlings, small reptiles, roots and tubers (Russell *et al.* 1989 Figure 9D). The nocturnal burrowing boodie is also omnivorous, and feeds on a variety of fruits, seeds, nuts, flowers and termites and hence has more of a vegetal component in its excrements (Figure 9E). Microbats, such as *Vespadelus finlaysoni*, eat a variety of small insects, hence their scats as found in Boodie Cave have a high chitin component (Figure 10D). Parente are carnivorous, consuming invertebrates and occasionally small vertebrates such as geckos and lizards as well as insects. Studies of monitor lizards has shown that individuals will specialise on whatever food items are available in their habitat (Traeholt 1997), including foraging amongst construction camps for small mammals and foraging gulls (Losos & Greene 1988). On Barrow Island, scats of *Varanus giganteus* consisted primarily of sea turtle eggs and hatchlings, and small mammals (Losos & Greene 1988). Figure 9G and H, show one such scat with highly birefringent, well-orientated elongate crystals of turtle egg and probably hair around an isotropic bone.

Contextual examples

Both herbivore and carnivore faeces were identified in the Carpenters Gap 1 and Riwi sequences (Vannieuwenhuyse 2016; Vannieuwenhuyse *et al.* 2017) and also Boodie Cave (Ward *et al.* 2017) suggesting animal occupation of the shelters (Figure 10A–F). The main implication of herbivorous scats (Figures 10A, B) is that partly degraded plant material in sediment profiles of archaeological excavations may not be cultural but rather a by-product of animals, and further indicates (alongside excremental fabrics) probable reworking of sediments. Similarly, bone from economic species, such as euro, hare-wallaby, golden bandicoot, brush-tail possum and even snakes and lizards, may actually represent remains of non-human prey rather than a product of human consumption (Manne & Veth 2015; Veth *et al.* 2017; Figure 9F). In these cases differences in fragmentation determined from whole fragments of micro- and small-bodied fauna may provide better indication of an anthropogenic origin.

Thin sections are more informative of post-depositional modification. Under relatively moist conditions, the decay of organic matter can lead to an enrichment of phosphate and hence to phosphate precipitations in or around the excrements (Canti & Brochier 2017). In Boodie Cave and Riwi, gypsum and/or anhydrite crystals were observed around bone and also phosphatic-rich faeces, such as bird droppings (Figure 10E). In well-drained sediments (neither waterlogged nor desiccated) organic material is usually not preserved and instead microscopic bio-mineral components like silica phytoliths or calcitic crystalline faecal spherulites (5–15 μm, Figure 10B) may be the only indication of presence of organic matter in the past (Canti & Brochier 2017).

However, spherulites are easily dissolved hence generally only survive in alkaline sediments or where water throughflow is minimal, such as limestone caves or rockshelters. Some examples include Boodie Cave (Figure 10C) and also Carpenters Gap 1 (Vannieuwenhuyse *et al.* 2017). They are also found in open areas characterised by rapid burial, aridity or a high pH in the sediments but are destroyed by heating at high temperatures (> 500°C; Canti & Brochier 2017). Whilst bushfire flames easily reach such temperatures, surface soil temperatures are generally buffered below 200°C and decrease with depth (McKenzie *et al.* 2004; Singh *et al.* 1991), hence spherulites should in theory not be affected.

### Macro and micro-botanical fraction

As indicated, UWA hosts existing and growing anthracology (wood charcoal) and carpological (seeds and fruits) reference collections from the Pilbara and Kimberley regions (Byrne *et al.* 2013; Dilkes-Hall 2014: Dotte-Sarout *et al.* 2015). These types of remains generally require identification from more than one cross-sectional angle and/or in three-dimensions by specialist archaeologists, and hence are less suited to a thin section reference collection. Microbotanical remains include ash, phytoliths, pollens and spores, starch, diatoms and other microfossils. Identification of these particles in thin sections is described in relevant chapters of Nicosia and Stoops (2017). Northwest Australian regional studies and reference collection are still scarce, especially those related to archaeological contexts (Wallis 2001).

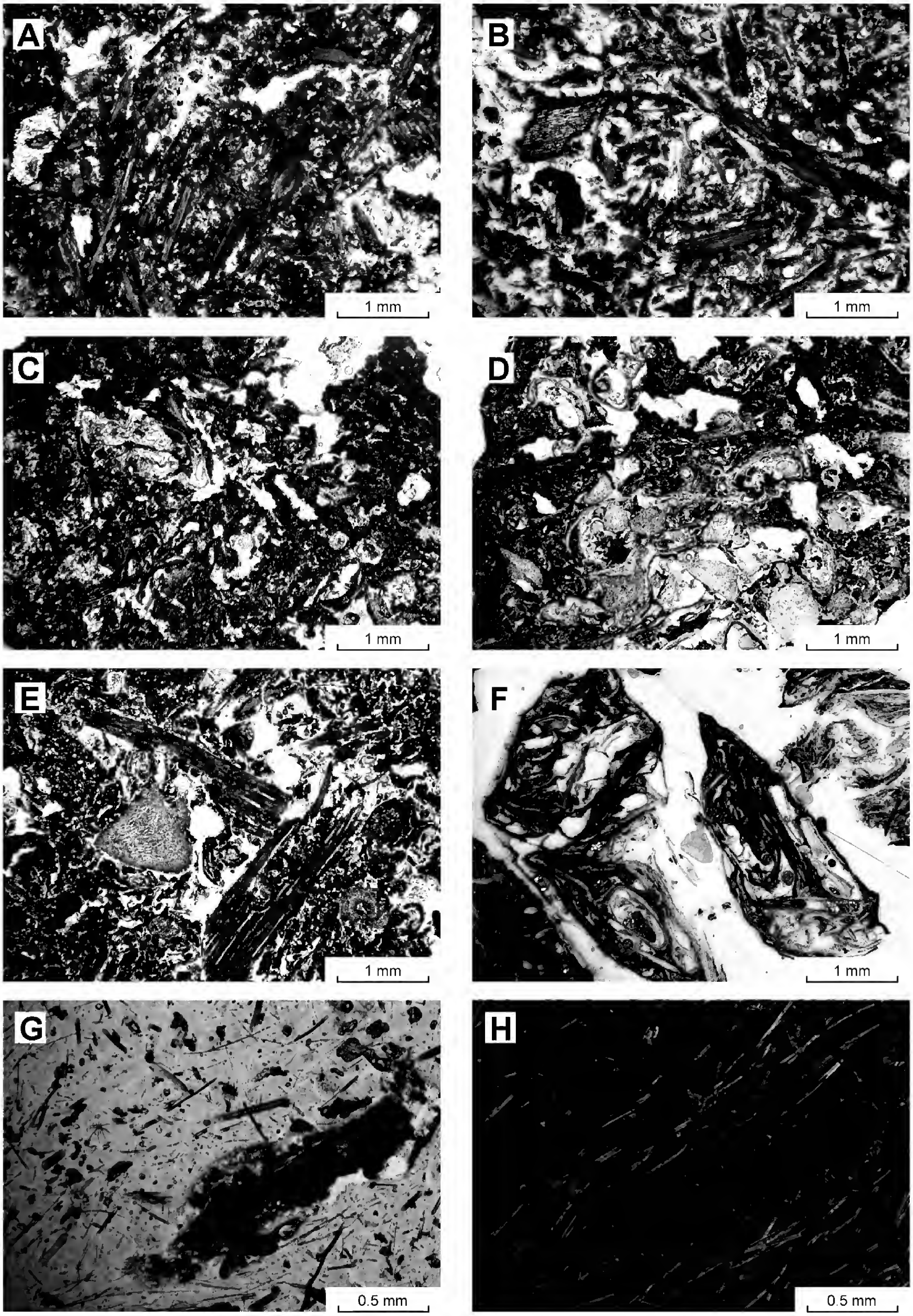

**Figure 9**. Thin-section microphotographs of native fauna scats from Barrow Island: A, euro, *Macropus* sp.; B, Wallaby, *Petrogale* sp.; C, possum, *Trichosurus* sp.; D, bandicoot, *Isodon* sp.; E, burrowing boodie, *Bettongia* sp.; F, microbat, *Vespadelus* sp.; G, H, parente, *Varanus giganteus*. All images are PPL except H, which is XPL.

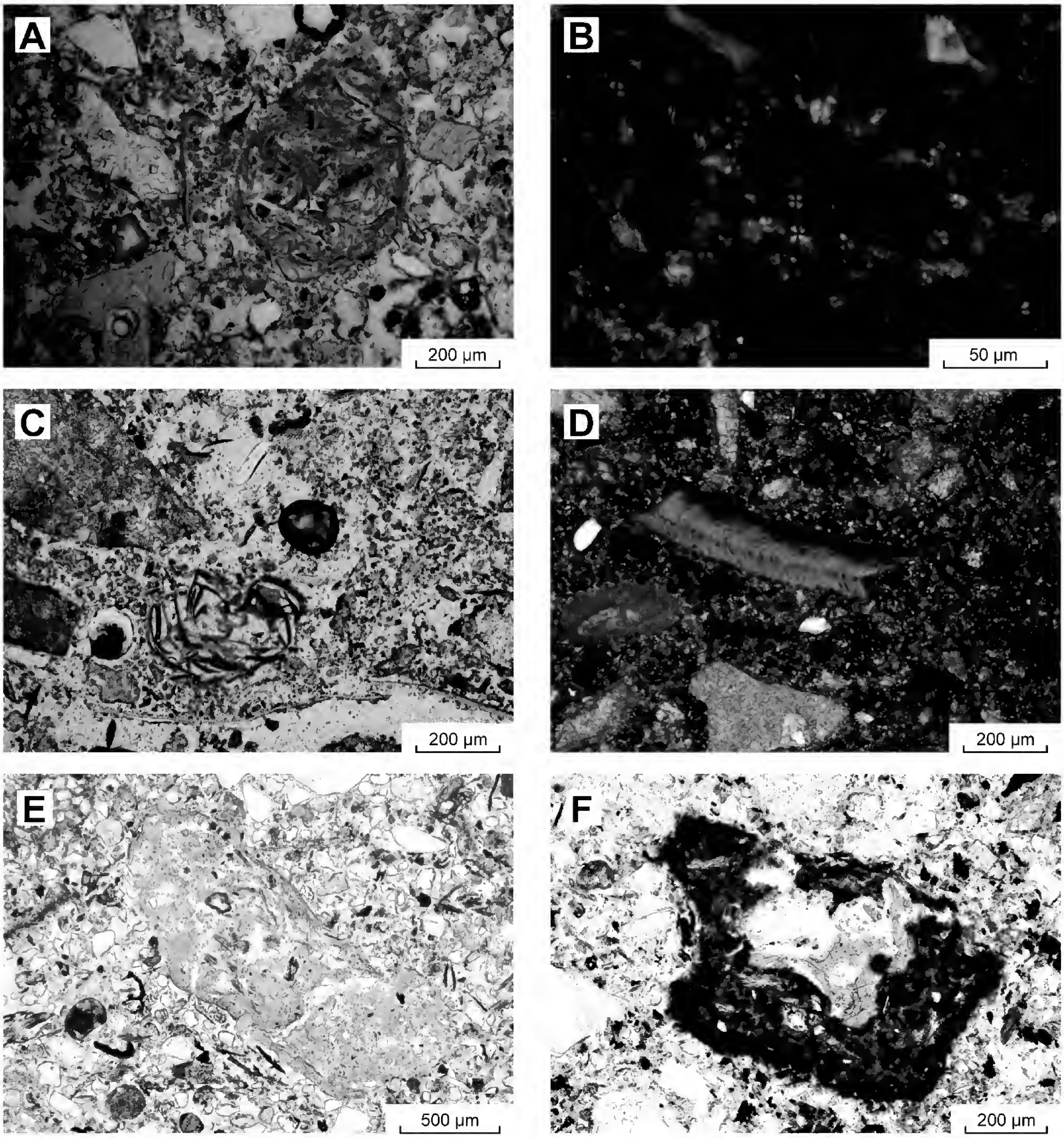

**Figure 10**. Microphotographs of scats found in Kimberley and Pilbara archaeological sites: A, partially digested plant matter in well preserved macropod coprolite (PPL, Boodie Cave); B, same as A, at high magnification showing spherulites with typical cross-pattern extinction (XPL); C, microbat scat with insect chitin (PPL, Boodie Cave); D, chitin (insect parts, XPL, Boodie Cave; Ward *et al.* 2017); E, apatite-rich bird dropping with vegetal tissue residues and phytolith inclusions (PPL & XPL, Riwi, Vannieuwenhuyse 2016); and F, carnivorous scat with bone fragments (PPL, Carpenters Gap 1, Vannieuwenhuyse *et al.* 2017).

Palaeobotanical analyses extend the focus to human signatures rather than simply palaeoenvironment. A large focus has been given to the micromorphological study of combustion features, documented in many publications (refer Nicosi & Stoops 2017 and references therein). The palaeobotanical and micromorphological analysis of combustion features have proven to be quite informative in terms of human behaviour (plant collection, food production and various use of light and heating properties), as demonstrated by the combined anthracological and micromorphological results from Riwi combustion features (Whitau *et al.* 2017).

Microbotanical particles such as ash and phytoliths have a commonly polymorphic nature, which means that

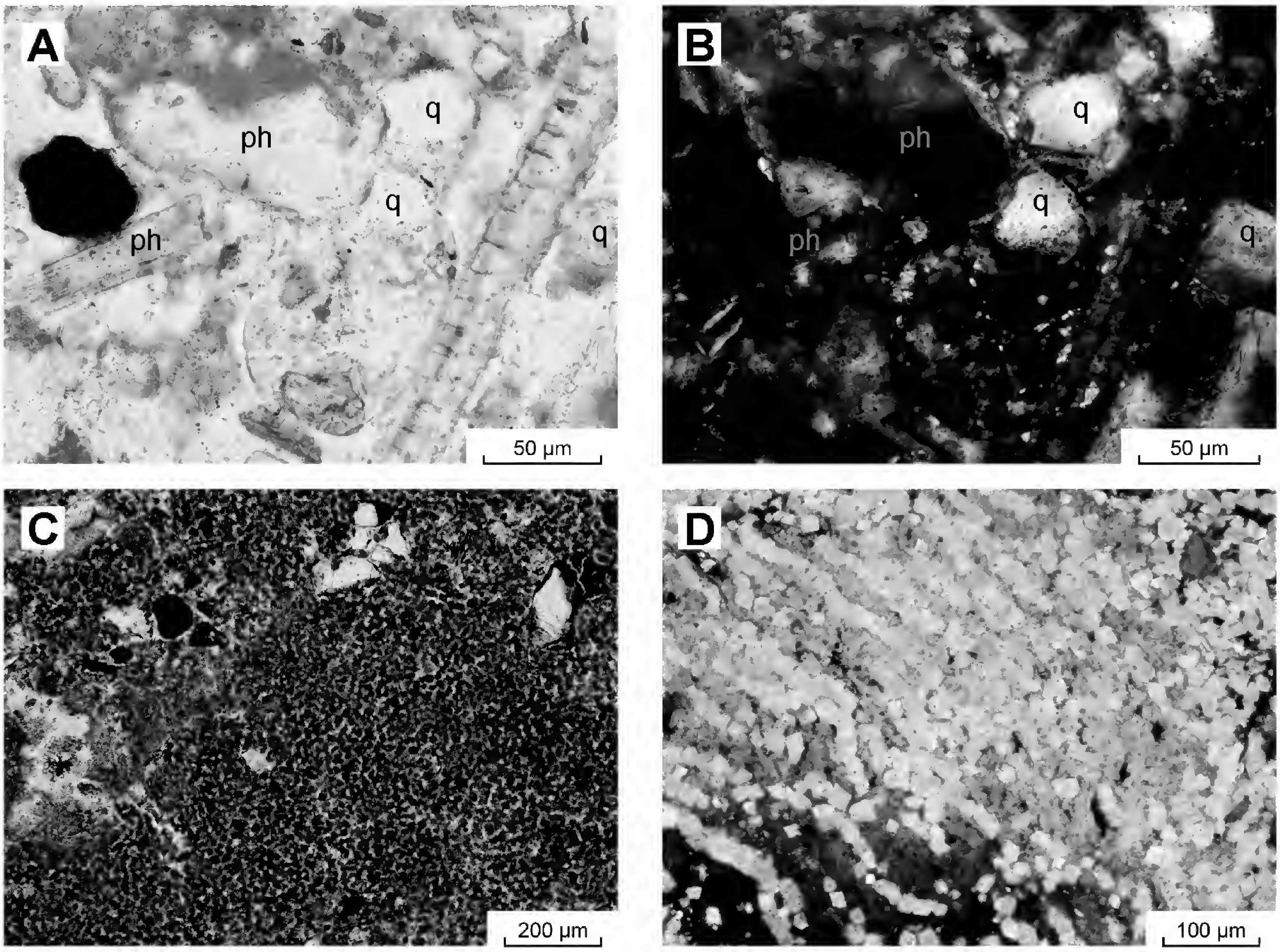

**Figure 11**. Microphotographs of polymorphic phytoliths in Riwi: A&B (PPL & XPL) are sourced from Vannieuwenhuyse (2016) and Whitau *et al.* (2017); and C&D (PPL & XPL) showing phytoliths that are typically anisotropic in XPL and calcitic rhomboedric ash particles.

similar shapes can be found in different wood species and there may be different shapes in the same wood species (Wattez 1988; Brochier & Thinon 2003). While studies in the Kimberley have demonstrated that phytoliths have a high range of polymorphism (e.g. Wallis 2001, Figure 11A and B), calcitic ash particles observed in archaeological sequences all have a similar rhomboidal shape (Figure 11C and D). This is probably best explained by the similarity in woody anatomical structure among Australian Eucalypt and Acacia species (observations based on anthracological study, Whitau & Dotte-Sarout, pers. comm. 2015).

Preservation of plant and charcoal are best explored by identifying the effects of post-depositional processes using micromorphology. For example, the mineralisation of wood charcoal in Boodie Cave was presumably produced by precipitation of minerals from water dripping through the cave ceiling (Ward *et al.* 2017). Similar examples of secondary carbonates or gypsum growing in charcoal voids have been observed in karstic contexts in Australia and France (DV personal observation) so may be a common phenomenon of limestone caves in arid zones.

## DISCUSSION

### Creating and sharing reference collections

The extreme weathering conditions of northern Australia exacerbate the poor preservation of largely temporally and spatially discontinuous archaeological and environmental evidence left by mobile Aboriginal occupation. Micromorphology thus allows for a forensic style characterisation and analysis to aid any or macro-scale study of archaeological sites; and, perhaps more critically, providing information about the formation history and integrity of cultural material and their microstratigraphic context.

According to Hughes (1983, p. 114):

> *A wealth of information can be gained from the analysis of thin sections of samples of impregnated deposit (...). However, (...) the preparation of the samples and their subsequent analysis is a specialised, expensive and time-consuming process that only a few institutions in Australia are capable of undertaking. For these reasons thin section analysis should only be considered for long-term archaeological projects of an interdisciplinary nature.*

Although time-consuming, most institutions have a geological facility capable of preparing inexpensive thin sections. Unfortunately the large micromorphological thin sections, typically 5 x 7 cm or more, needed to better understand depositional and post-depositional features (Courty *et al.* 1989) are more expensive to produce. Nevertheless, it must also be taken into consideration that large thin sections can supplement and/or replace mineral identification (e.g. X-ray diffraction) and grain-size analysis (especially identifying grain size of different minerals), or can be used for complementary analyses such as scanning electron microscopy and quantitative mineral mapping (e.g. Ward *et al.* 2018). Thin sections are particularly useful in detecting diagnostic remains or features that would otherwise be overlooked in any macro-scale analysis, such as the painted wall fragments from Mount Behn rockshelter or microcharcoal fragments in cultural units where macroscopic evidence of charcoal or burning is entirely absent (Lowe *et al.* 2018). Regardless of any sophisticated techniques, as Courty (1991) reminded us, the primary goal of micromorphology is understanding sedimentary context.

Another consideration is the destructive aspect of thin section analysis, particularly for stone artefacts. Nevertheless, numerous examples demonstrate the value of stone artefact petrology to determine the provenance of such items (e.g. Binns & McBryde 1972; Glover *et al.* 1975; McBryde & Watchman 1976; Martin 1982; Benbow & Nicholson 1992; Webb *et al.* 2013; O'Leary *et al.* 2017). From a broader micromorphological perspective it is not just the potential source of stone artefacts that is of interest but also what they might indicate about depositional and post-depositional history. For example, different patterns of heat fracturing (both cracking and shattering) may be important in identifying deliberate heat treatment as opposed to natural transformation through fire (Mercieca 2000). Similarly, orientation might provide clues to directional water movement, sloped deposits or even faunal activity (Vannieuwenhuyse 2016), whilst petrons or other forms of size sorting may be indicative of a lag deposit or development of stone lines through bioturbation (Fitzpatrick 2012), all of which may be important in distinguishing natural from cultural deposits and/or their stratigraphic integrity (Hiscock 1985).

There can be great value in undertaking micromorphological analyses for short-term and single site studies, for example, to aid facies characterisation and integrity of any radiometric dating (e.g. Janowski *et al.* 2015; Green *et al.* 2017; Vannieuwenhuyse *et al.* 2017; Ward *et al.* 2017). It is encouraging to see micromorphology techniques increasingly being integrated with standard sedimentological (including geochemical), geochronological and magnetic susceptibility analyses to better understand the record of human impact and site formation processes and site integrity (Clarkson *et al.* 2017; Lowe *et al.* 2018). It has also been applied successfully to understand site formation of abandoned mud brick structures in arid environments in the near East (Friesem *et al.* 2011), which may find analogy in the historic wattle-and-daub structures in Australia and elsewhere (Kruger 2015).

In isolation the small-scale data offered by micromorphology is generally insufficient to reach meaningful interpretations of archaeological site formation. Rather it works best in conjunction with other microscale (e.g. mineralogy, palynology, phytolith and isotopic analyses) and macro-scale evidence (e.g. lithic analysis, zooarchaeology, anthrocology, archaeomalacology) as a guide to intra-deposit relationships and to gain a more holistic view of site formation (e.g. Villagran *et al.* 2011; Vannieuwenhuyse *et al.* 2017; Ward *et al.* 2017; Whitau *et al.* 2018a, 2018b). As Courty (1991) explained, micromorphology is best utilised when combined with other methods to answer specific questions.

The time-consuming aspect of micromorphological analysis is perhaps unavoidable but objective comparison of sediments and component features can be significantly aided by development of reference databases and contextual (large thin section) studies. The UWA archaeological micromorphological reference collection is themed around material from northwest Australia and will hopefully be expanded in future years. This is important as the present reference collection is unlikely to be representative of the wide range of archaeological contexts of this region. Even this preliminary micromorphological reference collection demonstrates how different the types of remains, contexts and site formation processes can be in northwest Australia compared to more temperate regions.

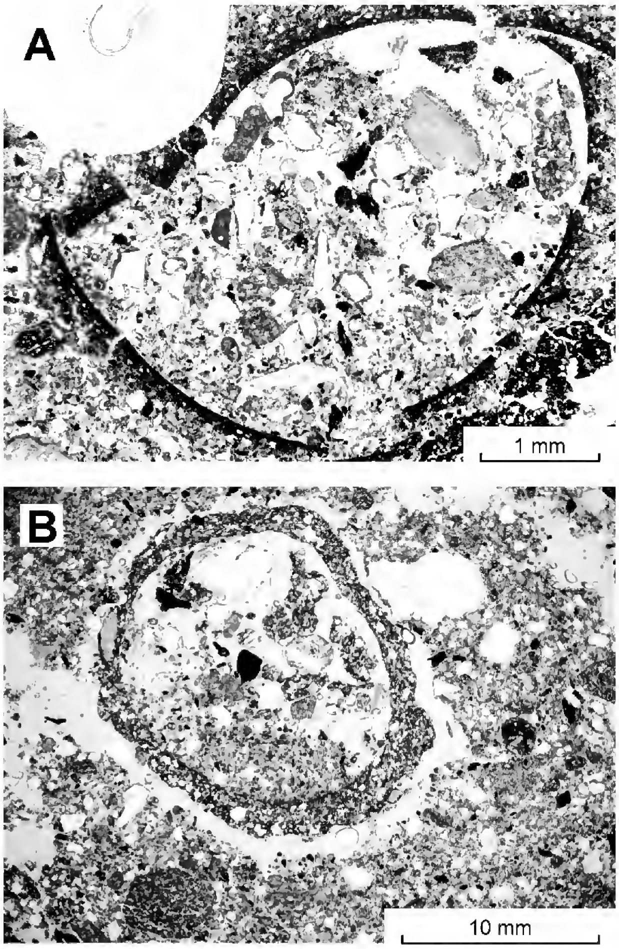

**Figure 12**. Insect galleries from Mount Behn (both PPL, sourced from Vannieuwenhuyse 2016).

As noted by van der Meer & Menzies (2011, p. 228), for the plethora of individual microstructures within sediments, it is the overall assemblage that is more indicative of a particular sedimentary environment than any single microstructure type. More typical of arid and semi-arid contexts, for example, are dissolution features (especially of carbonates and phosphates including bone, ash and guano); calcification (cave breccia, secondary carbonates) and argillic, calcic, and gypsic features. Examples of many of these are present in the caves, rockshelters and open sites of northwest Australia (Vannieuwenhuyse 2016; Ward *et al.* 2017) and other sites in arid and semi-arid zones (e.g. Amit & Yaalon 1996; Khademia & Mermut 2003). Biological activity can also offset or obscure effects of other processes (Courty & Fédoroff 1985). For example in arid and semi-arid zones termites and other burrowing arthropods (e.g. mudwasps, antlions, burrowing bees) essentially fill the role of earthworms in more temperate climates (McBeaty 1990; Williams 1978; Figure 12) and probably play a greater role in post-depositional disturbance than larger fauna (Venn 2008; Kourampas *et al.* 2009; Vannieuwenhuyse *et al.* 2017).

The reference collection provides a preliminary valuable regional reference against which to help identify archaeological and non-archaeological (including post-depositional) remains and features in thin sections obtained from other sites in northwest Australia and in other arid-zone areas. Just as with the anthracology reference collection (Dotte-Sarout *et al.* 2015), the micromorphology reference collection ultimately needs to be transformed into an atlas or database that is readily available to help with the development of the discipline in this and other arid and semi-arid zone regions. To this end, the reference collection supplements the comprehensive micromorphological and encyclopaedic references of Stoops *et al.* (2010) and Nicosia & Stoops (2017). We will continue to build on our arid zone database as comparative experimental studies and reference collections for cooler climates (e.g. Villagran *et al.* 2011; Banerjea *et al.* 2015) show that such databases are invaluable aids for the identification of anthropogenic sctivity.

## CONCLUSION

Although archaeological micromorphology is still a developing field in Australia, new projects focused on prehistoric sites are starting to reverse this trend (and may eventually extend to historical and marine contexts). The examples presented for northwestern Australia indicate that there is great advantage in developing local frameworks and resources for micromorphological and related work. Whilst acknowledging the conceptual capacities to process micromorphological data already collected and continually increasing, the development of archaeological micromorphology, as Courty (1991) explains, requires a close collaboration with archaeologists, using relatable terminology and an understanding of common objective towards understanding past human activities and the associated environmental context (see also Goldberg & Aldeias 2016). The best way to achieve this is through collaborative projects associating archaeologists, geoarchaeologists and other specialist scientists, so that adequate samples can be obtained from excavations. Such datasets are useful in teaching and training but ultimately are aimed at strengthening, or transforming, interpretation of archaeological sites in these Australian dryland contexts.

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# Professor Barbara York Main

## BSc, PhD (UWA), OAM

## 27th January 1929 – 14th May 2019

The Lady of the Spiders, Barbara Main (nee York), left a consummate scientific and literary legacy that was generated by her passion for the natural environment, dedicating her working life to documenting the spiders and other invertebrate inhabitants of Australia.

Barbara was born and raised along with four brothers on a farm in the Western Australian wheatbelt. Being home-schooled enabled her to help her mother with household duties but also gave her time to roam about the family property. She later maintained that this instilled a life-long love of the Western Australian landscape. After attending Northam High School, in 1947 she enrolled in a science degree at The University of Western Australia. In 1951 she was employed as an Assistant Lecturer at Otago University, New Zealand, before returning to Perth to commence a PhD at The University of Western Australia in 1952. Disregarding popular topics for post-graduate projects such as plants, mammals, and birds, Barbara turned her attention to spiders. Her amblings in the Western Australian wheatbelt taught her that there were many more species than previously known and she set about to understand their diversity, their role in the ecosystem and how they had evolved within the landscape. This passion for spiders and the environment set the course for a lifelong career and a glowing international reputation.

Not content with dealing with the rigours of undertaking a PhD project, in 1952 Barbara married fellow University of Western Australia PhD candidate, Albert (Bert) Main (1919–2009), and started a family. Bert went on to forge an impressive career of his own in zoology and the environment. It was probably inevitable that she would marry a fellow biologist, as it was well known that Barbara kept spiders in her room at the University Women's College, deterring many potential suitors.

Barbara completed her thesis in 1956 and became the first female PhD in the Department of Zoology at The University of Western Australia. The zoology building at the time was situated "on the hill" on Mounts Bay Road near the Women's College.

While raising her family in suburban Perth during the 1960s, Barbara continued to study and write about spiders and the environment. She described several new species, including the only Australian blind trapdoor spider, which lives in the deep recesses of various Nullarbor caves. Her published books *Between Wodjil and Tor* (1967) and *Twice Trodden Ground* (1971) represent passionate accounts of the loss of biodiversity after the extensive clearing of the Western Australian woodlands in the early 20th century, focusing on the "Wodjil country" near the family farm. Her strong connection to natural landscapes was evinced in *Twice Trodden Ground*, where she declared that she longed "to return to a wild, lonely, forgotten piece of unwanted 'useless' land no good for farming ... the sort of place where one finds a kind of earthly anointment".

At UWA with friend in 2012 (photo John Banister)

She was the subject of a BBC and ABC documentary, *Lady of the Spiders*, narrated by David Attenborough and filmed by pioneering cinematographers Jim Frazier and Densey Clyne. The documentary included footage of a population of giant spiny trapdoor spiders that Barbara had commenced studying in the early 1970s. Knowing that the spiders never left their burrows, apart from the adult males during the mating season, she painstakingly tagged each burrow with a metal disc stamped with a unique number. Despite rarely seeing the spiders themselves, this allowed her to document and understand their complex lives in intimate detail, despite their being tucked away at the bottom of deep burrows. She could even tell when a female's babies had emerged from the maternal burrow and made a home of

At North Bungulla Reserve in 2015 (photo Grant Wardell-Johnson)

On receipt of the Royal Society of Western Australia Medal in July 2018 (photo Monica Main)

their own, due to the tell-tale sign of a 'fairy-ring' of tiny new holes a metre or two from the mother's home. Little did she know that a spider tagged in those early years (Number 16) would live until 2016, finally succumbing at the age of 43. This study showcased Barbara's passion and patience, remaining the longest study of any spider population in the world.

Barbara's work explored the close connection that spiders and other organisms have with their surroundings. Land clearing, trampling by stock, weeds, fire, and reduced rainfall (climate change), were all sadly having an effect on her beloved spiders all over Western Australia. She was never more distraught than when she returned to a site she had visited in the 1950s, only to find that a once-thriving population of trapdoor spiders was gone. Landscapes once sprinkled with many different species were now desolate and empty. It was a dagger to her heart.

Barbara's publications inspired an entire generation of scientists. Her 1976 book *Spiders* stimulated young Australian biologists to study spiders more closely. Barbara's collection of museum specimens and her perceptive observations on their environmental requirements have fostered new research on the evolution and taxonomy of these iconic animals, including studies using DNA sequence data. These studies vindicate Barbara's ideas that trapdoor spiders have been part of the Australian landscape for over 200 million years, slowly changing over time to adapt to different climates, soils and environmental conditions. Her taxonomic contributions resulted in the scientific description of over 70 different spider species and genera.

Barbara was an ardent supporter of community organisations, including a lifelong member and most recently Patron of the Western Australian Naturalists' Club. She also served on many boards and committees, one of which was as a member of the WA Museum Board of Trustees from 1982 to 1993, being the first woman to be appointed to this role.

Barbara received numerous accolades during her career, including the Order of Australia in 2011 and the Royal Society of Western Australia Medal in 2018. She was also recognised by other scientists who named numerous spiders and other invertebrates in her honour, including the genera *Bymainiella* (a trapdoor spider), *Barbaraella* (a pseudoscorpion) and *Mainosa* (a wolf spider).

She is survived by her children Rebecca, Gilbert, and Monica, and her grandchildren Eleanor, Marjorie, and Harold.

We are unlikely to see someone like Barbara again. Vale Lady of the Spiders.

**Dr Mark Harvey**
**Department of Arachnology**
**Western Australian Museum**

The text for this obituary is reproduced from the Western Australian Museum website http://museum.wa.gov.au/explore/articles/professor-barbara-york-main

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# Settling the West: 50 000 years in a changing land

**JOE DORTCH [1*], JANE BALME [2], JO MCDONALD [1], KATE MORSE [2, 3], SUE O'CONNOR [4], PETER VETH [1, 5]**

[1] *Centre for Rock Art Research and Management, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia*

[2] *School of Social Sciences, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia*

[3] *Big Island Research Pty Ltd, 41 Cliff Street, Fremantle WA 6160, Australia*

[4] *School of Culture, History & Language, The Australian National University, Canberra ACT 2600, Australia*

[5] *UWA Oceans Institute, The University of Western Australia, 35 Stirling Highway, Crawley WA 6009, Australia*

[*] *Corresponding author: ✉ joe.dortch@uwa.edu.au*

## Abstract

Australia was first colonised more than two thousand human generations ago. In this paper we show how, over this period, ancestors of Western Australia's Aboriginal peoples adapted to changing environments, in tropical savannahs, deserts, woodlands, forests and coastlines. Throughout this history, there is evidence for intra-regional genetic and economic continuities, and exchanges and dynamism in religion, language and art. These relationships are remarkably well-documented in Western Australia, which features many of the oldest sites on the continent. The evidence reviewed here derives from the Kimberley, Western Desert, Pilbara and South West. Each region contains at least one site first occupied c. 50 000 years ago, and numerous other sites first occupied in the late Pleistocene. We describe the archaeological evidence for the early development of a range of complex modern behaviour from each region, including symbolic behaviour, information exchange, ground-stone technology, and ecosystem engineering. We also address the apparent tension between regional continuity and inter-regional contact and exchange.

**Keywords: Archaeology, Late Pleistocene, Holocene, Western Australia, Aboriginal people**

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## INTRODUCTION

Archaeological research across Western Australia demonstrates Aboriginal people have occupied all of the State's diverse biomes, spanning tropical, desert and temperate regions, for more than 50 000 years (Turney *et al.* 2001; Morse *et al.* 2014; Veth *et al.* 2017; Balme *et al.* 2018b; McDonald *et al.* 2018a). This remarkable coverage has implications for the timing of human dispersal across the world and the processes by which humans settled and managed new environments, including their social interactions across vast landscapes (Veth *et al.* 2011). The evidence for these achievements in Western Australia includes symbolic behaviours which have parallels in contemporary societies, including personal ornamentation, rock art, and long distance movement of exotic items (marine shell), and indicates the development of regional differentiation and identity persisting for much of the period of human occupation (Dortch 1979; Morse 1993a; Morse *et al.* 2014; O'Connor *et al.* 1998; McDonald *et al.* 2018a; Balme & O'Connor 2018; Balme *et al.* 2018, 2019). Genographic research supports the inference that distinct but interconnected regional populations emerged early in the history of the first Australians (Malaspinas *et al.* 2016). In this review, we aim to show that these regional signatures relate to negotiation of wide-spread, complex exchanges between autonomous groups who maintained long-distance connections at the same time as affirming strong affiliations to territory: a combination that was essential to the considerable achievement of occupying so many challenging terrains for this period.

As a global counterpoint to the dispersal of anatomically modern humans out of Africa, Western Australia provides a unique sampling point for adaptations of people to both familiar and unique landscapes (Veth *et al.* 2017). Evidence of long occupation from north to south of the State confirms the long-held view that ancestral Aboriginal peoples successfully crossed and settled a series of widely differing environments and adapted to endemic regional biodiversity on the way. At present, the wider Australian evidence does not support a preference for any of the possible colonising routes through various parts of the Indonesian–Malaysian archipelago (Bird *et al.* 2018). Nor does the evidence allow identification of the colonisation pathways within Australia. However, the oldest sites in each region of Western Australia appear to have been first occupied at about the same time, c. 50 000 years ago (50 ka), across almost 20 degrees of latitude, and from desert to coast, suggesting that whatever the pathways, colonisation was rapid and highly flexible.

The "colonising" narrative contrasts with most Aboriginal traditions of Indigenous origins, but there is common ground. Although the knowledge base differs, both scientific and traditional interpretations agree on the longevity of both cultural connections to landscapes

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**Figure 1.** Selected regions in Western Australia—southern Kimberley, North West (with sub-regions), Western Desert, South West—and archaeological sites mentioned in the text.

and changes in Aboriginal cultures within Australia. However, the nature of the archaeological record limits our present discussion to technological innovations, symbolic communication (including art, ornamentation and the materials used), and use of the environment for resources. We discuss these different lines of evidence under headings for each of four biogeographic zones reviewed here: Southern Kimberley; North West (divided into three sub-regions); Western Desert; and South West (Figure 1). These regions collectively cover more than 50% of Western Australia. They have been subject to archaeological investigation for some decades, but particularly in the last five years with several on-going projects—hence the present review.

## SOUTHERN KIMBERLEY

The traditional lands of Bunuba and Gooniyandi people are in the southern Kimberley of Western Australia. In the monsoonal tropics, the area is not as influenced by the moist monsoonal belt as the northern part of the Kimberley (Bureau of Meteorology 1996). The main topographic features in the southern part of this region are limestone ranges, including the Oscar, Napier, Emanuel and Lawford Ranges, which are relicts of a Devonian reef (Playford *et al.* 2009). In these reef systems caves and rockshelters have formed and preserve evidence, including hearths, artefacts and plant and animal remains, of Aboriginal people's use of the area for about 50 000 years (Balme *et al.* 2019).

Abundant evidence, including rock art, open campsites, stone quarries, and landscape features with religious significance, documents diversity in the long-term use of the area. This evidence provides a story of innovation, landscape learning, flexible use of a sometimes-difficult environments and, over time, the importance of wide social networks in people's lives. The earliest such evidence in the region comes from Carpenter's Gap 1 (CG1) in the Napier Range dating to between 51 and 45 ka (51 000 to 45 000 years; Maloney *et al.* 2018; Figure 2A) and Riwi, in the Lawford Range, with first occupation dating to between 46.4 and 44.6 ka (Wood *et al.* 2016; Figures 1, 2B). CG1 is less than two kilometres from the Lennard River and about eight from Windjana Gorge, which today usually maintains pools of water even in the dry season. Riwi is further south and closer to the desert boundary. At Riwi there is no permanent source of freshwater, but a small creek runs in front of the cave during the wet season.

At the time of first human occupation of these two sites, the climate was more humid than today (Fitzsimmons *et al.* 2013) and favourable for human occupation. People used these sites opportunistically, exploiting animals from the surrounding savannah on the rocky hill slopes and sand plains, and at CG1, from freshwater sources. Fruits and seeds from trees growing in monsoonal rainforest pockets in seasonal gullies in the limestone were particularly targeted for plant foods (Balme *et al.* 2019; Maloney *et al.* 2018). More fragile artefacts such as those made of fibre or other organic materials are not preserved in the oldest sediments but the presence of ochre fragments and, at CG1, a slab of painted rock at 40 000 years ago (O'Connor & Fankhauser 2001) indicates early symbolic activities.

Of particular note is the presence of a flake from an edge-ground axe found at CG1 associated with dates of 49–44 ka (Hiscock *et al.* 2016; Figure 2C). Evidence for edge-ground axe use is found in the oldest deposits of several other sites across northern Australia (e.g. Madjedbebe, on the edge of the Arnhem Land Plateau in the Northern Territory, where they are found in contexts older than 50 ka; Clarkson *et al.* 2017) but is not found in the southern two thirds of the continent, or indeed anywhere else in the world apart from Japan (Takashi 2012), until the Holocene (Balme & O'Connor 2014). Their consistent presence in the deepest layers of Pleistocene sites of northern Australia suggests their role as a colonising technology, perhaps for use on what would have initially been hardwood savannah trees. The restricted distribution suggests the existence of social links or cultural adaptations across northern Australia that did not penetrate to the south.

Between the earliest phases of occupation at these two sites and the Last Glacial Maximum (LGM, c. 22–18 ka), evidence for occupation is sporadic at both CG1 and Riwi (Maloney *at al.* 2018; Balme *et al.* 2019). There is little evidence of changing lifestyles during this period with people continuing to procure food primarily on the sand plain and in the rocky ranges at both sites with plants from monsoon rainforest pockets continuing to be economically important (Balme *et al.* 2019; Maloney *et al.* 2018). Considering the position of the sites on the edge of the present arid zone, we had expected that like many arid-zone sites (e.g. Morse 1988; O'Connor *et al.* 1999; Przywolnik 2005; Veth *et al.* 2014, 2017), evidence of occupation of sites in the southern Kimberley would be much reduced during the LGM, a period of reduced precipitation across Australia. However, this is not the case at either site. At CG1, the evidence suggests that people made greater use of freshwater sources, including fish and shellfish during the LGM (Maloney *et al.* 2018). Sponge spicules, sedges and diatoms increase in abundance at CG1 during the LGM (McConnell & O'Connor 1997; Wallis 2001) suggesting that, while resources on the plains may have been reduced, at least at times, water was available in the nearby river and gorge system. This suggestion is supported by the interpretation by Denniston *et al.* (2013) of a speleothem record from Ball Gown Cave, near Carpenter's Gap, indicating an active monsoon across the western Kimberley during the LGM between 24 and 22 ka. The same observations may also explain the strong record of occupation at Riwi during the LGM, despite the lack of permanent freshwater (Balme *et al.* 2019). These findings not only highlight the variation in LGM in different parts of Australia but are also consistent with opportunistic use of the landscape during periods of climate change.

During the Holocene, there is an increase in occupation intensity mainly indicated by the greater quantities of archaeological materials discarded at both sites. In this period, there is better preservation of organic materials, such as wood shavings and fibre (Balme *et al.* 2019; Maloney *et al.* 2018), illustrating the variety of technologies used by the sites' occupants. There is also evidence of more systematic use of the area, indicating better knowledge of the landscape. For example, amongst the higher number of re-touched stone tools at both sites is a greater selection of high-quality exotic stone for tool making, especially at CG1 (Maloney *et al.* 2018).

Landscape knowledge is supported by evidence for wider social networks. This is particularly demonstrated by the presence of 55 beads made from scaphopod shellfish recovered from levels dated at 9–2 ka from all five sites excavated in this area (Balme & O'Connor 2018; Balme *et al.* 2018; Figure 2D). Although isolated fragments of marine shells have been found in Pleistocene deposits at north-western sites 100–200 km from the coast at the time of the beads' deposition, the consistent presence of beads manufactured from a single species at sites up to 500 km from their original source at this time, suggests long-distance social networks were well established by the early Holocene.

At about 1 ka, the distinctive leaf-shaped, bifacial, pressure flaked Kimberley points appear in the archaeological record (Maloney *et al.* 2014) and continued to be made up to the present. Although the presence or absence of serrations along their edge can vary, the manufacture of these artefacts prior to the arrival of Europeans was confined to the Kimberley, suggesting a Kimberley cultural identity within which were several language groups (McGregor 1988) and other cultural alliances as represented in differences in rock art motifs (e.g. Layton 1992; Taçon *et al.* 2003; O'Connor *et al.* 2013; Akerman 2016) across the region.

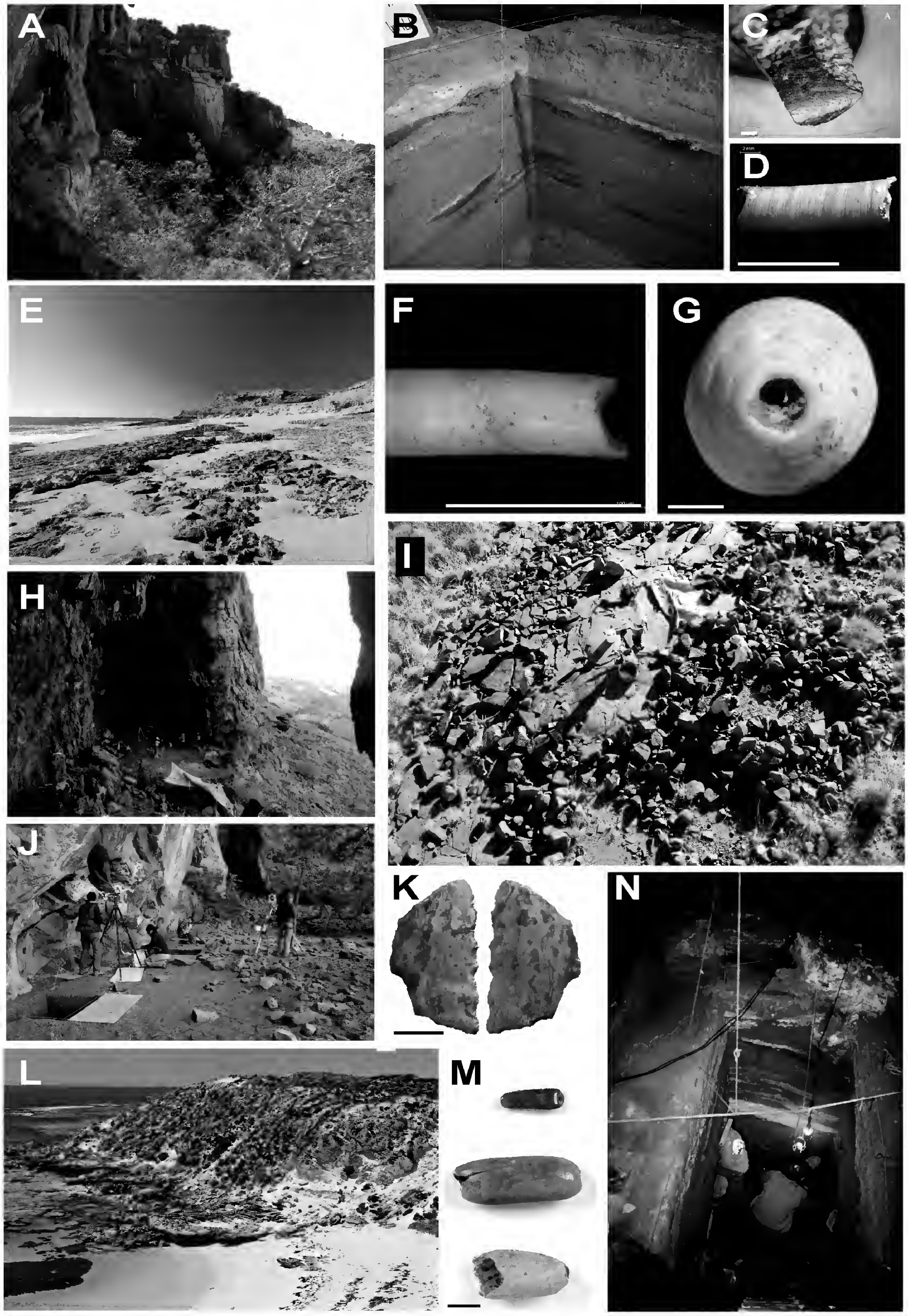

**Figure 2.** Selected sites and artefacts mentioned in the text: A. Carpenter's Gap, Southern Kimberley, B. Flake from an edge-ground axe at Carpenter's Gap (Hiscock *et al.* 2016), C. Hearths revealed in excavation walls at Riwi, dating from c. 47 ka to 6 ka, D. Scaphopod bead dated to the Holocene from Riwi, E. View of the cliffs containing Boodie Cave on Barrow Island, F. Scaphopod bead dated >10 ka from Boodie Cave, G. Shell bead dated c. 34 ka from Mandu Mandu Creek rockshelter, Cape Range (Morse 1993b), H. Excavations at Yurlu Kankala, Gorge Range, northeastern Pilbara (Morse *et al.* 2014), I. Stone circles interpreted as hut bases in the Dampier Archipelago, dated c. 8 ka (McDonald & Berry 2017), J. Excavations at Karnatukul, Western Desert (McDonald *et al.* 2018b), K. Backed artefact dated >40 ka, from Karnatukul, L. Calcarenite formations overlying palaeo-sol containing artefacts, dated c. 27 ka at Rottnest Island (Dortch & Dortch 2019), M. Beads made on macropod fibulae from Devil's Lair (photo: A. Carson), and N. Hearths dating from 21–13 ka revealed in excavation walls at Tunnel Cave. Scale bars for artefact images are 5 mm.

## NORTH WEST—COAST AND CONTINENTAL SHELF

There is little doubt that the island-foraging settlers dispersing through Wallacea and into Australia had well-developed maritime economies and technologies and were adept at exploiting marine resources backing onto sub-tropical hinterlands. Less known were the 'maritime deserts' south of the Kimberley, where highly productive coastal resource areas were backed by arid rangelands comprising spinifex plains, ancient limestone pavements, dune fields and piedmont uplands. This scenario describes a large part of the State's current littoral zone. At the time Australia was colonised, c. 65–55 ka (Clarkson *et al.* 2017), the expansive coastal plains of the North West Shelf extended over 100 km from the current coastline to as little as 12 km from the steeply dipping shelf off North West Cape (Morse 1993a). This unique coastal configuration provides a rare opportunity to investigate early and ongoing marine adaptations by Aboriginal people in the first 50 ka of coastal occupation of the north (Veth *et al.* 2017; cf. Brooke *et al.* 2017; Morse 1988).

The main study sites of Barrow Island and the Montebello Islands on the North West Shelf lie in the northern Carnarvon bioregion (Figure 1; Moro & Lagdon 2013; Veth *et al.* 2014). The limestone islands provide shelters and caves with excellent preservation for archaeological assemblages (Veth *et al.* 2007). The climate is arid with 300 mm of variable summer and winter rainfall (Kendrick & Mau 2002). Boodie Cave, on the north-western coast of Barrow Island, is optimally positioned near the edge of the Australian continental shelf to infer past use of the drowned coastal plains. The exceptional preservation offered by caves and shelters in limestone substrate has provided a range of significant finds from rockshelter sites on Cape Range and Barrow and Montebello Islands:

a) Some of the earliest evidence for consumption of dietary shellfish outside of Africa (coeval with Borneo and Timor Leste);

b) Early evidence for a mixed coastal and arid plains fauna as a maritime desert adaptation;

c) Transport of dietary and utilitarian shellfish species c 15 km over the emergent continental shelf;

d) Pleistocene shell beads from personal adornment (e.g. hair, head, wrist or ankle ornaments) and manufactured shell tools (at both Boodie Cave and Mandu Mandu Creek rockshelter; Morse 1993b; Figures 2E–G);

e) Ongoing use of marine species from before and after the LGM; and

f) Marine and terrestrial species increasing significantly with proximity of the sea.

Boodie Cave (Figure 2E) registers first human occupation between 51.1 and 46.2 ka, consistent with the majority of other early dated assemblages across northern Australia (Clarkson *et al.* 2017; Veth *et al.* 2017). The cave has evidence for repeated occupation, with a discontinuity straddling the LGM, and then abandonment by 6.8 ka when the island becomes separated from the mainland (Veth *et al.* 2017). This abandonment coincides with that for the nearby Montebello Islands (first occupied at c. 30 ka) and is a likely function of distance offshore and the diminished carrying capacity of the islands (Veth *et al.* 2007).

By 42 ka coastal foragers collected and transported four taxa of shellfish from mangrove, mudflat and rocky substrates up to 15 km over the coastal plain (Veth *et al.* 2017). Whereas three (*Terebralia, Tellina* and *Nerita*) are dietary, the fourth taxon (*Melo* sp.) is a common robust much larger gastropod used for water carrying, ornamentation and shell artefact production (Balme & Morse 2006). *Nerita, Tellina* and *Terebralia* could have been safely transported in wet clumps for later consumption at Boodie Cave (Veth *et al.* 2017).

Boodie Cave also contains many modified shell fragments including dentate pieces likely to have been used for marine mammal butchering, chisels and polished edge scrapers. The presence of shell tools is expected given the lack of hard rocks in the vicinity. Twenty-two fragments of Tusk shell (scaphopod) with consistent wear patterns probably served as personal ornaments such as beads in a necklace (Figure 2F). These beads are directly dated as > c. 10 ka.

Prior to the LGM, the terrestrial fauna from Boodie Cave was dominated by arid zone species, including the spectacled hare wallaby (*Lagorchestes conspicillatus*) and euro (*Macropus robustus*), which may have been speared and consumed by small hunting parties (Veth *et al.* 2017). With rising sea levels and a closer coastline, the post-LGM diet expanded significantly to include 40 molluscan and 13 terrestrial species. The latter comprise largely small-to-medium game consistent with foraging by family groups. Early Holocene assemblages are rich and contain marine faunal remains including fish, turtle, marine mammal, crocodile, crab and sea urchin. A similar, though more recent, history is well documented at rockshelter sites on the western coastal margin of the North West Cape (Morse 1993a,b; Pryzwolnik 2005).

### Productivity of the coastal zone before current sea levels

The early dietary shellfish assemblages from Boodie Cave, and recent cores capturing estuarine shellfish at the LGM within the present Bonaparte Gulf (Ishiwa *et al.* 2016) increasingly lend support to models for productive coastal zones during times of sea level change (Ward *et al.* 2015). The prevalence of the estuarine gastropod *Terebralia* in these assemblages, dating from 42.5 ka until the abandonment of Barrow Island, indicates utilisation of mangrove habitats. The early appearance of dietary shellfish in the Boodie Cave assemblages and their presence until abandonment of the island supports our modelling for continuing productivity of the Pleistocene coastline for coastal foragers (d'Alpoim Guedes *et al.* 2016; Manne and Veth 2015; Ward *et al.* 2015).

Recent analysis from John Wayne Country Rockshelter (JWCR), a perched shelter several kilometres from Boodie Cave (Ditchfield *et al.* 2018), also shows that during the Pleistocene mangrove resources were available and transported up to 10 km inland, becoming especially abundant during the 'Big Swamp' phase of the early Holocene. These patterns accord well with the nearby

Barrow Island sites and a suite of rockshelter and open sites analysed on Cape Range to the South West (e.g. Morse 1993a, b, 1999) and from the Pilbara maritime provinces to the east (e.g. McDonald & Berry 2017). At JWCR crustaceans and marine molluscs from mangrove habitats were most intensively discarded between 10 759 ± 880 to 8588 ± 1227 cal. Before Present (BP; Demuro *et al.* 2019). This age range is earlier than many sites on Cape Range (Morse 1999; Veth *et al.* 2014) but overlaps with dates for the Dampier Archipelago (McDonald & Berry 2017). At the regional level this demonstrates that Aboriginal people exploited productive mangrove ecosystems as sea levels rose towards Barrow Island and beyond. These data do not support notions that rapid sea level rise (including melt-water pulse events) significantly diminished marine productivity (O'Connell & Allen 2012). When combined with earlier coastal assemblages from the region (e.g. Morse 1999; Przywolnik 2005; Veth *et al.* 2017), we conclude that the JWCR record represents a continuation of a much older coastal economy which integrated marine resources from Pleistocene coastlines with those from the arid coastal plains on the now drowned continental shelf.

These findings allow us to entertain new levels of maritime capabilities for modern humans dispersing along the southern arc from Africa, through southern Asia across the islands of Wallacea to Australia (Bird *et al.* 2018; Norman *et al.* 2017). The presence of dietary shellfish from the earliest occupation units of Boodie Cave, and from karstic sites to the north including East Timor and Borneo (Barker 2013; O'Connor *et al.* 2011) provide irrefutable evidence for maritime competencies at the end of the Southern Dispersal Route (Kealy *et al.* 2016). Remarkably the early colonists of the now-submerged shelf of Greater Australia did not turn their back on the sea or remain coastally tethered, but instead rapidly adapted to the marsupial fauna and arid zone plants of the extensive maritime deserts of north-west Australia.

## NORTH WEST—DAMPIER ARCHIPELAGO

The Dampier Archipelago now generally known as Murujuga is a significant rock art province in north-western Australia that documents the Pleistocene–Holocene arid-maritime transition in the cultural landscape (McDonald & Veth 2009). This archipelago of 42 islands has only existed since the mid-Holocene, when the sea rose to its current height. The highly weathered rock art depicts extinct fauna and early styles suggest that occupation and rock art production here was for the same 50 ka period as across the North West Shelf and Pilbara generally. The region today is within the jusistriction of Murujuga Aboriginal Corporation who co-manage the Murjuga National Park on behalf of the Ngarluma Yinddarbarndi, the Yaburara Mardudhunera and Wong-gg-tt-tto peoples.

Mulvaney's (2015) seven-phase art sequence predicts that art was produced at Murujuga from the earliest occupation of the region, and a model for Murujuga art production and occupation indices suggests these different art phases may be correlated with broad environmental events (McDonald 2015). The highly resistant weathering properties of the Dampier Archipelago's geology (Pillans & Fifield 2013), provides a durable canvas for the range of symbolic and social behaviours also being practised across this north-western coastal plain. The estimated one million petroglyphs of the Dampier Archipelago include many thousands of motifs that are highly weathered and include locally extinct fauna (McDonald & Veth 2009). The transition through various styles of production from terrestrial to fresher maritime themes records the change from inland desert range to maritime coastline due to rising sea levels.

Murujuga Rockshelter (MR1) on the Burrup Peninsula offers the oldest evidence for occupation of the then "Murujuga Ranges" (McDonald *et al.* 2018a). The earliest evidence for occupation of this site is dated to the LGM when this range lay over 160 km inland and probably served as one of several Pilbara refugia. In the terminal Pleistocene – early Holocene, likely in tandem with the last stages of sea level rise, the proportion of artefacts manufactured on exotic lithologies declined sharply. We infer a changed foraging range and reduced group territory sizes due to increased demographic packing as the coastline advanced over former territories. Abandonment of MR1 by 7 ka may haved resulted from a changing focus to the resources of the increasingly proximal coastline. This site shows how Aboriginal people adapted their Pleistocene procurement strategies in response to significant environmental and landscape changes in Murujuga.

A *Terebralia* midden excavated at Wadjuru Pool on Rosemary Island demonstrates again the exploitation of the extensive mangrove forest resources in the early Holocene (Bradshaw 1995; McDonald & Berry 2017). Ongoing work across the archipelago indicates that this occupation was part of a complex set of human behaviours which included art production and stone structure construction at the end Pleistocene – Early Holocene transition (Figure 2I). At both Boodie Cave and Wadjuru Pool people engaged in broad-spectrum, energy-intensive activities long before the mid-Holocene.

Mangrove habitats and hence species abundance in the North West appear to have declined around 4000 years ago and shell middens reveal that people switched their economic focus to a range of rocky shore, mudflat and sandy beach shellfish (Lorblanchet 1992; Clune & Harrison 2009). This switch is best exemplified by the change of focus from *Terebralia* species to *Anadara granosa*. On the inner island of the Dampier Archipelago, some *Anadara* mounds up to five metres high and >300 m long are as-yet unexcavated but on the basis of sea level history presumably are no older than the mid-Holocene. Most Burrup shell middens indicate mid- to late Holocene exploitation of a range of resources, including land animals such as euro (*Macropus robustus*), rock wallaby (*Petrogale rothschildi*), flying fox (*Pteropus alecto*) and quoll (*Dasyurus hallucatus*), and an extensive range of marine fauna including fish, dugong (*Dugong dugon*), turtles, crabs and birds (Lorblanchet 1992; Vinnicombe 1986).

The sundering of islands off the Australian coast often resulted in their abandonment by people for many millennia (e.g. O'Connor 1999). The outer islands of Murujuga—located 20 km offshore—are potentially distant enough to have made long-term occupation difficult. Rosemary and Enderby Islands, on the outer rim of the archipelago, were cut off by continued rising sea levels by c. 7 ka (Lewis *et al.* 2013). These islands provide an opportunity to explore early Holocene island use and art production—unlike Barrow and the Montebello Islands, where no art has been found. The distance between Rosemary and Enderby Islands and their nearest landfall in the Dampier Archipelago (5 and 3 km, respectively) is minor compared with the c. 50 km to Barrow Island from the current coast. Current systematic survey recording and dating demonstrates a complex signature of symbolic behaviour and archaeological evidence on these outer islands during the Holocene and perhaps only a small hiatus in outer island use.

## NORTH WEST—INLAND PILBARA

Covering some 500 000 km$^2$ from Barrow Island near the western edge of the continental shelf across some 64 km of Indian Ocean to the remarkable rocky peninsula of Murujuga, the ancient and diverse Pilbara landscape continues inland through vast spinifex plains cut by seasonally flooding river systems and a plateau and escarpment geography of steep ironstone ranges to the borders of the Western Desert. There are now over 20 published Pleistocene archaeological sites in the Pilbara (Morse *et al.* 2014; Marsh *et al.*2018; McDonald *et al.* 2018a; Slack *et al.* 2017) with other sites known but as yet unpublished (Morse 2009).

The Aboriginal history of the Pilbara is best known in pockets of land investigated in response to mining exploration. Concentrated largely in the rich ironstone Hamersley Range (Morse & White 2009; Slack *et al.* 2018) these sites, excavated rockshelters and caves tell us much about early human occupation and adaptation to an arid and changing landscape. Unlike many other sites discussed here, the typically ironstone-rich acidic sediments of rockshelter sites rarely preserve the organic material that helps our understandings of cultural life or symbolic behaviour. Stone artefacts dominate the archaeological landscape of the Pilbara. Surface stone artefact scatters range from small discrete single flaking events to sites with hundreds of thousands of artefacts extending over tens of hectares. Many sites include quarries, grinding patches, stone arrangements and engraved rock art. All of these contribute much of what we know about how and where Aboriginal people lived, and what they were doing.

Deep in spinifex and ironstone country some 380 km east of Boodie Cave and 100 km south of the modern shoreline, Yurlu Kankala tells the story of early human occupation of this arid inland landscape from 45 ka to middle Holocene times (Morse *et al.* 2014; Reynen *et al.* 2018). The occupation of this site is further testament to the remarkable adaptive capacities of the first Australians and is significant in creating a narrative of adaptation to changing physical and social landscapes before, during and after the last glacial maximum.

Yurlu Kankala is situated on Njamal traditional land. Facing west-northwest, this 280 m$^2$ rockshelter near the top of the Gorge Range (Figure 2H) commands panoramic views over the surrounding spinifex plains. The area is well watered with a large permanent freshwater pool 500 m to the southwest and other perennial waterholes within three kilometres. Excavated in 2013 (Morse *et al.* 2014) and again in 2014 (Reynen *et al.* 2018), Yurlu Kankala provides a chronological sequence spanning 45 000 years and demonstrates that the occupants of this inland site adapted well to the changing Pilbara landscape. Stone artefacts, hearths, faunal remains, ochre and charcoal throughout the Yurlu Kankala sequence significantly demonstrate continued occupation during the LGM. Grinding material on the site's surface suggests the recent presence of family groups. Six hearths dated between 24 and 18 ka are all associated with stone artefacts and highly fragmented faunal material, predominantly euro, rock wallaby and bandicoot. A small proportion of the bone material is burnt (16.6%) but no evidence of butchering was identified. Stone artefacts throughout the deposit are made on locally abundant raw material, predominately quartz and comprise easily-produced informal, multi-purpose tools. Artefact discard rates peak between 24–23 and 17.6 ka and an increase in the types of tool-stone brought to the cave suggests that it was during this LGM period that the cave was occupied more frequently, or by larger groups of people (Reynen *et al.* 2018).

Unlike the LGM layers where discrete single-use hearths are clearly visible, the post LGM deposit (10–17 ka) is characterised by a high proportion of charcoal and ash and reduced geogenic sedimentation. Although the post-LGM stratigraphic record indicates continued human activity with trampling, fire maintenance, the building of new fires and consequent disturbance and cleaning out of existing hearths, the near absence of stone artefacts in this part of the deposit is surprising. Such a change in the pattern of excavated material suggests that at this time use of the site changed—perhaps as visitors came to undertake short-term task-specific activities that did not require stone tools. Wooden and other organic technologies were among the most adaptive and creative Aboriginal responses to the Australian landscape (Balme & O'Connor 2014), but the acidic deposits of Pilbara rockshelters preserve very little organic material. Yurlu Kankala is no exception and in the context of Pilbara archaeology, the near absence of stone artefacts, with an increased number of hearths in post-LGM Yurlu Kankala deposits, suggests that perhaps people living around the waterholes on the plains close to the rockshelter, armed with a tool kit of perishable materials, such as wooden dishes, spinifex string and other organic technology, were visiting the site to cook or prepare food or make artefacts such as string nets or baskets (Reynen *et al.* 2018).

Recently published data from Waturi Jurnti, a cavernous rockshelter some 130 km north-east of Yurlu Kankala in the Cundaline Ridge (Marsh *et al.* 2018), a resource-poor northern Pilbara upland, adds another Pleistocene site to the ever-expanding Pilbara story. First occupied at 45–42 ka, this site provides evidence of continued, albeit occasional or intermittent occupation associated with modifications of stone technology and resource use through the LGM and again in the late

Holocene. Like Yurlu Kankala, organic material at the site is rare and the most recent period of occupation—within the last 1300 years—contains the richest archaeological assemblage. A piece of string made from 'native [plant] fibre' was recovered from the most recent part of the deposit, as well as a fragment of baler shell on the floor surface (Marsh *et al.* 2018). This shell material indicates contact between the site's most recent occupants and the coast some 70 km away. The presence of small pieces of paperback (*Melaleuca* sp.) in Pleistocene layers at this site is also significant. Paperbark is a multi-purpose resource used by Aboriginal people to wrap food into bundles, to make water carriers, as bedding, to swaddle babies, bandages and as medicine (Isaacs 2002). Its repeated occurrence in Waturi Jurnti not only at the time of initial occupation but also in layers dating 31 and 28 ka provides a glimpse of a range of sophisticated behaviours being undertaken by the first Australians, including tasks traditionally associated with women.

The ever-present stone artefacts discarded on surface sites and found in archaeological deposits are key to the Pilbara narrative of small, highly skilled groups of people utilising a wide array of tool-stone, plant and animal resources as they negotiated changing and challenging landscapes and environments. The common presence of grindstone patches and 'grinding grounds' sometimes surrounded by extensive panels of engraved art on outcropping granite across many parts of the Pilbara demonstrates the range of technologies—including organic (e.g. spinifex fibre, seed grinding) and inorganic (stone tool sharpening) used by both women and men (Fullagar *et al* 2017; Hayes 2016; Reynen & Morse 2016). Their perseverance through perhaps the single greatest challenge of all, the Last Glacial Maximum, demonstrates the skilful adaptability of Pilbara Aboriginal people, not just in terms of resource use but in the continued use of critical long-distance social networks (cf. McDonald & Veth 2013a) which connected widely spread and continually moving groups of people. Together, these sites tell us much about the rich cultural lifeways of highly mobile hunter-gatherers, a tradition that continues in the Pilbara today in stories and histories told, and knowledge shared by many Traditional Owner groups.

## WESTERN DESERT

The Western Desert (WD) lies inland of the Pilbara uplands and to the south of the Kimberley. This vast and arid lowland comprises a series of sandy and stony deserts (Veth 1993) covering an enormous proportion of Western Australia. Drainage is internal and fragmented. Amongst the extensive dune fields are numerous subdued ranges, many of which contain permanent water. Although this was one of the last environments to be exploited by Europeans on this continent, archaeological evidence demonstrates that Aboriginal people were inhabiting even this most marginal of landscapes from around 50 ka. Work over the last 30 years with the Martu and Birriliburru custodians of this part of the Western Desert has continued to improve understanding how Australian desert people have used these arid landscapes, uncovering a rich record of evidence for occupation and symbolic behaviour through 50 ka (McDonald 2005; Veth *et al.* 2009; McDonald & Veth 2013a, table 1; McDonald *et al.* 2018b)—as well as uncovering the interplay between rock art and the *Jukurrpa* (the Dreaming) of those hunter-gatherer peoples who are amongst the last groups to come into contact with settler societies (McDonald & Veth 2013b).

Serpent's Glen rockshelter, known as Karnatukul to its traditional custodians, is in the Carnarvon Ranges (Katjarra). This rockshelter was the first Pleistocene site identified in the Western Desert (O'Connor *et al.* 1998). Recent excavation (McDonald *et al.* 2018b, 2018c; Figure 2J) has refined the previous occupation sequence and identified earliest occupation from around 50 ka: an LGM occupation signal; a Late Pleistocene–Holocene transition; and a Holocene sequence with defined occupation pulses during the last millennium. The stone artefacts at Karnatukul (Figure 2K) represent a long-term record of artefact use, transport and discard. The site also has a complex painted assemblage, direct-dating of which (McDonald *et al.* 2014) demonstrates that the most recent use of this shelter was as a homebase with industrial quanitites of stone tool and wood-working, as well as the extensive decoration of the walls using a local style of pigment art.

The Karnatukul pre-glacial Pleistocene assemblage shows an early preference for high-quality chert that is not found near the site (McDonald *et al.* 2018b). The oldest assemblage includes a retouched ironstone scraper and a backed chert artefact. These hafted artefacts signify early experimentation in this specialised technology in Australia by highly mobile foragers (McDonald *et al.* 2018c).

Artefact discard rates increase slightly during the glacial and terminal Pleistocene period and indicate continued, episodic site visits by highly residentially-mobile groups (McDonald *et al.* 2018b). This is significant, as no LGM dates had been found in the Western Desert before this excavation. The earliest of two distinct pulses of artefact discard during the Holocene is marked by an increase in assemblage diversity, in the mid-Holocene. Grinding technologies appear in the sequence for the first time, demonstrating a variety of animal, plant and seed processing. The toolkit carried by people visiting Karnatukul at this time appears to be designed for a more generalised rather than a specialised subsistence economy.

Occupation during the last millennium at Karnatukul reflects a regional shift in settlement patterns. Artefact discard rates increased substantially. Chert micro-debitage dominates the assemblage, signalling the technological change to specialised tula and backed artefact production. On-site manufacture, maintenance and discard of backed artefacts took place at Karnatukul.

Many aspects of the Karnatukul assemblage resonate with broader regional patterns found across arid inland Australia during the late Holocene. Increased intensity of site occupation, a preference for high-quality stone and increasing conservation strategies are key trends seen at other Western Desert sites. Other WD sites (e.g. Bush Turkey 3, Veth *et al.* 2008; and Kaalpi, Veth *et al.* 2001) show increased residential mobility and logistical provisioning during the last millennia. Karnatukul shows not only a marked increase in use of this locale, but its transition from a satellite site visited episodically, to a more regularly visited and territorially tethered 'home-base' where intensive reduction and tool manufacture took place, and art production similarly showed people's attachment to this place. Western Desert sites demonstrate considerable variability in individual site histories, affirming greater complexity in the use of the arid landscape than previously recognised.

## SOUTH WEST AUSTRALIA

Contrasting with adjoining semi-arid regions and desert further north, the southwestern corner of the continent has a Mediterranean climate: cool, wet winters and warm dry summers, with rainfall increasing southward and westward. The highest rainfall areas (800–1400 mm) are covered by mosaics of wet and dry sclerophyll forest, woodland, heath and wetlands. Devils Lair in the midst of this biodiversity was one of the first sites in Australia to provide evidence of human occupation by 45 ka (Turney *et al.* 2001), and remains one of the country's most important sites for its wealth of stratigraphic, palaeontological and zooarchaeological detail (Balme 2014). The site is emblematic of the archaeological potential of limestone sites along the Western Australian coast.

The region between Capes Leeuwin and Naturaliste (Leeuwin–Naturaliste Region, or LNR) in the extreme southwest is particularly rich, providing evidence for Aboriginal occupation in five caves, including Devils Lair (Balme *et al.* 1978; Dortch 1979; Dortch *et al.* 2014). Tunnel Cave also features hearths and dense archaeological remains deposited over several main occupation episodes between 26 and 8 ka (Figure 2N). Archaeological materials at all cave sites include artefacts made of quartz and fossiliferous chert (sources of this rock appear to have been rendered inaccessible by post-glacial sea levels rise: O'Leary *et al.* 2017; Dortch & Dortch 2019); ochre fragments; emu eggshell fragments; and worked bone, including points at several sites, and three bone beads (Figure 2M) from Devils Lair (Dortch 1979).

Beyond the capes region, Yellabidde Cave, in the Northern Swan Coastal Plain, provides evidence for Pleistocene occupation, with artefacts dated at 28 ka (Monks *et al.* 2016). Another five limestone sites north and south of the LNR were occupied in the last 2–1 ka, a period featuring substantial increases in occupation episodes at open sites as well (Dortch 2004). Despite possible biases due to better preservation of younger material, the possibility of a late Holocene population rise is an important question here (Balme 2014).

Human occupation at Devils Lair is dated from 48 to 12 ka and spans several episodes when the cave entrance closed and then re-opened (Dortch 2004). The lack of archaeological evidence in the three metres of deposit accumulated before 48 ka has been taken to indicate that people first arrived in the region at 48 ka, which following more recent dating work would now be well after the first arrival of humans in Australia (Clarkson *et al.* 2017). This regional interpretation requires much more support, given that Devils Lair provides the only record in the region at this time. Also, the nature of the evidence is complex: the oldest evidence for occupation within the site, as opposed to the re-working of ancient artefacts into levels dated 48 ka, derives from a somewhat younger hearth, at c. 45 ka.

The rich vertebrate remains from the Pleistocene cave sites record environments of the LGM, when sea level was 130 m lower than today and there was an extensive coastal plain west of the present coastline. Analyses of faunal remains and charcoal derived from nearby canopy trees reveal an arid-adapted fauna and woodland/open-forest at this time, changing to closed habitats and karri (*Eucalyptus diversicolor*) from c. 11 000 years ago (Balme 2014; Dortch & Wright 2010; Faith *et al.* 2017). Given land management practices richly recorded in oral and written history (Hallam 2014; Lullfitz *et al.* 2017), these climatic fluctuations over tens of millennia of occupation probably involved changes in land management by Aboriginal populations.

Besides the iconic cave sites, some hundreds of open-air sites have been reported. Although relatively few have been excavated, the dated open-air deposits attest to diverse economic and social behaviours associated with environmental features such as wetlands and coastal woodlands (Dortch & Dortch 2019). Pleistocene archaeological deposits are recorded at Perth (Upper Swan, Helena River, Fiona Stanley Hospital, Rottnest Island (Figure 2L), Minim Cove, Perth Airport; Dortch & Dortch 2019; Pearce & Barbetti 1981; Schwede 1990); in the LNR (Quininup Brook, Dunsborough, Arumvale, Ellenbrook: Dortch 2004); and on the south coast Kalgan Hall (Ferguson 1985) and Cheetup (Smith 1993). Lacking organic remains, the open sites' chief archaeological value is providing stone artefacts in datable contexts indicating the positioning by populations relative to resource zones, generally consistent with historic landscape-use patterns (Dortch & Dortch 2019). The largest and most complex of the Pleistocene open-air sites—at Perth Airport, Helena River, Dunsborough, Kalgan Hall—are near permanent swamps, wetlands or river crossings, places that continued to be used in late Holocene and historic times (cf. Hallam 1987).

The Holocene record suggests the continuation if not the intensification of these patterns. As an example of finely-tuned use of wetland environments, Lake Jasper near Northcliffe formed 3800 years ago, inundating occupation sites, forest trees and former waterholes (Dortch 2002b). The distribution of occupation sites (as interpreted from artefact concentrations in the lake floor), tree trunks in growth position and former swamps, indicates the spatial arrangement of sites in relation to local environments. Additional late Holocene subsistence modes are demonstrated by sites such as fish traps (Dortch 1999; Dortch *et al.* 2006); rock platforms used for processing fish bait and shell scatters (Dortch *et al.* 1984); and trees notched for climbing to catch possums (Meagher 1974).

The region's rich oral and written historic record of past and present landscape use by Nyoongar people is a vital source for generating testable archaeological claims. The Nyoongar language group corresponds approximately to the region's biogeographic boundary and encompasses 13 neighbouring dialect groups, with movements of people documented between each neighbour (Dortch 2002a). Considering the region's historic record, which details early 19th century Noongar economic and settlement patterns (e.g. Meagher 1974), several adaptations to forests are suggested. Use of forests, including the right to burn vegetation, followed traditional controls such as inherited and kinship rights and obligations based on places and totem species, tied to religious and spiritual beliefs (Dortch 2002a; Hallam 2002; Lullfitz *et al.* 2017). The longevity of the cultural connection is further confirmed by oral histories of rising post-glacial sea levels (c. 18 000–6000 years ago; Stocker *et al.* 2016) and continuing traditions of plant use (Rusack *et al.* 2011).

Management of woodland, estuarine, and forest resources had subtle impacts that researchers are only beginning to understand. Oral and written records provide a useful starting point (Kelly 1999; Kost 2013; cf. Hallam 2002). Whereas site occupation histories suggests people sometimes relocated sites to deal with post-glacial environmental changes (Ferguson 1985; Dortch *et al.* 2012), there is also evidence that Aboriginal land management influenced habitats (Lullfitz *et al.* 2017). Use of various sites in karri forest suggests people either fired the forest to keep it open or maintained pathways (Dortch 2005; Dortch *et al.* 2010). Marked changes in abundance of marsupials, suggesting changes in habitat, are correlated with the posited population changes at c. 1 ka, and following European disruption of Aboriginal burning c. 150–100 years ago (Dortch *et al.* 2014; Faith *et al.* 2017; Monks 2018).

The material culture that survives indicates connections with other regions and continuities through time. Backed stone artefacts appear from c. 4000 BP, in accordance with their continental proliferation (Dortch *et al.* 2012). Bone points were still being made in recent decades (Bird & Beeck 1988). Rock art is not widespread in the region, ostensibly due to a lack of suitable rock surfaces. One art site in the far South West suggests motifs forms in common with early art from other regions, yet was executed on what appears to be a Late Holocene rock formation (Gunn *et al.* 2011).

Historically, as shown in linguistic and genetic evidence, Nyoongar people had long-distance connections with neighbouring groups (Malaspinas *et al.* 2016). Archaeological evidence for these connections may include ochres from the South West in other regions, putatively traded over long distances (Hallam 2014). Recent advances in ochre-sourcing (Scadding *et al.* 2015) suggest potential for identifying long-distance exchange of archaeological ochres. As with the internal boundaries between dialect groups, the boundaries between language regions were permeable (Dortch 2002a). Like the peoples of other regions discussed in this paper, this record of connection to the region and with neighbouring groups may explain the persistence of occupation by the Nyoongar people for nearly 50 000 years.

## DISCUSSION

This overview of the archaeology of the first peoples of Western Australian identifies many different cultural groups each with distinct regional histories. Despite this heterogeneity, a series of observations are common to all four major regions discussed here:

- At a broad scale, there is continuous occupation from 50 ka demonstrated by at least one site in each region. There is little reason to suppose that large regions were entirely abandoned after initial colonisation except for the possible exception of sandridge deserts at the LGM (Veth 1993), and, as we suggest below, genetic and archaeological records suggest continuity within regions.
- At the available resolution it is not possible to establish pathways or rates of colonisation. Although colonisation was most likely from the north, our sample is too small to determine any further details from the chronologies available or by current dating methods.
- Occupation persists at certain sites or localities in each region through the LGM, especially in the high rainfall Kimberley and South West and in the inand ranges of the Pilbara.
- Aboriginal populations appear to have increased in the Holocene, although archaeological and genomic estimates are still crude, and it is not possible to identify a consistent demographic pulse across all regions.
- Aboriginal groups formed extensive social networks within and between regions as shown by the distribution and stylistic connection of regional art bodies in all but the South West.
- Technological innovations once thought to be confined to the Holocene—e.g. ground stone technology; backed blades; hafted implements—appear in the Pleistocene, as early as 40 ka in some cases.
- All groups engaged in art production, or at least used ochre for art or ornamentation, and produced personal ornaments in the form of shell or bone beads, from the earliest periods of occupation.
- All groups exploited localised resources, including marine foods and shellfish in coastal regions, indicating familiarity with different environments from an early point in occupation history.

All of these traits are evident in the Pleistocene when overall population may have been relatively low (Malaspinas *et al.* 2016; Veth *et al.* 2011; Williams *et al.* 2015). As evidence for how regional populations organised themselves at this time is limited, it is difficult to identify any particular social structure, much less societies analogous to the ethnographically recorded, dense populations of the last few centuries. However, based on ethnographic examples of sparse populations worldwide, the putative lower population density would almost certainly have promoted an even greater extension of long-range social networks in order to maintain viable social groups. These extended networks are consistent with the appearance of materials used for ornamentation in the Kimberley, North West and South West, such as marine shells and ochre, suggesting transport over considerable distances in the Pleistocene, most likely through inter-group exchange, as the distances are too great for the annual round of a single group. Interpretation of the number of dated occupation layers in successive periods as a proxy for population, while disputed, suggests on the whole that Pleistocene populations were small (Williams *et al.* 2015). Nevertheless, broad genetic estimates of effective population size (the minimum population required to sustain the observed genetic diversity) suggest that regional populations rose relatively quickly after 40 ka, becoming differentiated by 30 ka, dipped at the LGM, and rose again with post-glacial amelioration well before the late Holocene (Malaspinas *et al.* 2016). The genetic differentiation may well have correlated with cultural differentiation; the relatively early changes in population size suggest groups had adapted early to Pleistocene conditions. If taphonomic corrections are valid, late Holocene spikes in dated occupation layers are not explained by better preservation, and could represent real population rise (Williams *et al.* 2015).

Use of broad suites of resources from almost every ecosystem available is a trait of many foraging peoples and of all Australian societies in ethnographically recorded times. The limitations of most Western Australian environments go some way to explaining the use of diverse environmental zones including marine and coastal environments, montane deserts, and nearly every environment apart from sand-ridge deserts during full glacial aridity (Veth 1993). Broad foraging modes in each region would have required considerable familiarity with landscapes and capacity to transmit knowledge through generations, which in turn implies continuity in regions—all facilitated by attachment to place, which is renowned among Aboriginal people today.

Land management can be claimed in locations where ethnographic information allows the construction of testable hypotheses. Such models can be developed in all regions reviewed here: existing ones are well known in the anthropological and historical literature for the Western Desert and South West (Bird *et al.* 2018; Hallam 2014). It is highly likely that earlier generations of Aboriginal people had the technical and organisational capacity to manage many ecosystems. However, archaeological evidence supporting these views remains to be acquired and investigated.

The emerging evidence for long-term continuities in archaeological and genetic records in Western Australia as a whole implies long-term intimacy with ecosystems and detailed knowledge of land and seascapes. The complex land-management practices observed during and after each region's European colonisation imply technical expertise, social controls, and inherited responsibilities and affiliations to land. These practices would seem to require a substantial development period—nonetheless achievable well within in the long period reviewed here, if not even in the first few millennia of occupation. However the process of successful landscape learning is for now shrouded in uncertainty, given that impacts of hunter-gatherer colonisation events are highly disputed on all continents. The Western Australian records reviewed here, particularly from limestone caves and other well-stratified deposits, seem to offer considerable potential to explore landscape learning in the earliest millennia of Aboriginal occupation.

## CONCLUSION

The record of human occupation of Western Australia is characterised by creation and persistence of regional cultural identities, associated with dynamic, social responses to environmental challenges. Among these responses, technological innovation, symbolic behaviour and development of a wide resource base were critical factors in the history of human adaptation to fifty millennia of change. The need to adapt to local environments—landscape learning—would have been balanced with the necessity for social interaction over extensive areas with shared resources. The early solution in many regions was the development of a common symbolic vocabulary enabling mutual comprehension between regionally-differentiated social groups across the continent. Further possible tensions would have been resolved through the historically documented, mutually recognised affiliations to place, and long-distance networking between knowledge-holders of stories and rituals concerning sites. More recently, social groups became increasingly territorially embedded in place, distinct style boundaries developed with easily recogniseable and iconic rock-art styles (e.g. Wanjina art in the Kimberley) in each of the regions discussed. Australia's persistent societies have long geneaologies, genetically, linguistically and culturally. We suggest the Songlines and shared Dreamings of the modern era have an ancient history in connecting past communities of Aboriginal societies.

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# Synthetic Aperture Radar scenes of the North West Shelf, Western Australia, suggest this is an underutilised method to remotely study mass coral spawning

**ANNA K. CRESSWELL** [1,2,3*], **PAUL C. TILDESLEY** [4] **AND GEORGE R. CRESSWELL** [4]

[1] *School of Biological Sciences, University of Western Australia, 35 Stirling Highway, Crawley WA, 6009, Australia*

[2] *CSIRO Oceans and Atmosphere, Indian Ocean Marine Research Centre, 64 Fairway, Crawley, WA, 6009, Australia*

[3] *The UWA Oceans Institute, University of Western Australia, 35 Stirling Highway, Crawley, WA, 6009, Australia*

[4] *formerly CSIRO Oceans and Atmosphere, Castray Esplanade, Battery Point Tas 7004, Australia (retired)*

* *Corresponding author:* ✉ *annacresswell@gmail.com*

## Abstract

Corals reproduce during annual 'mass spawning' when gametes are released into the water column in near-unison. While mass spawning events have been well studied, there remain key questions about their timing, triggers and resilience. We report the second occasion to our knowledge in which a mass spawning has been captured serendipitously with satellite-borne synthetic aperture radar (SAR). SAR can collect information through cloud and in both day and night by detecting changes in ocean surface roughness, including, as we shown here, those caused by mass coral spawning, which creates slicks or films of spawn on the sea surface. We examined four SAR scenes of coral reefs on the North West Shelf, Western Australia, from a 10-day interval bracketing the expected time of mass spawning in March 2001. The scene from 19 March 2001 shows what we classify as a snapshot of mass coral spawn slicks, from reefs extending over an area of roughly 100 km. The locations of the slicks correlated spatially with underlying carbonate reefs. We suggest SAR monitoring of coral reefs at spawning time may be an underutilised method that can provide new information on this natural phenomena.

**Keywords: Barrow Island, coral reproduction, coral reef, RADARSAT, remote sensing, SAR, monitoring, methodology**

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## INTRODUCTION

Understanding coral life cycles is becoming more important as ocean warming drives mass coral mortality events (Hughes *et al.* 2017). Reproduction in corals is a synchronised phenomenon, known as "mass spawning", where a large proportion of corals release gametes over only a few consecutive nights at certain times of the year (Simpson *et al.* 1991, Keith *et al.* 2016). The reproductive matter floats to the surface and in reefs of dense coral this often leads to coral spawn 'slicks' or 'films' on the water surface (Oliver & Willis 1987). Depending on weather conditions, these slicks can persist for several days, allowing the possibility of tracking both the extent and the movement of coral embryos and larvae following a mass spawning.

Satellite-borne SAR sends microwave pulses to Earth, and based on the return of echoes back to the satellite, makes an image, which can provide information on the surface from which it was reflected (Gens 2008). Roughened ocean surfaces scatter part of the SAR signal back to the satellite whereas a smooth ocean surface, where capillary waves are dampened, reflects the signal away (Gens 2008). When Jones *et al.* (2006) detected surface slicks in a SAR scene obtained with the Canadian Space Agency's RADARSAT of the Vulcan and Goeree Shoals in the Timor Sea on 16 April 1998 they interpreted these to be coral spawning slicks, the first documented by SAR. Their case was strong because the shapes of the slicks matched those of the underlying reefs, and the conditions were right to expect mass spawning in this region: autumn, 4½ days after full moon, shortly after sunset, an ebb tide one hour before low tide with wind speed 4.6 $ms^{-1}$.

Coral spawn slicks are composed of coral eggs and embryos and their breakdown products, and can form dense, highly viscous patches (Oliver & Willis 1987). SAR has commonly been used to detect natural hydrocarbon seeps and oil spills in the ocean (Tian *et al.* 2015), the principles of which may be applied to coral slicks (Jones *et al.* 2006). There are challenges associated with detecting slicks, mainly linked to the wind and swell conditions at the ocean surface. Harahsheh *et al.* (2001) assign optimum wind speeds for oil slick detection to be between 3 and 6 $ms^{-1}$, given that wind speeds less than this will cause minimal difference in backscatter between slicks and calm seas, and wind speeds greater are likely to cause disintegration of slicks (Ivanov 2000; Brekke & Solberg 2005).

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In Western Australia mass coral spawning was first recorded in the Dampier Archipelago (Simpson 1985). In this region corals generally spawn around the third quarter of the moon (*i.e.* one week after full moon) on neap, nocturnal, ebb tides (Rosser & Gilmour 2008, Baird *et al.* 2011, Gilmour *et al.* 2016). In some cases where the full moon falls near the edge of the spawning window only some corals will have mature gametes and spawn, whereas others will delay spawning until the following full moon, resulting in a 'split-spawning' (Gilmour *et al.* 2016).

There are still questions about the timing of coral spawning, geographic variation in spawning season and the environmental triggers (Rosser & Gilmour 2008, Baird *et al.* 2011, Gilmour *et al.* 2016, Keith *et al.* 2016). Recently, remote sensing has been recognised as an important tool for the interdisciplinary assessment of coral reef processes (Hedley *et al.* 2016). Here, we present four SAR scenes of the waters around the Barrow and Montebello Islands, which bracket the time of an expected coral spawning event in March 2001. SAR has not previously been used in targeted studies of coral spawning events, and we discuss the utility of this method for adding to the knowledge base on coral spawning.

## METHODS

Four SAR scenes were obtained over a ten-day interval in March 2001 as part of Project 250 of RADARSAT-1 of the Canadian Space Agency/Agence spatiale canadienne (Parashar *et al.* 1993). They were initially acquired to investigate oceanic internal waves in the region (Jackson 2004, fig. 3). The scenes are "ScanSAR Wide", i.e. 500 km square with a resolution of 100 m, and cover the region around the Barrow and Montebello Islands, part of a group of islands to the northwest of the Australian coast at ~21°S (Fig. 1). The date and times of the scenes, as well as whether the satellite was in ascending or descending orbit, are as follows: 17 March (05:44, descending), 19 March (18:50, ascending), 24 March (05:40, descending) and 26 March (18:46, ascending). The SAR scenes were interpreted visually; generally, white areas due to high backscatter of the reflected signal indicate roughened water surfaces, and black or low backscatter areas indicate smooth surfaces (Gens 2008). Images required interpretation with reference to additional factors as low backscatter can be indicative of windless, smooth water surfaces (Gens 2008), oil slicks (Nunziata *et al.* 2013) and phytoplankton blooms (Wu *et al.* 2018) amongst other things (Harahsheh *et al.* 2001).

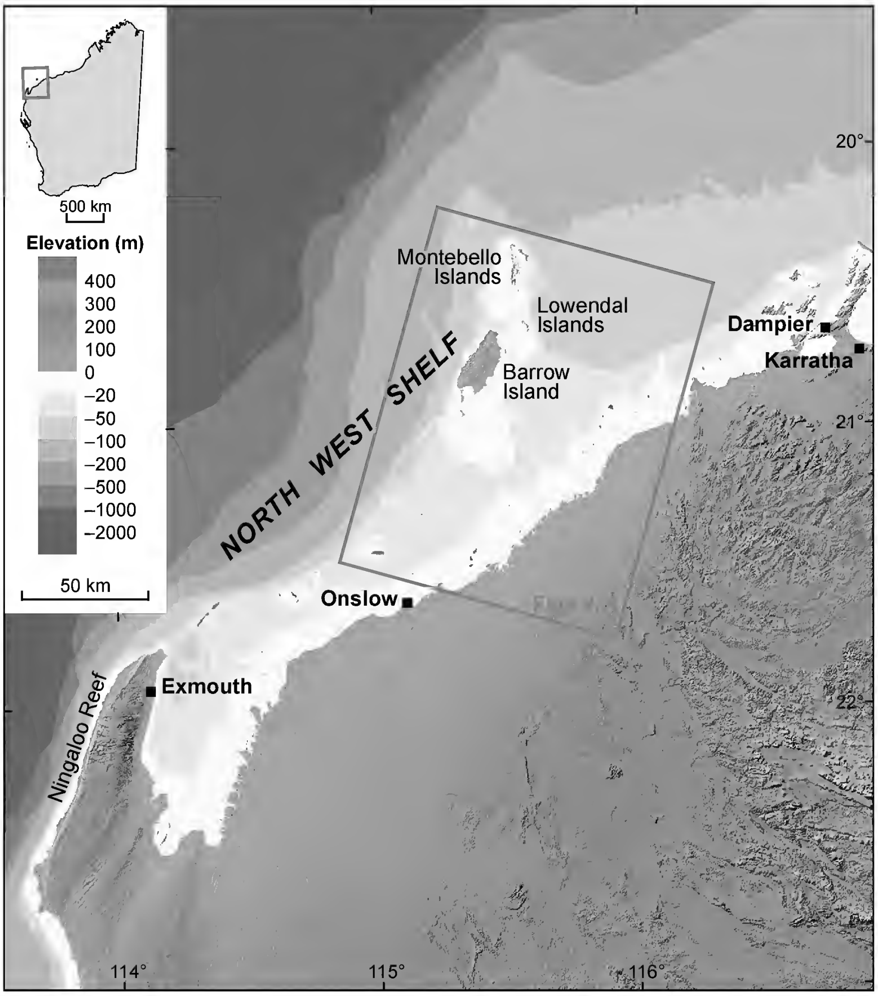

**Figure 1**. The North West Shelf of Australia showing the region covered by the RADARSAT SAR scenes examined for this study. The coastline and isobaths from 100–1000 m are from the General Bathymetric Chart of the Oceans (GEBCO) https://www.gebco.net/ and the 20 m isobath was copied from the Australian National Bathymetric Map Series.

In order to narrow the classification to coral spawn we followed the advice of Jones *et al.* (2006) to increase the accuracy of interpretation. Ancillary data—bathymetry, current velocities, wind speeds and directions—were investigated alongside the SAR scenes. We examined the scenes with reference to the expected time and days of coral spawning in 2001, the proximity to underlying carbonate reefs, and the states of the tides and winds. We also checked for any historical reports of oil spills at the time of the SAR scenes.

With reference to the time, moon phase and tide, a spawning event was expected 7–10 days after the full moon on a neap, nocturnal, ebb tide (Gilmour *et al.* 2016). Tide data for the time of the SAR scenes was sourced for Barrow Island from http://tides.mobilegeographics.com. Tides in the region are semidiurnal and the magnitude varies around the islands with a maximum spring tide on the east coasts of >4 m compared with <2.5 m on the west coasts of the offshore islands (Richards & Rosser 2012).

Wind measurements from the Barrow Island Airport were obtained from the Australian Bureau of Meteorology for the times of the SAR scenes. We considered the locations of the subtidal and intertidal carbonate reefs as indicators of a coral population, overlaying spatial data from SAR scenes illustrated by the Western Australia Department of Environment and Conservation (2007, fig. 3).

All references to time are in Western Standard Time, WST (Coordinated Universal Time, UTC + 8 hours), with local time in the study region being WST-20 minutes.

## RESULTS AND DISCUSSION

The four SAR scenes (Fig. 2) and information on wind, moon phase and time of day (Fig. 3), suggest that a mass spawning event can be captured using SAR. The 17 March 2001 scene (Fig 2a), six days after the full moon, was captured at dawn on what was a strong ebb tide with Barrow Island airport recording a 9 ms$^{-1}$ southwesterly wind. This is equivalent to five on the Beaufort Scale (Mather 2005), which translates to "Fresh breeze. Moderate waves (1.8 m), many whitecaps". Although the time of the lunar month, the tide and time of day satisfied Gilmour's *et al.* (2016) conditions for mass coral spawning for the region, no coral spawn slicks were detected. However, the strong wind and breaking waves would likely have demolished any coral spawn slicks that may have been present.

The 19 March 2001 scene (Fig. 2b), ten days after full moon at neap tide (weak ebb), was captured at

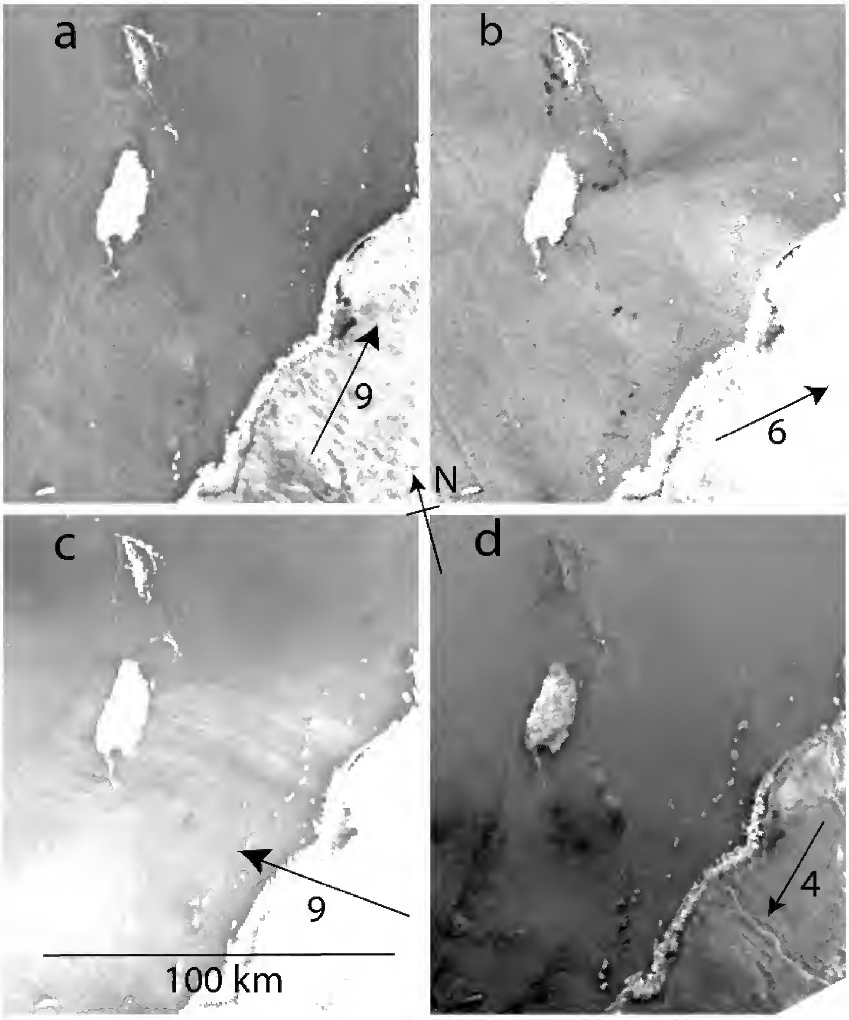

**Figure 2**. The RADARSAT SAR scenes from the Montebello and Barrow Islands region for a) 17, b) 19, c) 24 and d) 26 March 2001. The vectors represent the winds (ms$^{-1}$) measured at Barrow Island Airport at the times of the satellite passes.

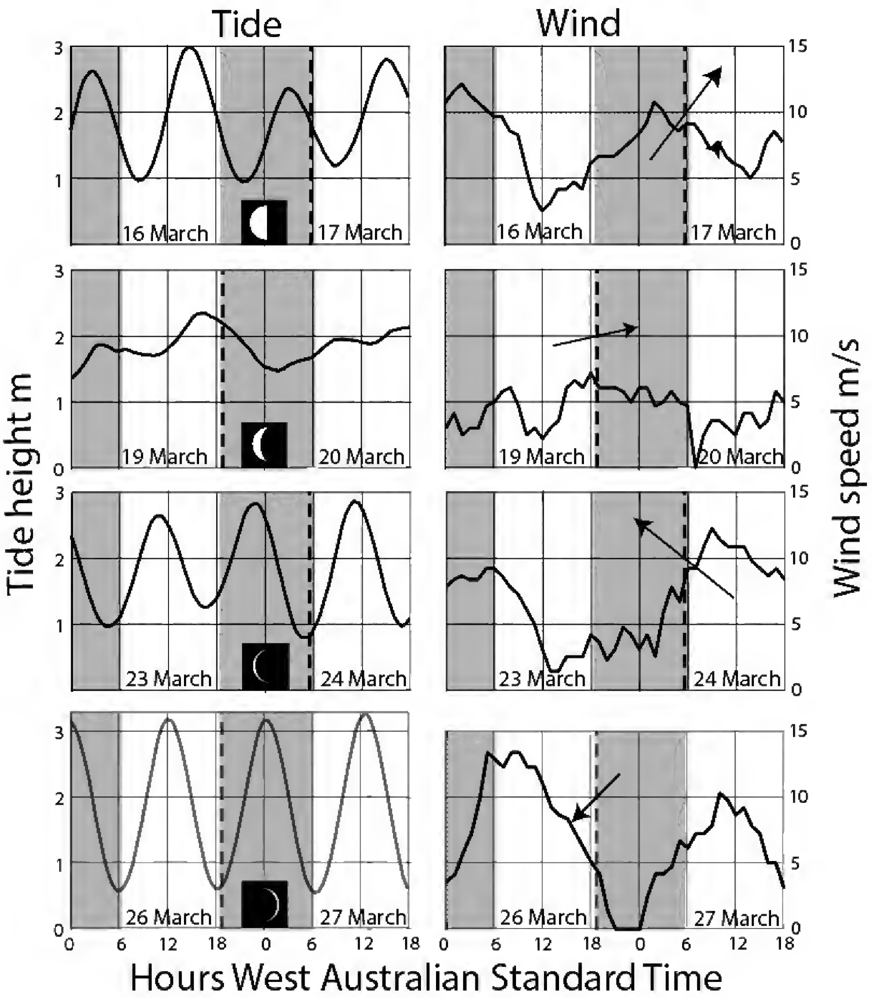

**Figure 3.** Predicted tide at Barrow Island and wind speed measured at Barrow Island airport around the times of the RADARSAT SAR scenes, which are marked with vertical dashed lines. The shading indicates night, the small black boxes show the phases of the moon, and wind vectors at the times of the scenes are added at the intersections of the dashed lines with the 10 ms$^{-1}$ grid lines.

early twilight and a 6 ms$^{-1}$ westerly wind was recorded, equivalent to four on the Beaufort Scale—"Moderate breeze. Small waves (1 m), some whitecaps." Gilmour's *et al.* (2016) conditions for mass coral spawning—phase of the moon, tidal conditions and time of day (early evening)—were satisfied and the wind speed fell within the optimum range for slick detection (Harahsheh *et al.* 2001). These factors in combination with low backscatter shown by black areas near the islands, and between there and the NW Australian coast, indicate slicks. Slicks appear to have originated from multiple reefs across the study region.

The 24 March 2001 scene (Fig. 2c) was captured just before dawn, at new moon and low water with a 9 ms$^{-1}$ southeasterly wind, equivalent to five on the Beaufort Scale, as was that for the 16 March scene. Roughened waters, some aligned with the wind direction, can be seen between the northwestern Australia coast and Barrow Island. As with Figure 2a, there appear to be no regions of smooth water or slicks, in keeping with the strong winds.

The 26 March 2001 scene (Fig. 2d) was captured just after sunset at new moon at low water with a 4 ms$^{-1}$ northeasterly wind, equivalent to three on the Beaufort Scale—"Gentle breeze. Large wavelets (0.6 m), crests begin to break". The gentle breeze may be the reason for the extensive smooth areas in the southwest part of the scene. To the west of the Montebello Islands localised areas of low backscatter are likely due to calm water surfaces, as in this region coral spawning has not been documented to continue for this many days after the full moon (Gilmour *et al.* 2016, Simpson *et al.* 1991).

The complex distribution of subtidal and intertidal reefs around Barrow and the Montebello Islands is represented in the yellow and green overlay on the 19 March 2001 scene in Figure 4b, as this was the scene that showed strong evidence of coral spawn slicks. There appears to be a strong relationship between the reefs and the dark pixels (low backscatter) of the SAR image. We suggest these dark pixels represent a mass coral spawning in progress on the evening of 19 March. The slicks are more distinct in some locations, particularly west of the Montebello Islands, east of Barrow Island and at the subtidal reefs further south. Eastward from Barrow Island is a fan of water that is smooth relative to its surroundings, as shown by the darker pixels. We speculate that this may be due to coral spawn being carried eastward by current and/or wind, though it could also be a result of smooth water in the windward lee of the land. Dark pixels on the eastern sides of two small reefs west of Barrow Island can be interpreted as having a similar origin. Along part of the southeast coast of Barrow Island there is also smooth water, possibly from coral spawn or from being in the lee of the island.

Aerial photographic surveys are one method that has historically been used to quantify the extent of coral spawn slicks, which appear as pink or white patches on the water surface (Oliver & Willis 1987). The advantage of SAR over photography is that it can collect data at night (coral generally spawn in the evening), and through cloud cover (Gens 2008). However, there are potential problems associated with false positive detections. Smooth water, oil spills, phytoplankton blooms (Wu *et al.* 2018), in particular *Trichodesmium* spp. slicks (Oliver & Willis 1987), and natural carbon seeps all have the potential to give a false positive for coral spawn (Gens 2008). Low wind speeds may cause pseudo slicks which would be indistinguishable from coral spawn, as Figure 2d showed, whereas high wind speeds can cause coral spawn to be quickly dispersed thus not forming slicks that can be detected by SAR (Brekke & Solberg 2005).

Nevertheless, our study, along with that of Jones *et al.* (2006), suggest it would be worthwhile to trial SAR as a method for targeted studies of coral spawning on a large scale, if measures can be taken to remove the likelihood of false positives through consideration of the weather, tide, and predicted coral spawning time. Combining SAR with data such as in situ documentation of coral spawning, and monitoring of oil slicks or phytoplankton blooms that could confuse the SAR interpretation would allow this method to be used more accurately. Alternatively, or additionally, optical satellite (e.g. from Landsat (https://landsat.gsfc.nasa.gov/)) or airborne imagery, in daylight hours if cloud was absent, would help to confirm SAR identifications (Hedley *et al.* 2016).

SAR may be particularly useful to assess remote or difficult to access coral reefs where monitoring coral spawning can be logistically and/or economically challenging. In the years since the SAR scenes of the present study were collected, SAR technology (and remote sensing satellite technology more generally) has advanced. There are now more than 15 space-borne SAR systems in operation for a diverse range of applications, with continued advances in the capability to collect ecological information (Moreira *et al.* 2013). This includes the Sentinel-1 satellite (https://sentinel.esa.int/web/sentinel/missions/sentinel-1/data-distribution-schedule), which has freely distributed SAR scenes. There are various ways SAR acquisition could be adapted to directly target coral spawning. The SAR scenes interpreted in this study were the "ScanSAR Wide" option, but higher resolution, smaller scenes could be

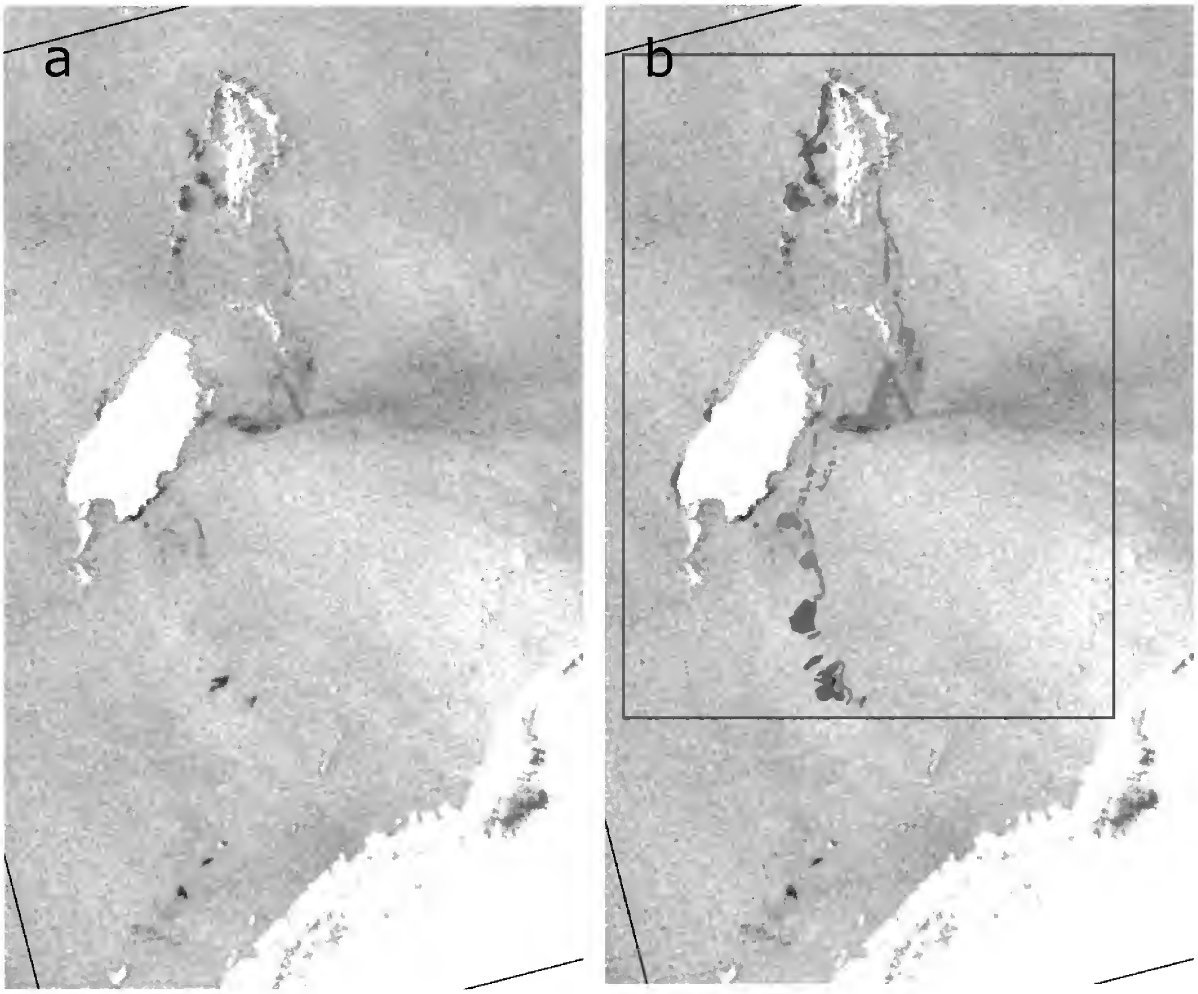

**Figure 4**. a) RADARSAT SAR scene for 19:50 hrs WST 19 March 2001; b) with yellow and green overlays showing the positions of subtidal and intertidal reefs, respectively. Note, the spatial data for reef locations are smaller than the SAR scene, indicated by blue outline.

collected in the future. There are likely to be issues with satellite location lining up with the timing and location of coral spawning in cases where the satellite overpass does not align with the targeted reef(s). Ideally, several satellite passes each day could capture the evolution of coral spawn slicks. However, access to a number of SAR satellites would be required to achieve this, as the return frequency of an individual satellite is generally every few days, as was the case in the present study. With a greater number of satellites operating SAR, this becomes more possible. Nonetheless, targeting a large reef system such as the Great Barrier Reef, or being flexible with location, would allow higher likelihood of capturing the event.

## CONCLUSIONS

Of the four SAR scenes we examined, that for 19 March 2001 captured a mass coral spawning event off north Western Australia that was synchronised at reefs extending over 100 km. This is, to our knowledge, the second time SAR has serendipitously captured mass coral spawning. This suggests that if targeted, SAR can be a method to provide important synoptic information on the timing, extent and surface longevity of coral spawn slicks, which would increase our understanding of this phenomenon. New information could be applied in many fields, including modelling studies focused on reproduction, connectivity and dispersal in coral reefs, as parameters surrounding the extent and timing of mass spawning events are important for such models (Wood *et al.* 2014). It could also directly benefit managers; for example, in situ monitoring in north Western Australia is used to detect spawning events on reefs in areas of dredging and industrial development, yet Styan & Rosser (2012) suggest that current practices often miss significant mass spawning events. We do not suggest SAR as a replacement to existing monitoring, rather as a complementary tool, with limitations discussed above. Greater availability of SAR, including freely available images from Sentinel-1, promises to continue to allow better connections between field observations of spawning events with satellite-borne imagery.

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## CONFLICT OF INTEREST STATEMENT

On behalf of all authors, the corresponding author states that there are no conflicts of interest.

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# The greening of Western Australian landscapes: the Phanerozoic plant record

**DANIEL PEYROT** [1*], **GEOFFREY PLAYFORD** [2], **DANIEL J. MANTLE** [3], **JOHN BACKHOUSE** [1], **LYNNE A. MILNE** [4], **RAYMOND J. CARPENTER** [5], **CLINTON FOSTER** [1,8], **ARTHUR J. MORY** [1,6], **STEPHEN MCLOUGHLIN** [7], **JESSE VITACCA** [1], **JOE SCIBIORSKI** [1], **CHARLOTTE L. MACK** [4] & **JENNY BEVAN** [1]

[1] *School of Earth Sciences, The University of Western Australia WA 6009, Australia*

[2] *School of Earth and Environmental Sciences, The University of Queensland Qld 4072, Australia*

[3] *MGPalaeo, 1/5 Arvida St Malaga WA 6090, Australia*

[4] *School of Earth and Planetary Sciences, Curtin University WA 6102, Australia*

[5] *School of Biological Sciences, University of Adelaide, SA 5005, Australia*

[6] *Geological Survey and Resource Strategy, 100 Plain Street, East Perth WA 6004, Australia*

[7] *Swedish Museum of Natural History, SE-104 05 Stockholm, Sweden*

[8] *Research School of Earth Sciences, Australian National University, Canberra, ACT 2601, Australia*

* *Corresponding author: ✉ daniel.peyrot@uwa.edu.au*

## Abstract

Western Australian terrestrial floras first appeared in the Middle Ordovician (c. 460 Ma) and developed Gondwanan affinities in the Permian. During the Mesozoic, these floras transitioned to acquire a distinctly austral character in response to further changes in the continent's palaeolatitude and its increasing isolation from other parts of Gondwana. This synthesis of landscape evolution is based on palaeobotanical and palynological evidence mostly assembled during the last 60 years. The composition of the plant communities and the structure of vegetation changed markedly through the Phanerozoic. The Middle Ordovician – Middle Devonian was characterised by diminutive vegetation in low-diversity communities. An increase in plant size is inferred from the Devonian record, particularly from that of the Late Devonian when a significant part of the flora was arborescent. Changes in plant growth-forms accompanied a major expansion of vegetation cover to episodically or permanently flooded lowland settings and, from the latest Mississippian onwards, to dry hinterland environments. Wetter conditions during the Permian yielded water-logged environments with complex swamp communities dominated by *Glossopteris*. In response to the Permian–Triassic extinction event, a transitional vegetation characterised by herbaceous lycopsids became dominant but was largely replaced by the Middle Triassic with seed ferns and shrubs or trees attributed to *Dicroidium*. Another floristic turnover at the Triassic–Jurassic boundary introduced precursors of Australia's modern vegetation and other southern hemisphere regions. Most importantly, flowering plants gained ascendancy during the Late Cretaceous. Characteristics of the state's modern vegetation, such as sclerophylly and xeromorphy, arose during the Late Cretaceous and Paleogene. The vegetation progressively developed its present-day structure and composition in response to the increasing aridity during the Neogene–Quaternary.

**Keywords: palaeobotany, palynology, vegetation, palaeoclimate, Western Australia**

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## INTRODUCTION

Terrestrial vegetation of the geological past can be reconstructed using molecular, micro- and megascopic fossil remains. This article focuses mainly on palynological and palaeobotanical material corresponding to the 'micro-' and 'megascopic' remains preserved in the fossil record. Although outside the scope of this paper, molecular biogeochemical studies of fossil plants are increasingly significant in understanding the evolution of plant life (Spaak *et al.* 2017). Although a substantial amount of palynological information can be obtained from publicly available reports commissioned by petroleum industries and governmental institutions, the majority of data considered herein is from published sources. As study techniques and the results obtained depend on the nature and size of the material examined, this article initially addresses methodological aspects. For each time interval, representative palynological and megafloral assemblages of the terrestrial flora are discussed and their most significant representatives illustrated. General tectonic and geological settings are illustrated in Figure 1, and locality information is

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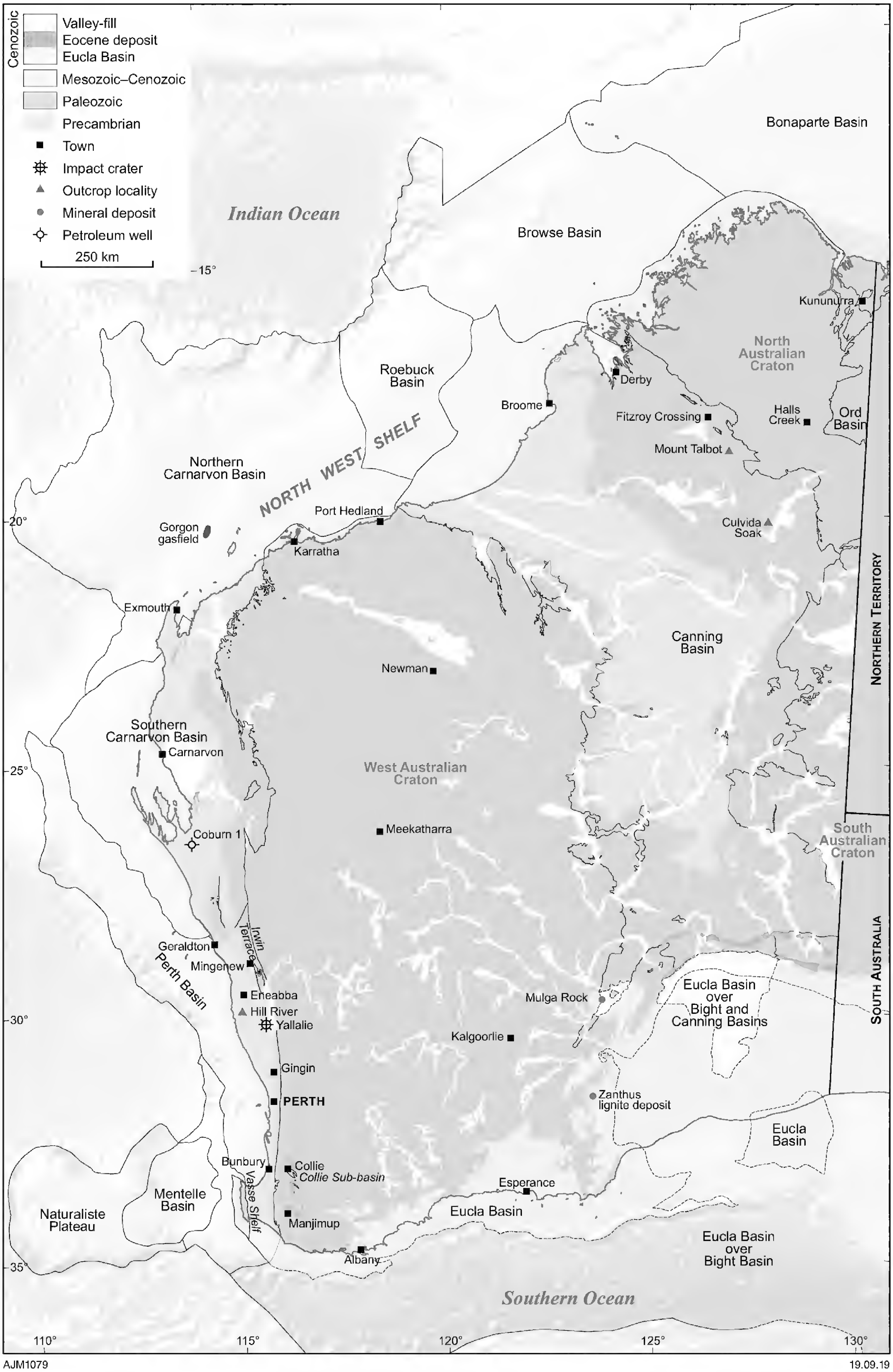

**Figure 1**. Onshore and offshore Western Australia showing major tectonic elements and localities cited in text.

listed in Appendix 1. Figures 2–8 include type material housed in the collections maintained by the School of Earth Sciences of The University of Western Australia (UWA), the Western Australian Museum (WAM), the Australian Museum (AMF) and the Swedish Museum of Natural History (NRM). Significant contributions to this paper include those from CF and GP on the Ordovician–Devonian; JB, CF, GP and SMcL on the Carboniferous–Permian; DJM and SMcL on the Triassic–Jurassic; and RJC and LAM on the Late Cretaceous – Holocene. Full names of taxa are provided in Appendix 2.

## Classification and preservation of plant fossils

Fossilised plant remains initially can be grouped according to size: miospores, which are less than 200 μm in diameter; mesofossils, which include megaspores and 0.2 – 5 mm plant fragments; and larger remains, usually termed megafossils (or macrofossils).

The term miospore collectively embraces spores from non-flowering plants and fungi, and pollen grains (aka pollen) from both flowering and non-flowering plants. Spores are organic-walled, commonly with distinctive shapes, unicellular or multicellular reproductive bodies associated with sexual reproduction in land plants and asexual reproduction in fungi. In land plants, spores are the result of a final meiotic division. They are further categorised according to their size and morphological characteristics. Isospores and microspores represent small (commonly <200 μm) unicellular, dispersal units produced by homosporous plants (mosses, most ferns) and heterosporous plants (quillworts, water ferns, *Selaginella*), respectively. Megaspores are larger dispersal units produced by heterosporous plants. Despite having similar functional characteristics to micro- and isospores, megaspores (usually >200 μm) are often excluded from routine palynological analyses, which tend to focus on smaller and commonly more abundant plant microfossils. Pollen are the male counterparts of the ovules and represent the microgametophyte generation of seed plants (Chaloner 1970). Miospores characteristically have a highly durable organic external wall, which includes the chemically inert biopolymer sporopollenin. General introductions to pollen and spores are too numerous to be listed here. Enthusiasts may find instructive the superbly illustrated book *Pollen* (Kesseler & Harley 2008). Undergraduate and postgraduate students will find authoritative compendia in the three volumes edited by Jansonius & McGregor (1996); the second edition of *Paleopalynology* (Traverse 2007); and in *Quaternary palynology* (Moore *et al.* 1991; focused on Holocene palynomorphs).

Mesofossils include relatively small plant fragments and large megaspores. The former comprise conductive tissues, cuticles, roots, stems, leaves, fruits or any other plant debris <5 mm in diameter. The nature of the recovered assemblage is largely dependent on depositional and diagenetic processes. The initial biochemical composition of the plant remains will influence their abundance in the stratigraphic record. In particular, the presence of the extremely stable organic polymers lignin and cutin, which strengthen cell walls and form a chemically stable component of plant cuticles respectively, greatly enhances their preservational potential in sedimentary facies. Burial under anaerobic conditions (e.g. either in permanently flooded terrestrial mires and swamps, or in marine settings below a stratified water column) may lead to coalification. This process represents a complex series of physical, chemical and structural changes associated with an increase in carbon content and aromaticity, and a concomitant decrease in oxygen and other volatile components. Coalification generates significant changes in colour and physical properties of plant remains that have to be considered during their laboratory extraction and later analysis. More advanced (i.e., higher rank) coalification destroys minute anatomical characteristics such that only gross morphological features may be preserved. Conversely, oxygen-depleted conditions may enhance plant preservation via partial burning or charring to produce fusains, which are highly inert chemically and moderately resistant to degradation by microbial attack—a process sometimes called charcoalification. The presence of charcoalified fossil plant debris has important applications in palaeoenvironmental and climatic reconstructions as it typically signifies episodes of intensive wildfires. Examples of such inferences are the recognition of dry climatic conditions during the Middle to Late Triassic in the Northern Carnarvon Basin (Scibiorski *et al.* 2018) and the expansion of fire-prone sclerophyll vegetation during the Neogene in Western Australia (van der Kaars *et al.* 2000; Atahan *et al.* 2004).

Although various preservational styles of plant megafossils have been recorded (as discussed by, inter alia, Schopf 1975), compression/impression (adpression) and permineralisation (petrifaction) constitute the most common modes of preservation (Chaloner 1999). The former involves transformation during the incorporation of comparatively soft plant fragments within the surrounding matrix and their progressive flattening with increasing depth of burial. Whereas internal structures are usually destroyed by the collapse of the plant tissues, coalification of the organic material forms dark carbonaceous layers that retain the original outline of the plant fragments (Taylor *et al.* 2009). This process can preserve delicate superficial structures (trichomes, stomata) and cuticles, and can create fracture planes separating the organic remains from the mineral matrix. The adjacent mineral layer may retain an exact imprint (mould) of the coalified remains. When such plant fragments have a dorsiventral architecture (as do most leaves), they tend to accumulate more or less parallel to the bedding plane, creating closely stacked layers. Spectacular examples are present within the Permian Irwin River Coal Measures near Mingenew in the northern Perth Basin and in coeval strata at Collie.

In environments characterised by anoxia, acidic conditions and high primary productivity, accumulating plant material can form thick deposits of peat. When plant remains are buried to suitable depths, they undergo a gradual transformation, progressing successively with increasing burial and/or temperature, from lignite to sub-bituminous and bituminous coal, and ultimately to anthracite. The higher ranks of coal (sub-bituminous and above) are typically characterised by plant fragments altered beyond recognition. Although palaeobotanically and palaeoenvironmentally less informative, high-rank coals are economically important and can contribute to hydrocarbon generation. In Western Australia, economic (and potentially economic) sub-bituminous coalfields have been discovered in the Collie Sub-basin, an eastern outlier of the southern Perth Basin, and in the main part of the basin (Irwin Terrace, Hill River area, Vasse Shelf). Apart from the Lower Jurassic Cattamarra Coal Measures near Hill River and Eneabba, these coal measures contain Permian palyno- and megafloras (Backhouse 1991; Hocking & Preston 1998). Coalification processes are often associated with the generation of gas, for which Western Australia is particularly notable given its numerous offshore gas fields incorporating some of the world's largest proven reserves (e.g. Greater Gorgon, Scibiorski *et al.* 2018).

As noted above, permineralisation is a common mode of plant fossilisation. During the early phases of diagenesis, mineral-charged groundwater permeates cells and plant tissues, precipitating mineral fractions of varying composition. Silicate or carbonate precipitates are common but other minerals (gypsum, phosphate, fluorides, pyrite, oxides) may be involved in this process. Permineralisation can provide outstanding three-dimensional preservation of cell wall and anatomical structures (Taylor *et al.* 2009). In exceptional cases, this process can even preserve soft parts down to the level of cell nuclei and other organelles (Bomfleur *et al.* 2014). General introductions to palaeobotany aimed at undergraduates, collectors or enthusiasts include the texts by Cleal & Thomas (2009) and Willis & McElwain (2002). More expansive and detailed palaeobotanical treatises are those of, inter alia, Stewart & Rothwell (1993) and Taylor *et al.* (2009).

## Techniques of extraction

Appropriate methods of extraction depend on the type and chemical composition of the fossils, the nature of the host rock or sediment, the available laboratory facilities and the techniques originally employed to obtain the samples. The extraction of palynological material described by Gray (1965), Phipps and Playford (1984), Wood *et al.* (1996) and Batten (1999) is summarised below. Indurated samples are usually macerated in acid reagents to dissolve the bulk of the mineral components. Hydrochloric and hydrofluoric acids (this with particular care!) are used to remove calcium carbonate and silicate minerals respectively. Oxidation, followed by alkali treatment, is then necessary for removal of unwanted organic debris. Sieving through a Buchner funnel, or 10-micron nylon cloth, possibly accompanied by a brief session of ultrasonic vibration, may be employed to disaggregate amorphous organic matter and remove fine particles. Finally, staining of the residue may prove useful to enhance the optical contrast of palynomorphs. For Neogene–Holocene samples, particularly if unconsolidated, instead of oxidation the workflow usually includes maceration of the residue by a process called acetolysis (Erdtman 1960); this uses 9:1 acetic anhydride and sulphuric acid to remove unwanted cytoplasmic content, pollenkitt and cellulosic polymers.

The next steps are determined by the focus of the intended analysis. Biostratigraphic studies entail transmitted bright-field light microscopy (TLM) of residues mounted on a slide with a coverslip using a mounting medium of suitable durability and refractive index. Palynological residues destined for detailed morphological or ultrastructural analyses by electron microscopy require additional coating with gold, graphite or other conductive media. Among other techniques, transmission and/or scanning electron microscopy (TEM/SEM) can provide excellent details of miospore ultrastructure and morphology (Milne 1998a; Haig *et al.* 2018, figs 2G–I; Figs 7B, C) and have been successfully utilised in palynological research for over 50 years. TEM facilitates ultrastructural characterisation of the walls of fossil spores/pollen with an unrivalled level of detail: Foster & Balme (1994), for example, used TEM to reveal the ultrastructure of the oldest saccate miospore from the Upper Devonian of Western Australia. Milne (1998a) developed a technique to facilitate quick sectioning and precise orientation of the grain, enabling a single fossil grain to be studied in TLM, SEM and ultimately TEM (Figs 7A–D). These techniques, however, involve time-consuming preliminary conditioning of the material (Kennaway *et al.* 2008); in particular embedding, sectioning and staining. For this reason, the use of alternative techniques, such as Focused Ion Beam (FIB) milling, have recently gained favour among some palynologists (Villanueva-Amadoz *et al.* 2012). The use of more advanced transmitted-light techniques enhancing contrast, such as Confocal Laser Scanning Microscopy (CLSM; Feist-Burkhardt & Pross 1998; Peyrot *et al.* 2007) or Phase and Differential Interference Contrast (PC/DIC) microscopies, remain limited largely to projects carried out in academia, given the high price of the optical devices.

Most of the techniques used to study palynological material are also applicable to meso- and megascopic remains. Where the sedimentary rock is fissile, palaeobotanical material can be partially or totally isolated from the surrounding matrix with the use of needle and hammer (Fairon-Demaret *et al.* 1999). Immersion in hot water or hydrogen peroxide may facilitate the disaggregation of weakly consolidated, fossiliferous sediments. In some cases, whole leaves and other plant parts can be floated out with this method. Foliar fossils, even highly fragmented remains, can also yield plant cuticles. These carry important details that can be used for identification purposes, as well as for palaeoclimatic interpretation. Cuticles are usually isolated by soaking leaf remains in weak chromium trioxide solution, hydrogen peroxide or household bleach. The cuticle can then be stained and mounted on a glass slide for microscopic examination. Impression fossils that lack organic preservation can preserve exquisite leaf venation details, which are best interpreted under low-angle illumination. Thin sections and acetate peels are the techniques of choice for anatomical studies of permineralised material. Procedures described in a companion paper (Haig *et al.* 2018) are not reiterated here. Observational techniques vary depending on the scale of the material. Mesofossils and small megafossils are usually studied via low-magnification light, and/or scanning electron microscopy. Thin sections and small sectioned body parts can be examined using TEM, which may benefit from supplementary mineralogical (X-ray diffraction) or geochemical (ICP-MS, inductively coupled plasma-mass spectrometry or other) analyses.

Undergraduate and postgraduate students will find useful information on diverse techniques commonly utilised for the extraction and study of plant mega- and microfossils in the summary provided by Jones & Rowe (1999).

## SUMMARY OF PUBLISHED RECORD

### Factors influencing the record

The presence of sporopollenin gives miospores an exceptional resistance to post-burial degradation. This, together with the outstanding aero- and hydrodynamic properties of non-animal dispersed miospores, explains their prolific stratigraphic record (in Western Australia from the Middle Ordovician Goldwyer Formation, Canning Basin, to Holocene and historical successions) and their presence in strata that accumulated in a wide range of depositional settings (from deep marine to terrestrial and aeolian). The outstanding physico-chemical durability of spores and pollen means that they are readily recycled (reworked) together with other resistant sedimentary particles. Nonetheless, miospores remain susceptible to oxidation and, to a certain extent, weathering processes (e.g. Cenozoic lateritisation that affected much of the Australian continent). Palynological material is best preserved in, and recovered from, fine-grained, dark-coloured, sedimentary rocks (shale, claystone and siltstone). In Western Australia, the deep weathering profile and extensive leaching explains the poor or nil recovery from surface samples (Balme & Hassell 1962). Hence, for palynological endeavours, there is a reliance on subsurface samples (preferably drillcores) or those from deeply incised terrains. The nature of the sedimentary rock plays an important role in the preservation of megafossils. Finer grain-sizes (mud, volcanic ash) will enhance the fossilisation and allow better preservation of the original plant material as compressions and impressions. Permineralisation depends on very specific depositional circumstances, particularly pore waters saturated in silicates, gypsum, pyrite and/or oxides.

## Paleozoic: evolving vegetation and landscapes

### ORDOVICIAN–DEVONIAN: FROM EARLY TERRESTRIALISATION TO THE FIRST FORESTS

The earliest land plant spores, known as cryptospores, formed obligate tetrad configurations (Figs 2A, B), and are interpreted as having been produced by small, millimetre-sized plants related to modern liverworts (Steemans & Wellman 2004). Their oldest records date back to the Middle Ordovician (c. 469 Ma) in Argentina (Rubinstein *et al.* 2010) and Sweden (Rubinstein & Vajda 2019), which pre-dates the Western Australian record by a minimum of 2–12 Ma (Foster *et al.* 2018). The oldest cryptospores found in Western Australia, including *Velatitetras laevigata* (Fig. 2A), are from the Middle Ordovician Goldwyer Formation of the Canning Basin (Spaak *et al.* 2017). These strata were deposited in a broad, shallow epeiric sea where the earliest land plants grew on emergent banks and would have provided the first greenish tinge to the land surface of Western Australia. Younger records of the cryptospore *Tetrahedraletes medinensis*, possibly of Late Ordovician to Silurian age, have been recovered from the Mallowa Salt, Carribuddy Group, Canning Basin (Foster & Williams 1991). Currently, there are no other Australian Ordovician cryptospore records beyond the Canning Basin.

Western Australian Silurian successions have been the subject of relatively sparse palynological characterisation by Gorter *et al.* (1994) and Backhouse (in Yasin & Mory 1999). Both reported (but did not figure) cryptospores, including *Tetrahedraletes medinensis*, together with rare trilete spores and acritarchs, from petroleum exploration wells in the Southern Carnarvon Basin. More palynological work is required, as coeval strata in Victoria contain one of the oldest known lycopsids (*Baragwanathia longifolia* Lang & Cookson 1935). These herbaceous plants, related to modern clubmosses, produced trilete spores and consisted of photosynthetic, vascularised, decimetric, erect stems bearing elongate leaves in tight helices. The reduction from tetrad unit to a monad trilete spore might arguably have conferred better dispersal capabilities for the reproductive units. However, it is well established that the acquisition of a more robust vascular system effectively enhanced support and water/nutrient conductive capabilities, allowing these plants to colonise a wider range of terrestrial habitats.

Devonian successions are relatively well represented in Western Australian outcrop and subsurface sections, and have been described from the Carnarvon and the Canning basins. Spore assemblages from the Gneudna Formation (Southern Carnarvon Basin)—described in detail by Balme (1962, 1988)—can be considered as representative of the early Late Devonian terrestrial palynoflora of Western Australia. The palynoflora is relatively diverse (up to 45 miospore species) and is dominated by *Geminospora lemurata* (Figs 2C, D), together with significant numbers of other cosmopolitan species, such as *Rhabdosporites langii* (Fig. 2E), *Verrucosisporites scurrus* (Fig. 2F), *Emphanisporites annulatus* (Fig. 2G), *E. rotatus* (Fig. 2H), *Gneudnaspora divellomedia* (Fig. 2I) and *Ancyrospora langii* (Fig. 2J). The presence of the last two species is particularly notable as it highlights a substantial increase in diversity of spore morphologies. *Gneudnaspora divellomedia* is a hilate spore, a relatively uncommon apertural type, and *Ancyrospora langii* bears anchor-like processes reminiscent of those present in modern water fern spores. The record of these spores in the Gneudna Formation and other deposits in the Canning Basin indicates the presence of heterosporous land plants in Australia during the Late Devonian. Heterospory presents significant evolutionary advantages and has been recorded in at least six distinct lineages of land plants during the Devonian (Bateman & DiMichele 1994). Relationships between dispersed miospores and their parental plants are often difficult to establish. However, several lines of evidence indicate that the spores *Geminospora lemurata* and *Rhabdosporites langii* were produced by progymnosperms (Balme 1995), a group considered to include the first arborescent plants. As such, the Gneudna Formation's spore content is

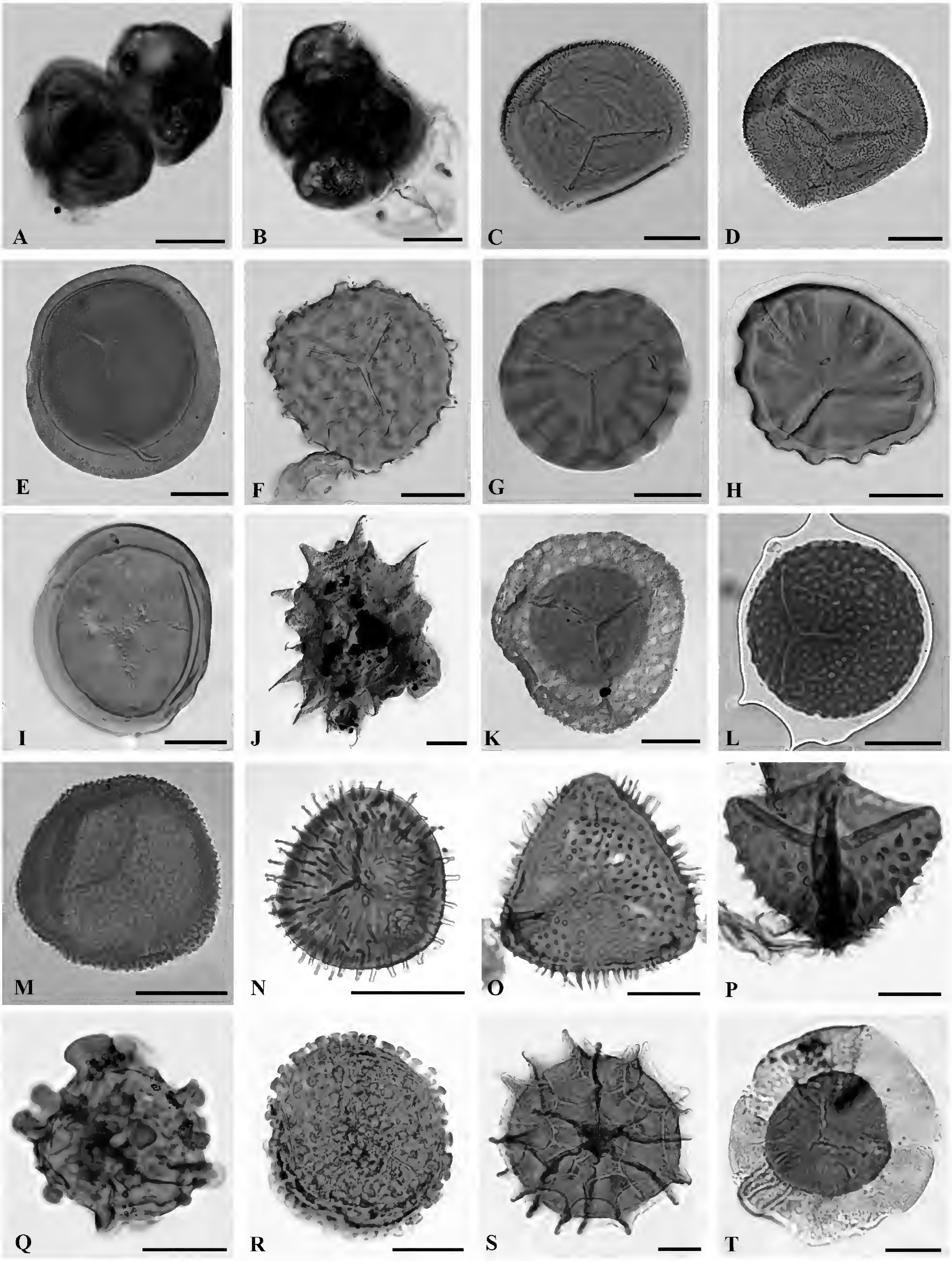

**Figure 2.** Representative early and later Paleozoic spores from Western Australia: A *Velatitetras laevigata*; B indeterminate cryptospore; C, D *Geminospora lemurata*, proximal and medial foci; E *Rhabdosporites langii*; F *Verrucosisporites scurrus*; G *Emphanisporites annulatus*; H *Emphanisporites rotatus*; I *Gneudnaspora divellomedia*; J *Ancyrospora langii*; K *Retispora lepidophyta*; L *Convolutispora fromensis*, holotype, UWA-45113; M *Granulatisporites frustulentus*, holotype, UWA-45119; N *Claytonispora distincta*; O *Diatomozonotriletes birkheadensis*; P *Anapiculatisporites amplus*; Q *Raistrickia accincta*; R *Raistrickia corymbiata*, holotype, GSWA-F53066; S *Reticulatisporites magnidictyus*; T *Auroraspora solisorta*. Scale bars: 20 μm. Ages: A, B, Ordovician; C–M, Late Devonian; N–T, Carboniferous. See appendices for additional information.

considered representative of swamp, alluvial plain or riparian vegetation that included the first trees in Western Australia during the early Late Devonian. By the latest Devonian, the state's vegetation experienced a near-complete turnover as shown by the substantially different spore assemblages preserved in uppermost Devonian and lower Mississippian strata of the Canning and Bonaparte basins. These assemblages include elements belonging to the cosmopolitan *Retispora lepidophyta* palynoflora, which includes, together with the eponymous species (Fig. 2K), certain taxa that are recorded elsewhere in coeval successions (Playford 1976, 1982). Some of Western Australia's oldest plant megafossils, represented by tree-sized lycopsid (lepidodendrid) stem casts and impressions are preserved in uppermost Devonian strata of the Kellys Knob Sandstone, Bonaparte Basin, east of Kununurra (Fig. 4A).

## CARBONIFEROUS–PERMIAN: INCEPTION, PROLIFERATION AND DEMISE OF GONDWANAN SWAMP FORESTS

### Mississippian

Megascopic plant remains are extremely scarce in the Carboniferous strata of Western Australia (McLoughlin & McNamara 2001), being limited to a few herbaceous and short-stature lycophytes recovered from the Southern Carnarvon and Canning basins. By contrast, the palynological assemblages of this age in Western Australia are diverse and well-characterised for the Canning Basin (Playford 1976), Bonaparte Basin (Playford 1971; Playford & Satterthwait 1985, 1986, 1988; Satterthwait & Playford 1986), and, more recently, for the Carnarvon and Perth basins (Quail Formation and/or lateral equivalents, Playford 2015; Playford & Mory 2017).

The Mississippian palynofloral succession has been subdivided into various palynostratigraphic units, the oldest being the Tournaisian–Visean *Granulatisporites frustulentus* Microflora (Kemp *et al.* 1977). That assemblage, so named as it is dominated by this species (Fig. 2M), includes elements present in the Famennian (latest Devonian), such as *Convolutispora fromensis* (Fig. 2L), together with cosmopolitan and stratigraphically more restricted species, such as *Claytonispora distincta* (Fig. 2N). Kemp *et al.* (1977) indicated a broad correspondence between this palynoflora and a *Lepidodendron* (Mega-) Flora on the basis of palynological correlations between eastern and Western Australian basins.

Younger Mississippian assemblages (mid-late Visean – early Serpukhovian, Mississippian), comprehensively described by Playford (2015) and Playford & Mory (2017) from the subsurface of the northern Perth and the Carnarvon basins, are relatively diverse (up to 45 species). These assemblages include the typical Gondwanan elements *Reticulatisporites magnidictyus* (Fig. 2S), *Grandispora maculosa* (Fig. 3A), *Psomospora detecta* (Fig. 3B), *Anapiculatisporites amplus* (Fig. 2P), *Indotriradites daemonii* (Fig. 3C), *Velamisporites cortaderensis* (Fig. 3E) and *Verrucosisporites quasigobbettii* (Fig. 3F), together with cosmopolitan species, such as *Anapiculatisporites concinnus* and *Auroraspora solisorta* (Fig. 2T).

In Western Australia spores with a more restricted geographic distribution and stratigraphic range include *Raistrickia accincta* (Fig. 2Q), *R. corymbiata* (Fig. 2R), *Diatomozonotriletes birkheadensis* (Fig. 2O), *Indotriradites kuttungensis* (Fig. 3D) and *Spelaeotriletes ybertii* (Fig. 3G). Collectively, these suites indicate an increasingly Gondwanan, less cosmopolitan flora. In eastern Australia, this assemblage is associated with the *Nothorhacopteris argentinica* Flora of Retallack (1980).

Upper Serpukhovian (uppermost Mississippian) and younger strata incorporate the first pollen (aka prepollen). These bilaterally symmetrical monosaccate pollen (of the genus *Potonieisporites*) were produced by early representatives of Voltziales, an extinct late Paleozoic group of arborescent gymnosperms distantly related to modern-day conifers. Together with radiosymmetric monosaccates, these pollen progressively assumed a major role in the palynological successions of this interval in Western Australia and elsewhere in Gondwana. The inception of gymnosperms (and their ensuing radiation through the Pennsylvanian) marks the most significant palaeofloristic event prior to the introduction of angiosperms in the Early Cretaceous.

### Pennsylvanian–Permian

The Pennsylvanian is characterised by major global cooling, leading to the establishment of an extensive ice sheet covering the bulk of Eastern Gondwana, including much of the region corresponding to Western Australia (Mory 2017; Martin *et al.* 2019). As a result, Pennsylvanian strata are poorly represented in the state and have been intersected by only a few wells, mainly in the northern Canning (Powis 1984; Apak & Backhouse 1999) and Bonaparte basins (Mory 2017). The palynofloras of this later Carboniferous are characterised by abundant monosaccate pollen—*Plicatipollenites* spp. (Fig. 3H) and *Potonieisporites* spp. (Fig. 3I)—and impoverished spore associations including the lycopsid element *Cristatisporites* and spores of uncertain affinities, such as *Calamospora* spp. (Fig. 3J), *Punctatisporites gretensis* (Fig. 3K) and *Secarisporites* spp. (Fig. 3L). The palynofloral assemblages of this interval have been linked to the *Sphenopteridium* (=*Fedekurtzia*) Flora described in eastern Australia (Retallack 1980; Coturel & Césari 2017).

Icehouse conditions of the Pennsylvanian ameliorated during the Cisuralian (Early Permian). Glacial meltwaters formed lakes and deposited thick mudstones that underlie younger sediments in almost all Phanerozoic sedimentary basins across Western Australia and elsewhere in much of Gondwana. The Permian is characterised by coal in most of the major basins of Western Australia, but thick (economically significant) deposits are confined to the southern Perth Basin (Hocking & Preston 1988). Given their known or prospective economic significance (Collie Sub-basin and Vasse Shelf) and/or good exposure (Irwin Terrace, northern Perth Basin), the coal-bearing successions have been the subject of numerous studies dealing with their spore-pollen (Balme & Hennelly 1955, 1956a, 1956b; Backhouse 1991) and megafloral content (Rigby 1966, 1993; McLoughlin 1992a, 1992b, 1993, 1995; McLoughlin & McNamara 2001).

The Collie Sub-basin's palynoflora is highly diverse (>100 species) and records the radiation of taeniate

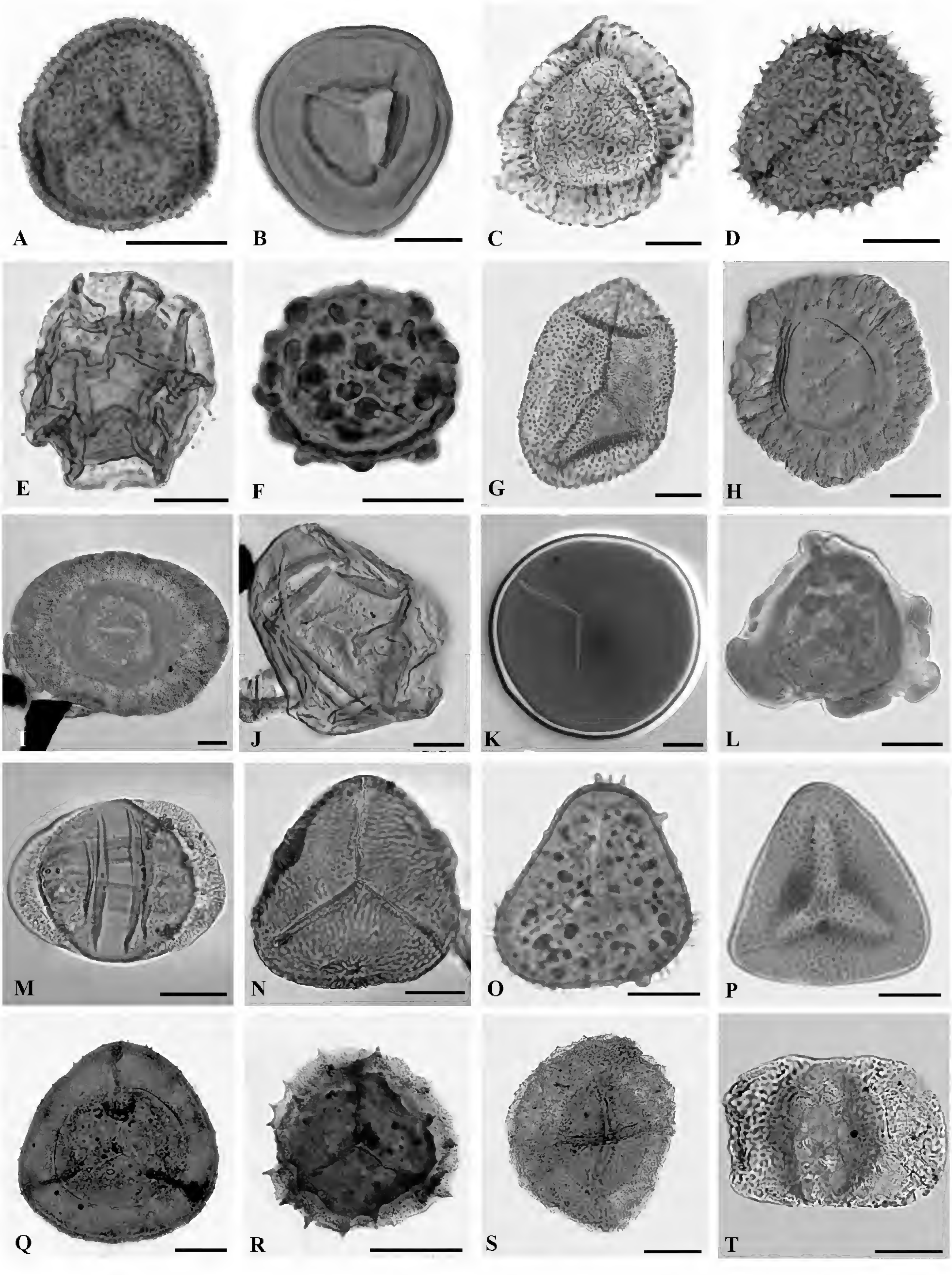

**Figure 3.** Representative late Paleozoic and early Mesozoic spores and pollen from Western Australia; A *Grandispora maculosa*; B *Psomospora detecta*; C *Indotriradites daemonii*; D *Indotriradites kuttungensis*; E *Velamisporites cortaderensis*; F *Verrucosisporites quasigobbettii*; G *Spelaeotriletes ybertii*; H *Plicatipollenites* sp.; I *Potonieisporites* sp.; J *Calamospora* sp.; K *Punctatisporites gretensis*, holotype, UWA-44984; L *Secarisporites* sp.; M *Protohaploxypinus samoilovichii*; N *Dulhuntyispora parvithola*; O *Horriditriletes tereteangulatus*; P *Microbaculispora tentula*; Q *Lundbladispora willmotii*; R *Kraeuselisporites cuspidus*; S *Aratrisporites banksii*; T *Falcisporites australis*. Scale bars: 20 μm. Ages: A–J, L, Carboniferous; K, N–P, Permian; M, Q–T, Triassic. See appendices for additional information.

pollen grains bearing transverse thickened bands on their proximal side (Backhouse 1991). Such thickened ribs have also been observed in pollen of extant Gnetales (e.g. *Welwitschia mirabilis*) and were interpreted by Foster (1979) as a morpho-functional adaptation to cope with dehydration. Taeniate pollen (e.g. *Protohaploxypinus samoilovichii*, Fig. 3M) are first recorded in Serpukhovian–Bashkirian (uppermost Mississippian – lowermost Pennsylvanian) strata and are frequently observed in Asselian and younger material, thus prompting some authors to recognise the *Striatites* Microflora (Balme 1964; Kemp *et al.* 1977). Early Permian spore associations typically include small ornamented trilete spores assigned to *Cyclogranisporites* spp., *Baculatisporites* spp. and locally abundant *Horriditriletes tereteangulatus* (Fig. 3O). Permian palynofloras also feature spores characterised by a combination of biconvex polar shape, rounded triangular equatorial outline and raised trilete scar. This group, known collectively as the 'cheilocardioid complex', diversified and became quantitatively significant during the Permian (Price & Filatoff 1990). The earliest Gondwanan cheilocardioid spore, *Microbaculispora tentula* (Fig. 3P), evolved during the Pennsylvanian, and the group diversified rapidly as the climate warmed and coal swamps developed throughout Gondwana. Unique to Gondwana, and particularly diverse in the Canning Basin during the Lopingian (Late Permian), are the highly distinctive, presumed fern spores of the genus *Dulhuntyispora* (Fig. 3N); these are regarded as the ultimate development of the cheilocardioid complex (Price & Filatoff 1990).

Permian megafloral assemblages are dominated by relatives of the Glossopteridales including leaves (*Glossopteris*; Fig. 4E), roots (*Vertebraria*; Fig. 4J), reproductive structures (*Arberia, Ottokaria*; Fig. 4B) and wood (*Araucarioxylon*) from gymnosperms up to 30 m tall. These arborescent plants were the main and/or monodominant colonisers of swamps and water-logged lowland settings as represented in the Collie Sub-basin. The megafloras of the Irwin Terrace are somewhat more diverse, including subarborescent and climbing sphenopsids (related to modern horsetails; Figs 4C, D, F, H, L), and low-stature lycophytes and ferns (Fig. 4G). Megascopic remains attributed to Cordaitales (*Noeggerathiopsis*; Fig. 4I) and the seed fern *Bergiopteris* (Fig. 4K), are also found at both locations and have been interpreted as allochthonous; i.e., the transported derivatives of 'upland' vegetation (McLoughlin 1995; McLoughlin & McNamara 2001). The profuse *Glossopteris* flora covered the Western Australian Permian landscape, as indeed throughout the Gondwana supercontinent. However, as the climate warmed and atmospheric conditions deteriorated at the close of the Permian (due to continental-scale volcanism in the northern hemisphere), the extensive *Glossopteris* vegetation vanished and, consequently, the associated striate pollen almost disappeared from the microfossil record. The collapse of this flora preceded, by a few hundred thousand years, the Permian–Triassic extinction event, which affected faunal communities on a global scale (Fielding *et al.* 2019).

## Early Mesozoic: changing landscapes and vegetation

### TRIASSIC: AUSTRALIAN VEGETATION IN A TIME OF CHANGE

Following the end-Permian mass extinction and the demise of the *Glossopteris* flora, Western Australia experienced prolonged recovery and low plant diversity during the Early Triassic (Retallack 1995a). The Induan–Olenekian plant communities of the Millyit Sandstone and basal Blina Shale in the Canning Basin are dominated by herbaceous lycophytes, such as *Pleuromeia*, along with variable abundances of conifers, sphenopsids and ferns (White & Yeates 1976; Gorter 1978). The Early Triassic spore-pollen associations of the Carnarvon and Perth basins record similar, low-diversity assemblages (Balme 1963; Dolby & Balme 1976; Haig *et al.* 2015) dominated by trilete, cavate lycopsid spores including *Densoisporites*, *Lundbladispora* (Fig. 3Q) and *Kraeuselisporites* (Fig. 3R). Micro- and megafloral attributes suggest a 'recovery flora' featuring abundant opportunistic spore-producers, such as herbaceous lycopsids, ferns (Fig. 5A) and other diminutive plants. This unusual floral physiognomy ('Lilliput effect') has been related to a high concentration of carbon dioxide, extreme chemical weathering and associated greenhouse conditions (Algeo & Twitchett 2010; Retallack *et al.* 2011; Sun *et al.* 2012). The increased nutrient run-off during this interval also led to short-lived episodes of enhanced marine productivity evidenced by recurrent spikes of acritarchs in the palynological record. These are manifest by the prodigious representation of *Micrhystridium* and *Veryhachium* in the Kockatea Shale assemblages of the Perth Basin (Balme 1963; Balme & Foster 1996; Haig *et al.* 2015, 2018). Similarly impoverished Early Triassic plant assemblages are well documented in eastern Australia and across southern Gondwana (Helby 1970, 1973; Retallack 1995b; McLoughlin *et al.* 1997; Vajda & McLoughlin 2007) and may relate to the lack of peat production (the 'coal gap') that persisted globally throughout the Early Triassic (Retallack *et al.* 1996). Initial vegetational recovery during this prolonged aridity in Western Australia began in the late Early Triassic, as shown by increasing diversity of arborescent gymnosperms and shrubby lycophytes; the latter reflected by abundant monolete spores (*Aratrisporites*; Fig. 3S) in palynological assemblages.

Early to early Middle Triassic (Olenekian–Anisian) megafloras from Culvida Soak in the Canning Basin (Retallack 1995a) are of low diversity and dominated by leaves attributed to *Dicroidium*. This foliage was produced by Umkomasiales, an order of seed ferns represented by seasonally deciduous shrubs and trees restricted to Gondwana (McLoughlin 2001; Kustatscher *et al.* 2018), where it is commonly predominant in deltaic megafloras (Retallack 1977). The near-ubiquity of *Dicroidium* in Gondwanan coastal and lowland plant communities until the end of the Triassic is manifested palynologically in Western Australia and elsewhere by its abundant bisaccate pollen *Falcisporites* (Fig. 3T). The remarkably

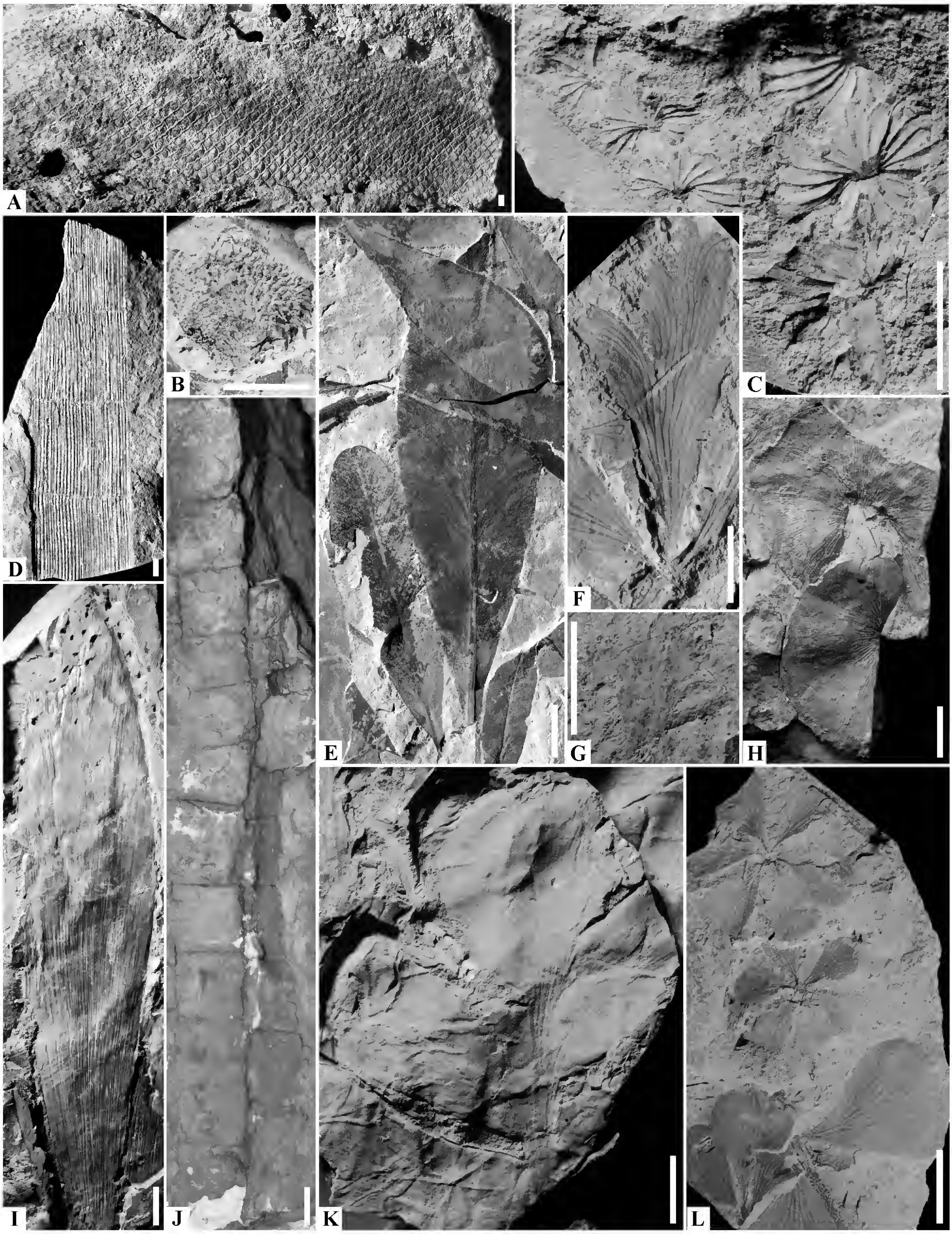

**Figure 4.** Representative Paleozoic plant megafossils from Western Australia: A Lepidodendroid lycopsid trunk in outcrop; B *Ottokaria bullata* (glossopterid seed-bearing organ), UWA-119121; C *Raniganjia minima* (sphenophyte leaf whorls), UWA-115334; D *Paracalamites australis* (sphenophyte stem), NRM-S048203; E *Glossopteris* sp. (mat of deciduous glossopterid leaves), NRM-S048236; F *Sphenophyllum morganae* (sphenophyte leaflet with reflexed lobes), UWA-115380; G *Liknopetalon* sp. (fertile fern pinnule), WAM-P.86.105; H *Gondwanophyton daymondii* (sphenophyte with fan-shaped leaves), WAM-P.86.58; I *Noeggerathiopsis* sp. (cordaitalean leaf), unregistered specimen; J *Vertebraria australis* (segmented glossopterid root), NRM-S166964; K *Bergiopteris* sp. cf. *B. archangelskyi* (lobed seed fern leaf), UWA-3902.5A; L *Sphenophyllum rhodesii* (sphenophyte leaf whorls), UWA-115434. Scale bars: 10 mm. Ages: A, Late Devonian; B–L, Permian. See appendices for additional information.

cosmopolitan Early Triassic floras were succeeded by increasing provincialism in the Middle and Late Triassic, as the recovery and evolution of new vegetation types intensified, and distinct floral communities developed across Gondwana and Laurasia. The increasingly diverse associations of pteridosperms, ferns, cycads, conifers, ginkgophytes and sphenopsids are best represented in Western Australia by their spore-pollen record (the Onslow Microflora; Dolby & Balme 1976) in the Northern Carnarvon Basin. This latitudinally restricted and warm temperate palaeobotanical province stretched from Timor, through northwestern Australia, India, easternmost Antarctica, northern Madagascar and east Africa to northwestern Argentina (Peyrot *et al*., 2019; Césari & Colombi 2013; Kustatscher *et al.* 2018). It differs from the more southerly Ipswich Microflora (Dolby & Balme 1976) by its greater diversity of gymnosperms and the presence of distinctive Eurasian palynofloral components, such as *Camerosporites*, *Enzonalasporites*, *Ephedripites* (Fig. 5A), *Infernopollenites*, *Minutosaccus* (Fig. 5B), *Ovalipollis*, *Rimaesporites*, *Samaropollenites* (Fig. 5C) and *Aulisporites* (Fig. 5D). In Western Australia, these assemblages are well documented from the Bonaparte, Browse, Northern Carnarvon and Roebuck basins (Dolby & Balme 1976; Helby *et al.* 1987; Backhouse & Balme 2002; and many unpublished industry reports) and peaked in diversity during the Carnian and Norian (Late Triassic). The Ipswich Microflora is representative of low-diversity, cool temperate, *Dicroidium*/*Falcisporites*-dominated assemblages in eastern and southern Australia. This palaeobotanical province also ranged across much of Antarctica, southern Africa, Argentina and the Perth Basin in Western Australia where drier conditions persisted for longer than in the northern half of the state. These Middle–Late Triassic palynofloras prevailed without significant change until the end of that period.

## JURASSIC–EARLY CRETACEOUS: THE INITIATION OF MODERN VEGETATION

The Triassic–Jurassic boundary marks one of the 'big five' global extinction events (Hull & Darroch 2013). In Western Australia, it is usually manifest by the reduced frequency of *Falcisporites* (collapse of the *Dicroidium* flora) followed by an abundance of *Classopollis* in low-diversity assemblages. This substantial floristic modification, as implied by the distinctive changes in the palynological assemblages, was probably triggered by drastic and rapid palaeoenvironmental changes. The Jurassic and Early Cretaceous palynology of Western Australia has been documented by Balme (1957, 1964), Filatoff (1975), Helby *et al.* (1987) and Backhouse (1978, 1988). Detailed studies of the Cattamarra Coal Measures (formerly a member of the now-superseded Cockleshell Gully Formation), and the succeeding Cadda and Yarragadee formations in the Perth Basin reveal relatively diverse assemblages with abundant conifer pollen attributed to the taxodioid members of Cupresaceae (bald-cypress/redwood family) and Cheirolepidiaceae. The latter represents a group of extinct conifers traditionally associated with arid or saline coastal environments (Alvin 1982); however, in some regions, they also extended into seasonally humid settings (McLoughlin *et al.* 2002; Tosolini *et al.* 2015). Cheirolepid conifers produced the distinctive *Classopollis* (aka *Corollina*) pollen (Figs 5E, F). The Early Jurassic was also characterised by increasing abundance of pollen attributable to Araucariaceae (family of the extant Bunya and Norfolk pines). This circumstance, together with a proliferation of fern spores from families with extant representatives, established floral elements characteristic of modern Australia and elsewhere in the southern hemisphere. The proportion of Araucariaceae pollen, particularly *Callialasporites turbatus* (Fig. 5G), increased toward the end of the Early Jurassic. Other araucarian pollen, such as *C. dampieri* (Fig. 5H) and *Araucariacites australis* (Fig. 5I), also became common and increased in abundance through the Late Jurassic. Spores of the modern fern families Anemiaceae (Figs 5J, K), Gleicheniaceae (Fig. 5L), Cyatheaceae (Fig. 5M) and Osmundaceae (Fig. 5N) represent a conspicuous part of increasingly diverse (c. 100 species) assemblages. Western Australian Early Cretaceous palynofloras, as exemplified by assemblages from the Parmelia Group (Perth Basin), contain a higher proportion of spores compared to those from Jurassic strata (Backhouse 1988). The same families of ferns are represented and lycopod spores, such as *Staplinisporites caminus* (Fig. 5P), *Foveosporites subtriangularis* (Fig. 5Q), *Retitriletes circolumenus* (Figs 5R, S) and *R. clavatoides* (Fig. 5T), increased in abundance. Early Cretaceous palynofloras include lower proportions of conifer pollen, with Araucariaceae comprising 10–30% of the assemblages. Conversely, pollen of Podocarpaceae (e.g. plum pines), including *Microcachryidites antarcticus* (Fig. 5O), became better represented. The inception of monocolpate pollen attributed to flowering plants has not been precisely documented in Western Australia. However, their first appearance during the Barremian–Aptian (Early Cretaceous) is probable considering palynological records from eastern Australia (viz. Eromanga and Gippsland basins; Dettmann 1986; Burger 1990).

Jurassic and Cretaceous megafloras have been described from the Perth, Carnarvon and Canning basins. The review by McLoughlin & Pott (2009) of plant material from the Lower Jurassic Cattamarra Coal Measures and Upper Jurassic Yarragadee Formation of the Perth Basin, and the Dingo Claystone of the Northern Carnarvon Basin, revealed assemblages with subordinate ferns (Fig. 6B), abundant conifers (Figs 6C, E) and bennettitaleans (Figs 6D, F). The latter are extinct seed plants that bore cycad-like fronds, but with distinctive flower-like reproductive structures. Based on detailed analysis and comparison with other coeval Gondwanan floras, McLoughlin & Pott (2009) identified a mesothermal climatic signal. Moreover, some of these plants preserve the scars of feeding and egg-laying insects (Figs 6D, F), thereby providing some of the earliest evidence of plant–arthropod interactions in the Western Australian fossil record (McLoughlin *et al.* 2015). Lower Cretaceous megafloras from the Leederville and Bullsbrook formations (Perth Basin), the Birdrong Sandstone and Nanutarra Formation (Northern Carnarvon Basin) and the Broome Sandstone and Callawa Formation (Canning Basin) have been documented by McLoughlin & Guppy (1993), McLoughlin *et al.* (1995), McLoughlin (1996) and McLoughlin & McNamara (2001). These megafloras contain many taxa in common including conifers, Bennettitales (Figs 6J, M), Pentoxylales (Fig. 6K), umkomasialean seed ferns (Fig. 6O), the lycophytes

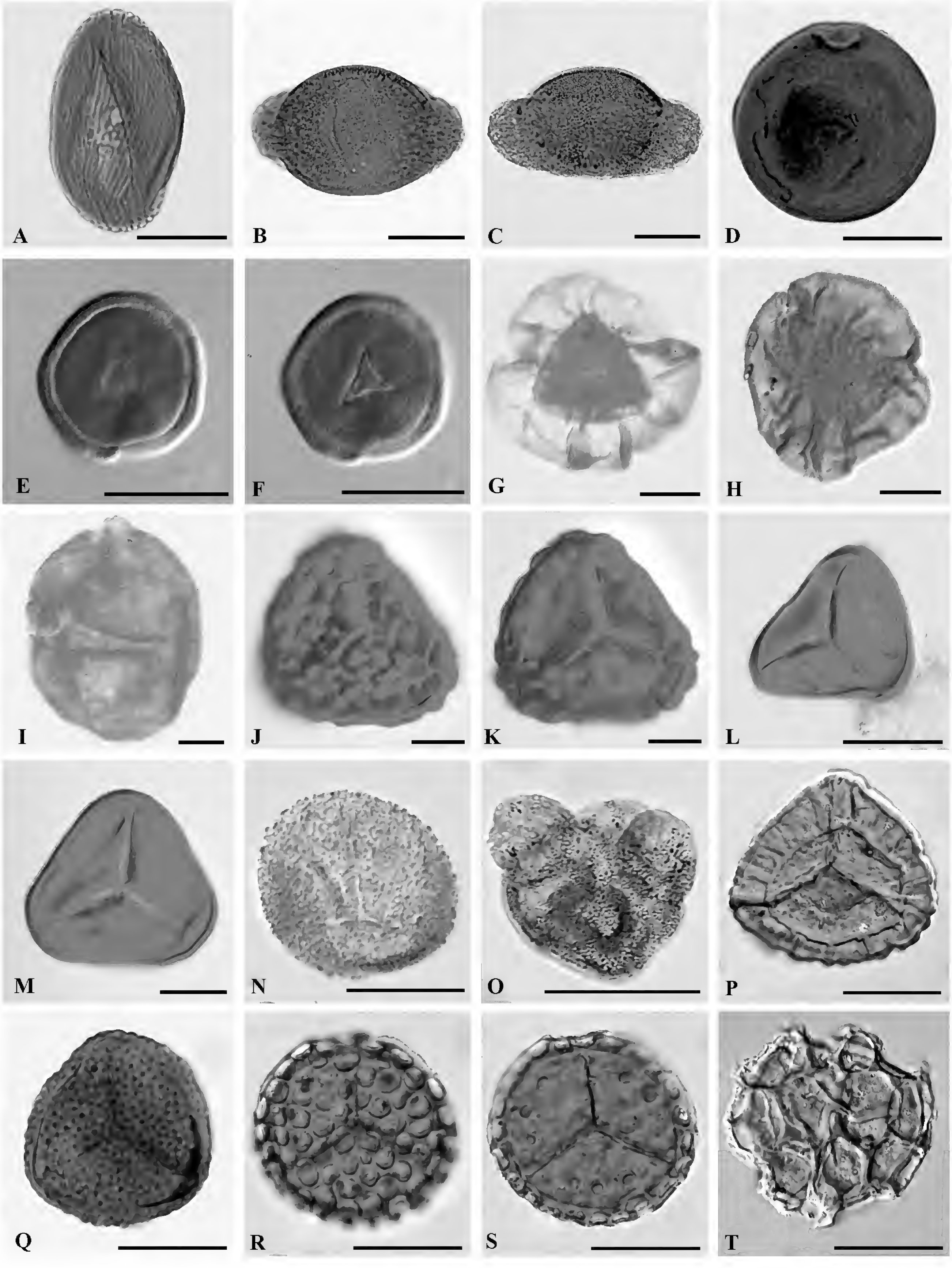

**Figure 5.** Representative Mesozoic spores and pollen from Western Australia: A *Ephedripites macistriatus*; B *Minutosaccus crenulatus*; C *Samaropollenites speciosus*; D *Aulisporites astigmosus*; E, F *Classopollis* sp., distal and proximal foci; G *Callialasporites turbatus*; H *Callialasporites dampieri*; I *Araucariacites australis*; J, K *Ischyosporites marburgensis*, distal and proximal foci; L *Matonisporites crassiangulatus*; M *Cyathidites minor*; N *Osmundacidites welmanii*; O *Microcachryidites antarcticus*; P *Staplinisporites caminus*; Q *Foveosporites subtriangularis*; R, S *Retitriletes circolumenus*, distal and proximal foci; T *Retitriletes clavatoides*. Scale bars: 20 μm. Ages: A–S, Triassic; E–N, Jurassic; O–T, Early Cretaceous. See appendices for additional information.

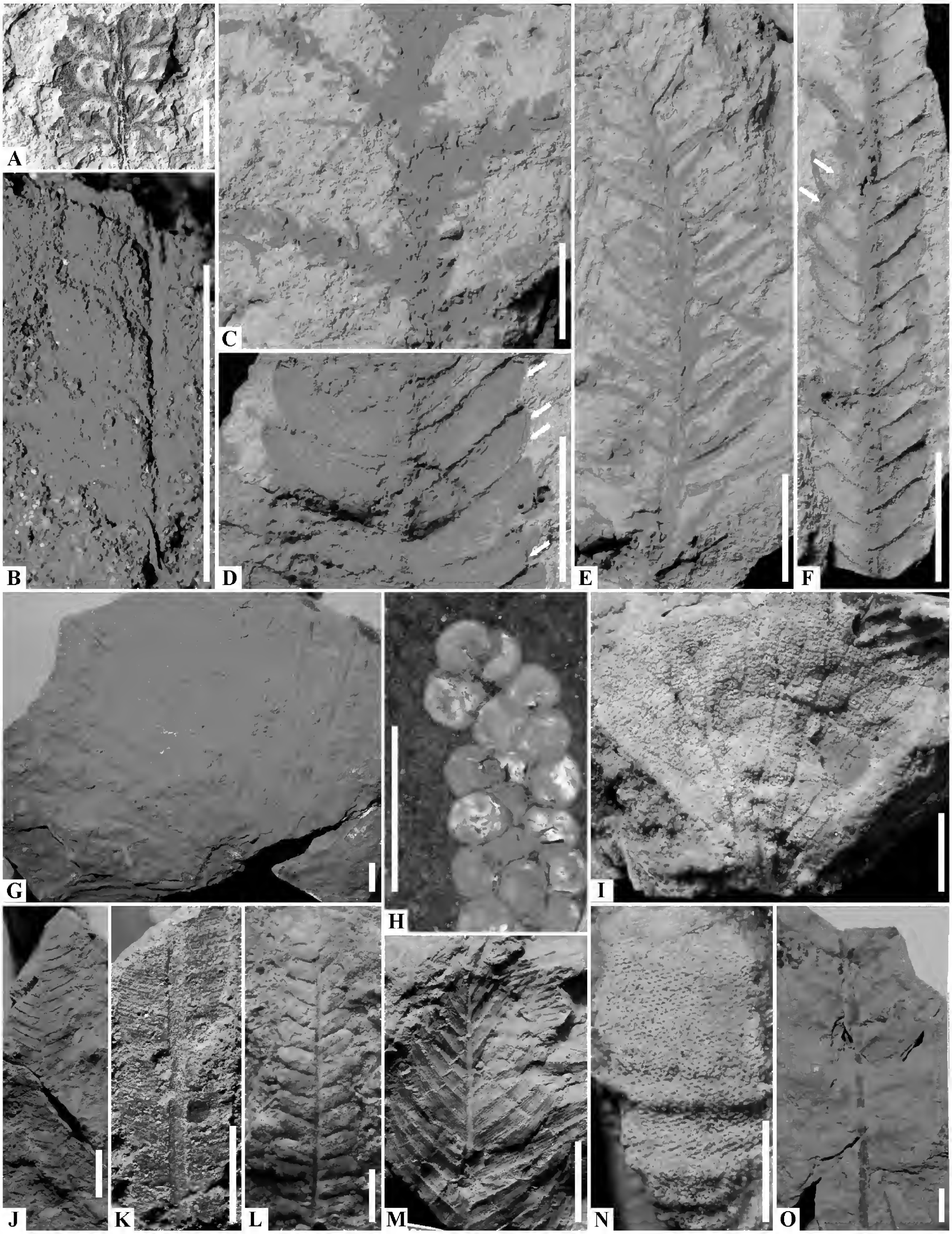

**Figure 6.** Representative Mesozoic plant megafossils from Western Australia: A cf. *Nymboidiantum multilobatum* (diminutive fern pinna); B *Sphenopteris* sp. (fern pinna), AMF58770; C *Pagiophyllum amanguanus* (conifer shoot with awl-shaped leaves), AMF53736; D *Otozamites linearis* (central portion of a bennettitalean leaf with arrow indicating insect oviposition scars on pinnules), AMF-58731B; E *Elatocladus confertus* (planated coniferous short shoot), AMF-58726; F *Ptilophyllum cutchense* (bennettitalean leaf with arrow indicating insect feeding damage to pinnule apices), AMF-58756; G *Isoetites elegans* (tuft of isoetalean microphylls), UWA-16687; H Cluster of megaspores associated with *Isoetites elegans*, UWA-16687; I *Hausmannia* sp. (dipteridacean fern frond), WAM-P.88.13; J *Ptilophyllum cutchense* (bennettitalean leaf), UWA-16684; K *Taeniopteris daintreei* (pentoxylalean leaf), AMF-58781; L *Cladophlebis* sp. cf. *C. oblonga* (osmundaceous fern pinna), WAM-P.88.12; M *Ptilophyllum acutifolium* (bennettitalean leaf), WAM-P.96.2; N *Nathorstianella babbagensis* (isoetalean corm impression with spirally arranged leaf/root scars), WAM-P.88.2; O *Komlopteris* sp. cf. *K. indica* (seed fern leaf), UWA-16690. Scale bars: 10 mm, except for A: 2 mm, and H: 1 mm. Ages: A, Early Triassic; B–F, Early Jurassic; G–O, Early Cretaceous. See appendices for additional information.

*Nathorstianella babbagensis* (Fig. 6N) and *Isoetites elegans* (Figs 6G, H), and diverse ferns attributed to the families Dipteridaceae (Fig. 6I), Osmundaceae (Fig. 6L) and Gleicheniaceae.

## Late Cretaceous – Holocene: development of flowering plants

During the Cretaceous and early Cenozoic, global vegetation changed from mostly gymnosperms and ferns to predominantly angiosperms (flowering plants). The best known, reasonably well-dated, Late Cretaceous – Holocene floras in Western Australia are from the South West, a region now recognised as a biodiversity hotspot of global significance. In contrast to southeastern Australia, where some fossil palynofloras (pollen and spore assemblages) are well-known from continuous sedimentary successions, palynological studies in Western Australia have been limited, in part due to stratigraphic and geographic discontinuity. For this reason, many studies in the state document spore-pollen assemblages from a single palynozone, and substantial chronostratigraphic intervals are under-represented in the sedimentary record. For example, late Eocene plant megafossils and palynomorphs are well represented, whereas those from the early Eocene and late Oligocene are either absent or incompletely known.

Previous accounts of plant fossils, geology and climates through time in Western Australia (McLoughlin & Hill 1996; McLoughlin & McNamara 2001; Dodson *et al.* 2000; Dodson *et al.* 2002) are updated here to incorporate more recent research. The focus herein is on the mid-Late Cretaceous, the late Eocene and the Pliocene–Holocene for reasons mentioned above.

### MID-LATE CRETACEOUS (~83 Ma): RISE OF THE PROTEACEAE

In contrast to dinoflagellate cyst assemblages (Backhouse 2006), spore-pollen successions from the early Late Cretaceous (Cenomanian–Coniacian) of Western Australia have yet to be thoroughly documented. Available data suggest that non-magnoliid angiosperms were not introduced into Western Australian vegetation until the Cenomanian (Balme 1964). This contrasts with the records documented in southern Victoria (Dettmann 1986; Korasidis *et al.* 2016), Queensland (Dettmann 1973; Burger 1993) and Antarctica (Dettmann & Thomson 1987) that indicate the presence of this group in lower Albian (upper Lower Cretaceous) strata. Dettmann's (2017) regional study envisaged widespread Albian – early Late Cretaceous forests and woodlands dominated by Araucariaceae, Cheirolepidiaceae and Podocarpaceae with ground communities comprising ferns, lycopods and bryophytes. These conifer-dominated forests may have produced amber (Quinney *et al.* 2015) as in coeval northern hemisphere temperate forests (Barron *et al.* 2015; Peyrot *et al.* 2019).

Palynofloras are rare in mid-Upper Cretaceous (Santonian – lower Campanian) strata of the southern and central Perth Basin (Milne 2018). Numerous conifers, ferns and mosses probably grew in marshy areas near or adjacent to highly diverse communities dominated by Proteaceae (family of *Banksia* and *Grevillea*). Pollen of other flowering plants are still infrequent. The presence of charcoal indicates that the vegetation was burnt regularly. Overall, it is likely that the Perth Basin vegetation was similar to that reported from later in the Cretaceous by Carpenter *et al.* (2015, 2016); i.e., expanses of heathy vegetation with abundant Proteaceae, gymnosperms and palms, perhaps interspersed among pockets of more closed forest types with early representatives of Antarctic Beech (*Nothofagus*).

Although many of the Cretaceous proteaceous pollen types probably belong to extinct lineages, some of which continued into the early Cenozoic, several distinctive species bear striking resemblances to pollen of modern plants in Western Australia. Remarkably, *Proteacidites palisadus* (Figs 7E, F) shares important features with *Franklandia* pollen (Martin 1995; Sauquet *et al.* 2009); the two species of that genus are now found only in the state's South West. Other distinctive *Proteacidites* species include *P. annularis, P. adenanthoides* and *P. concretus. P. annularis* (Fig. 7G) is similar to pollen of *Xylomelum* (Woody Pear) and particularly to *X. occidentale*, the southernmost of the two Western Australian species (Milne 1994). *Proteacidites adenanthoides* (Fig. 7H) is akin to pollen from *Adenanthos* (Cookson 1950), a genus with its centre of diversity in the South West. *Proteacidites concretus* resembles pollen of *Macadamia* and *Helicia* (Dettmann & Jarzen 1996), genera that are native to eastern Australian rainforests. Common spores include *Cyathidites* spp., which are similar to spores produced by extant fern families Cyatheaceae and Dicksoniaceae (tree ferns), and *Clavifera triplex* (Fig. 7I), referable to Gleicheniaceae, which are now confined to northernmost regions of the state. Conifer pollen include *Phyllocladidites mawsonii* (Fig 7J) and *Lygistepollenites florinii* (Fig 7K), similar to that now produced by the Tasmanian Huon Pine and the New Zealand Rimu, respectively.

### LATE EOCENE (~40 Ma): RAINFORESTS AND HEATHLANDS CO-EXIST

Near the close of the Cretaceous, southern Western Australia was at similar latitudes to the present Antarctic coast, but a gulf then opened from the west to the Tasmanian region, with the final separation of the two continents at about 40 Ma. It is argued that climates in southern Australia during parts of the early Eocene were extremely warm (Carpenter *et al.* 2012), as elsewhere, partly due to high levels of carbon dioxide. The climate of southwestern Australia was also influenced by the combination of a shallow, sluggish, clockwise current within this gulf and warm Indian Ocean water from the tropics (Exon *et al.* 2004). The northward drifting of Australia and South America away from Antarctica resulted in the formation of a fully circumpolar ocean current and, consequently, a shift to a markedly cooler climate around the end of the Eocene.

Extensive palaeodrainage systems, such as those emptying into the vast Eucla Basin, point to overall much wetter climates in the Eocene than today (Clarke *et al.* 2003). However, pluvial climates do not necessarily produce densely rain-forested landscapes, especially

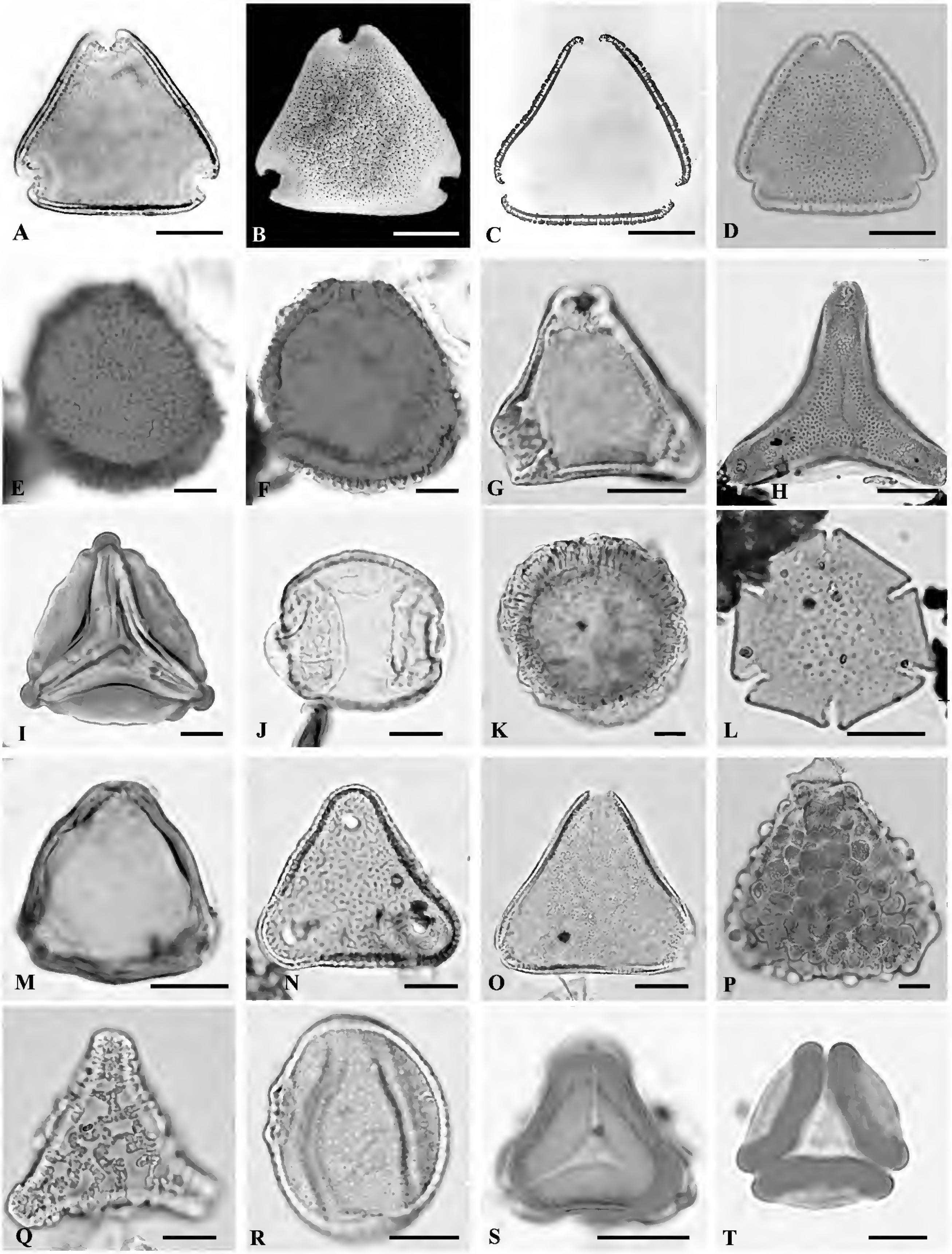

**Figure 7.** Representative Late Cretaceous and Cenozoic pollen from Western Australia: A–D *Proteacidites carobelindiae* (A medial focus TLM, B same specimen in SEM, C same specimen in TEM, D high focus); E, F *Proteacidites palisadus*, proximal and medial foci; G *Proteacidites annularis*; H *Proteacidites adenanthoides*; I *Clavifera triplex*; J *Phyllocladidites mawsonii*; K *Lygistepollenites florinii*; L *Nothofagidites* cf. *emarcidus*; M *Haloragacidites harrisii*; N *Anacolosidites acutullus*; O *Proteacidites punctiporus*; P *Proteacidites cumulus*; Q *Proteacidites reticulatus*; R *Milfordia homeopunctata*; S *Myrtaceidites eucalyptoides*; T *Eucalyptus marginata*. Scale bars: 10 μm. Ages: A–D, G, J, K, N–R, late Eocene; E, F, late Paleocene; H, I, Late Cretaceous; L, M, S, Miocene – early Pliocene; T, Holocene. See appendices for additional information.

when considering the extremely ancient and nutritionally poor nature of most Western Australian soils.

Late Eocene palynofloras include those described from the Bremer Basin (Stover & Partridge 1982), Zanthus on the western margin of the Eucla Basin (Milne 1988), Lake Lefroy near Kambalda (Itzstein-Davey 2004), the Muir–Unicup catchment near Manjimup (Al-Shawareb 2009) and Mulga Rock just north of the Eucla Basin (Mack & Milne 2015). Moss and fern spores are minor components of these assemblages. Conversely, pollen from wind-pollinated plants are abundant and include Araucariaceae; *Nothofagidites* spp. (Fig. 7L; related to the Southern Beech *Nothofagus*); and *Haloragacidites harrisii* (Fig. 7M) that embraces a range of Casuarinaceae species (she-oaks). Myrtaceae pollen, including that of *Eucalyptus* and *Melaleuca*, have been recorded in varying proportions in upper Eocene successions, being more common in the Mulga Rock assemblages than at Zanthus (Milne 1988; Mack & Milne 2015).

The late Eocene palynofloras include elements suggesting affinities with modern vegetation types characterising southern hemisphere high-latitude, temperate regions and high-altitude cool tropical regions. The rare presence of pollen assigned to *Anacolosidites acutullus* (Fig. 7N) and *Beaupreaidites elegansiformis* reflects the integration of tropical plants related to *Anacolosa* (Cookson & Pike 1954; Macphail 1999) and *Beauprea spathulaefolia* (Cookson 1950; Milne 1998b), the former of which is now confined in Australia to northern Cape York Peninsula in Queensland, and the latter is endemic to New Caledonia. These palynofloras also contain small numbers of presumably animal/insect pollinated proteaceous pollen types including *Banksieaeidites*, which have been related to modern Musgraveinae of the Queensland wet tropics and to *Banksia*; and *Proteacidites carobelindiae* (Figs 7A–D) and *P. cirritulus*, related to *Petrophile* (Mack & Milne 2015, 2016; Milne 1998b; Milne & Martin 1998). Other consistently recorded Proteaceae include *Proteacidites punctiporus* (Fig. 7O), *P. cumulus* (Fig. 7P) and *P. reticulatus* (Fig. 7Q). Collectively, these pollen signify the local presence of sclerophyllous plant communities, probably in mosaic with rainforest.

Western Australian late Eocene mega- and mesofossil evidence largely agrees with that from microfossils. Borehole samples have yielded diverse, well-preserved leaf cuticles—the outer resistant layer of a leaf that carries a 'fingerprint' of cellular details including stomata, glands, hairs and regular epidermal cells (Figs 8A, C, D, H, I; Carpenter & Pole 1995; Carpenter *et al.* 2017). The cuticular remains are generally indicative of warm and wet forest vegetation, especially *Gymnostoma* (Casuarinaceae), certain Proteaceae and Lauraceae (avocado and cinnamon family), which have numerous extant species in eastern Australian rainforests. Other fossils include the conifers, such as probable *Agathis* (Araucariaceae; Fig. 8A), *Libocedrus* (Cupressaceae), and the podocarps *Acmopyle*, *Dacrycarpus* (cf. Figs 8B, C) and *Dacrydium* (Fig. 8D). Foliage of *Nothofagus* (cf. Figs 8E, F) is also known, with one leaf species from the Kojonup Sandstone (Scriven *et al.* 1995) being strikingly similar to deciduous forms from South America. A noteworthy recent discovery from this region (by RJC) is that of the cycad *Bowenia* (Figs 8G, H), which is now represented globally by only two species in the Queensland tropics but was widespread across southern Australia during the late Paleogene (Hill *et al.* 2019).

There are also mega- and mesofossil signals of more open, sclerophyllous vegetation, which probably grew on variably swampy sites that could not support tall, closed rainforest. The apparent importance of Western Australia as a centre of sclerophyll evolution in the late Eocene (or earlier) is probably related to the state having some of the Earth's most impoverished soils (especially in phosphorus). Most notably, an apparent ancient diversification of *Banksia* is expressed in the Western Australian fossil record and may even reflect the strengthening of seasonal climates in the region. In particular, two very different late Eocene fossil *Banksia* leaf types exhibit morphologies that are classical transpiration-limiting adaptations (Hill 1998) of extant open heathland species of the South West. Thus, among the several *Banksia*-like leaf types (Figs 8J, L) in the Kojonup Sandstone is *B. paleocrypta* (Fig. 8L), which is remarkably similar to the extant *B. menziesii* (Fig. 8M) and *B. burdettii*, and features pronounced lower surface crypts with enclosed stomata (Carpenter *et al.* 2014). Another leaf type from the Zanthus lignite, *B.* sp. nov., is extremely small (< 1.5 mm wide) with leaf margins that are rolled under to almost meet at the lower midvein, a form shown by several extant South West species, including *B. nutans* and *B. tricuspis* (Carpenter & Milne in press). There is at least one other striking example of late Eocene mesofossils of Proteaceae that belong to a group well-represented in modern heathlands of the state's South West: Carpenter *et al.* (2017) documented the presence of cuticles (Fig. 8I) that are very similar to those of the snotty gobbles (*Persoonia* spp.). The Eocene–Oligocene plant assemblage preserved in lateritised strata at West Dale, southwestern Australia, represents another example of a megaflora incorporating diverse Proteaceae and Myrtaceae of sclerophyllous aspect (Hill & Merrifield 1993) associated with taxa more typical of rainforests (e.g. *Nothofagus, Gymnostoma, Agathis, Dacrycarpus* and *Retrophyllum*). The co-occurrence of mesomorphic and sclerophyllous leaf types at West Dale supports the existence of locally mixed communities incorporating some plants with high water requirements and others tolerant to water stress. It is likely that some of these plants, which evolved sclerophylly as an adaptation initially to growth on low-nutrient substrates, were pre-adapted to coping with drought as the Western Australian landscape became progressively drier following the Eocene.

## PLIOCENE–HOLOCENE: A LANDSCAPE SHAPED BY HIGHLY VARIABLE CLIMATES

Palynological studies of Neogene sediments in Western Australia are widely spread from the South West (Bint 1981) to offshore northwest (Martin & McMinn 1994); in the Yallalie Crater, c. 200 km north of Perth (Atahan *et al.* 2004; Dodson & Macphail 2004); and on the Nullarbor Plain on the state's south-easternmost border (Sniderman *et al.* 2016). All these deposits have been dated as Pliocene, but Macphail (1997) suggested that the lower part of Bint's (1981) Lake Tay deposit could be as old as late Miocene.

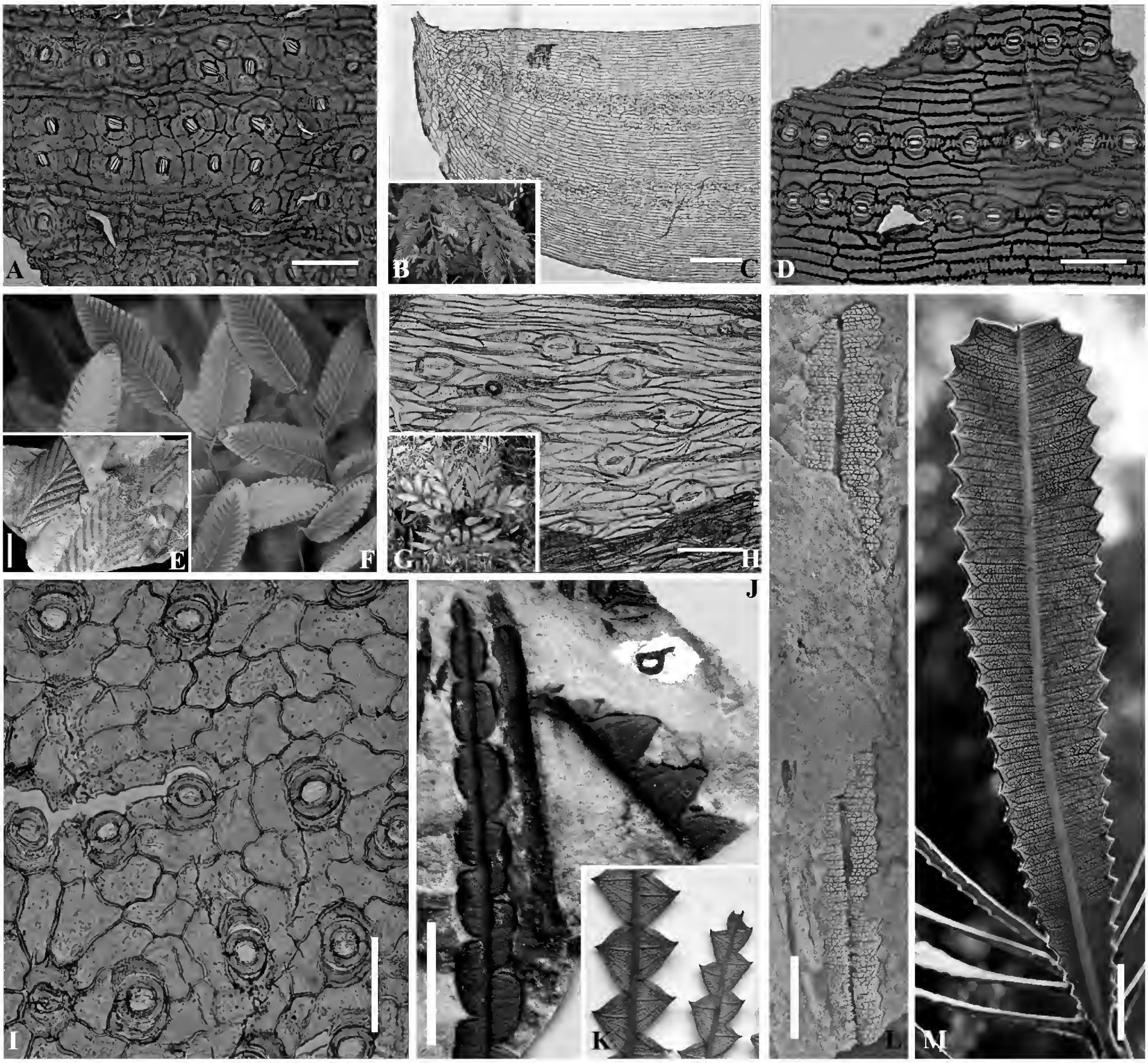

**Figure 8.** Representative Cenozoic plant mega- and mesofossils from Western Australia, and examples of extant relatives: A cuticle of Araucariaceae, probably *Agathis*; B extant *Dacrycarpus vieillardii* foliage; C apex of *Dacrycarpus* leaf; D cuticle of *Dacrydium*; E *Nothofagus plicata*; F extant *Nothofagus alpina*; G extant *Bowenia spectabilis*; H cuticle of *Bowenia*; I cuticle of Persoonieae; J *Banksia*-like foliage, UWA-118109; K extant *B. candolleana*, AQ333988; L *B. paleocrypta*, WAM; M extant *B. menziesii*. Scale bars: A, D, H, I 100 µm, C 200 µm, E, J, L 10 mm. Ages: A, C–E, H–J, L, Cenozoic; B, F, G, K, M, modern. See appendices for additional information.

A long-term trend of post-Eocene cooling and aridification is well recognised in Australia, but palynofloral evidence shows that, during the Pliocene, freshwater habitats and wet-forest plants were much more widespread than in present-day Western Australia. Sniderman *et al.* (2016) interpreted a warm/wet climatic interval within the early Pliocene on the basis of pollen assemblages from caves in the Nullarbor Plain. These authors showed that, soon after 5 Ma, in the early Pliocene, sparse shrub- or woodlands reflecting semi-aridity gave way to wetter eucalypt forests with understorey plants, including a type of *Banksia* and the spear-lily *Doryanthes*, that are now confined to coastal eastern Australia.

This relatively benign climate lasted for ~1.5 Ma (Sniderman *et al.* 2016), but mesic-adapted lineages appear to have persisted much longer, at least north of Perth. Important evidence for this comes from mid-Pliocene lake sediments within the Cretaceous 12-km-wide Yallalie asteroid impact crater (Atahan *et al.* 2004; Dodson & Macphail 2004). These sediments contain pollen of sclerophyll forest, heathland and semi-arid plant groups still present in southwestern Australia, along with other plants now confined to Australasian temperate and subtropical–tropical rainforests. The vegetation seems to have undergone repeated pronounced changes, probably in response to significant climatic fluctuations.

Despite climate variability, the overall palynological trends from the late Miocene to the Holocene show a decrease in Casuarinaceae pollen and a concomitant increase in Myrtaceae pollen (Fig. 7S), grasses, Chenopodiaceae (saltbushes) and daisies, whereas Restionaceae (Fig. 7R) abundances fluctuate. Most of the Pliocene assemblages include pollen of plants similar to extant species alongside a few wetter forest elements, such as *Araucaria, Agathis, Dacrycarpus, Dacrydium, Nothofagus* and ferns that were present as far back as the late Eocene. In contrast to Eocene sediments, even those with fossils of sclerophyllous vegetation, widespread evidence of frequent burning is apparent from the abundant charcoal observed in the Yallalie crater-fill (Dodson & Macphail 2004) and other upper Cenozoic deposits.

During the Pleistocene (~2.6 Ma to 11 700 years ago) there were even more extreme arid intervals with higher fire frequencies and successive prolonged glacial episodes (ice ages), characterising ~90% of this interval, separated by short, warm inter-glacials. These conditions likely contributed to the final demise of the remnant wetter forest elements in southwestern Australia. Nevertheless, frog fossils from the Nullarbor Plain indicate that at least seasonally moist conditions prevailed there in the early Pleistocene (Tyler & Prideaux 2016). This concurs with palynofloral evidence that the modern dominance of arid-adapted grasslands and shrublands, with chenopods and daisies, probably commenced in the middle Pleistocene (Sniderman *et al.* 2016).

During the last glacial maximum (global LGM: 21±3 ka) of the late Pleistocene, only a small region of Tasmania and southeastern Australia was glaciated (Barrows *et al.* 2002). However, very cold climatic conditions appear to have led to the demise of the eucalypt forests of the now wettest forested regions of the South West and were replaced by shrublands during an interval of perhaps 10 000 years (Sniderman *et al.* 2019).

The Holocene—the most recent epoch in Earth history—spans the last c. 11 700 years. Holocene palynofloras of the South West differ regionally, as does the vegetation of southern Western Australia today. For example, mid-Holocene palynological assemblages from Walpole (west of Albany) are dominated by eucalypt pollen (Churchill 1968; Newsome & Pickett 1993), whereas Casuarinaceae are the more prominent elements of the contemporary palynoflora of Two Mile Lake, south of the Stirling Ranges (Itzstein-Davey 2004). Palynofloras from peat near Manjimup indicate communities containing Casuarinaceae and eucalypts, with a heath understorey, in the early Holocene; and in the middle Holocene, alternating dominance of *Corymbia calophylla* (Marri) and *Eucalyptus marginata* (Jarrah, Fig. 7T) forests, with *Melaleuca* woodlands in wetland areas (Dodson & Lu 2000). The mid- to late Holocene palynofloras from Barker Swamp, Rottnest Island, suggest widespread *Callitris* (Rottnest Island Pine) forest with sedges (Cyperaceae) growing in the immediate vicinity, together with woodland incorporating tuart (*Eucalyptus gomphocephala*) and jarrah (Backhouse 1993). Late Holocene charcoal laminae in Barker Swamp are followed by a decline in *Callitris*, reflecting changes to a more open vegetation dominated by Asteraceae (daisies).

Newsome & Pickett (1992), Dodson & Lu (2000) and Itzstein-Davey (2004) concur that the mid- to late Holocene in southwestern Australia appears to have experienced relative climatic stability and that the vegetation was not unlike that of today. Fluctuations in pollen assemblages of lake and swamp sediments were evidently due more to local environmental changes (e.g. burning patterns, other species interactions, facies changes) than to major climatic changes.

## SUMMARY AND CONCLUSIONS

This review of broad trends in Western Australian plant communities and landscape evolution over the past 470 Ma (summarised in Fig. 9) is underpinned by substantial palaeobotanical and palynological data published since 1960. The earliest terrestrial Western Australian plant communities are Middle Ordovician based on palaeontological data, including palynological and molecular records, from the Canning Basin. Ordovician–Devonian palynological data are mainly from the Canning Basin. Late Devonian arborescent communities were widespread across the state. The Mississippian flora is inferred almost exclusively from palynological data sourced from the Canning, Carnarvon and Perth basins.

The oldest known pollen are dated as late Serpukhovian (latest Mississippian) indicating the colonisation of drylands by gymnosperms. The scarce record for the Pennsylvanian reflects a major cooling episode, resulting in the establishment of an extensive ice sheet covering the state. The Permian flora, developed in the aftermath of the preceeding ice age, is particularly well represented by palyno- and megafloral assemblages, both signifying the prevalence of swampy lowland plant communities dominated by arborescent *Glossopteris*.

The megafloral and palynological evidence from the Early–Middle Triassic indicates a distinctive, low-diversity flora comprising mainly herbaceous lycopsids, ferns and other low-stature plants replaced eventually by seed ferns typified by *Dicroidium*. The major turnover in Western Australia's vegetation during the Triassic–Jurassic transition is reflected by the replacement of *Falcisporites* (produced by *Dicroidium*) by *Classopollis* (Cheirolepidaceae), the latter becoming dominant in palynological assemblages. Upper Jurassic – Lower Cretaceous successions provide a rich and diverse megafloral and palynological record documenting the evolution and radiation of conifer and fern families with extant representatives. The colonisation of the landscape by flowering plants during the Barremian–Albian (late Early Cretaceous) remains poorly constrained temporally. Palynological successions of the Perth Basin indicate that Proteaceae were probably significant components of the Campanian vegetation.

Palynological and palaeobotanical evidence points to the presence of mixed floral communities (rainforests and sclerophyllous vegetation) during the Eocene. Palynological data from the Pliocene indicate short-lived resurgences of wetter conditions and associated expansion of wet forests within the long-term Neogene cooling and aridification of the Western Australian climate. In the middle Pleistocene, arid-adapted,

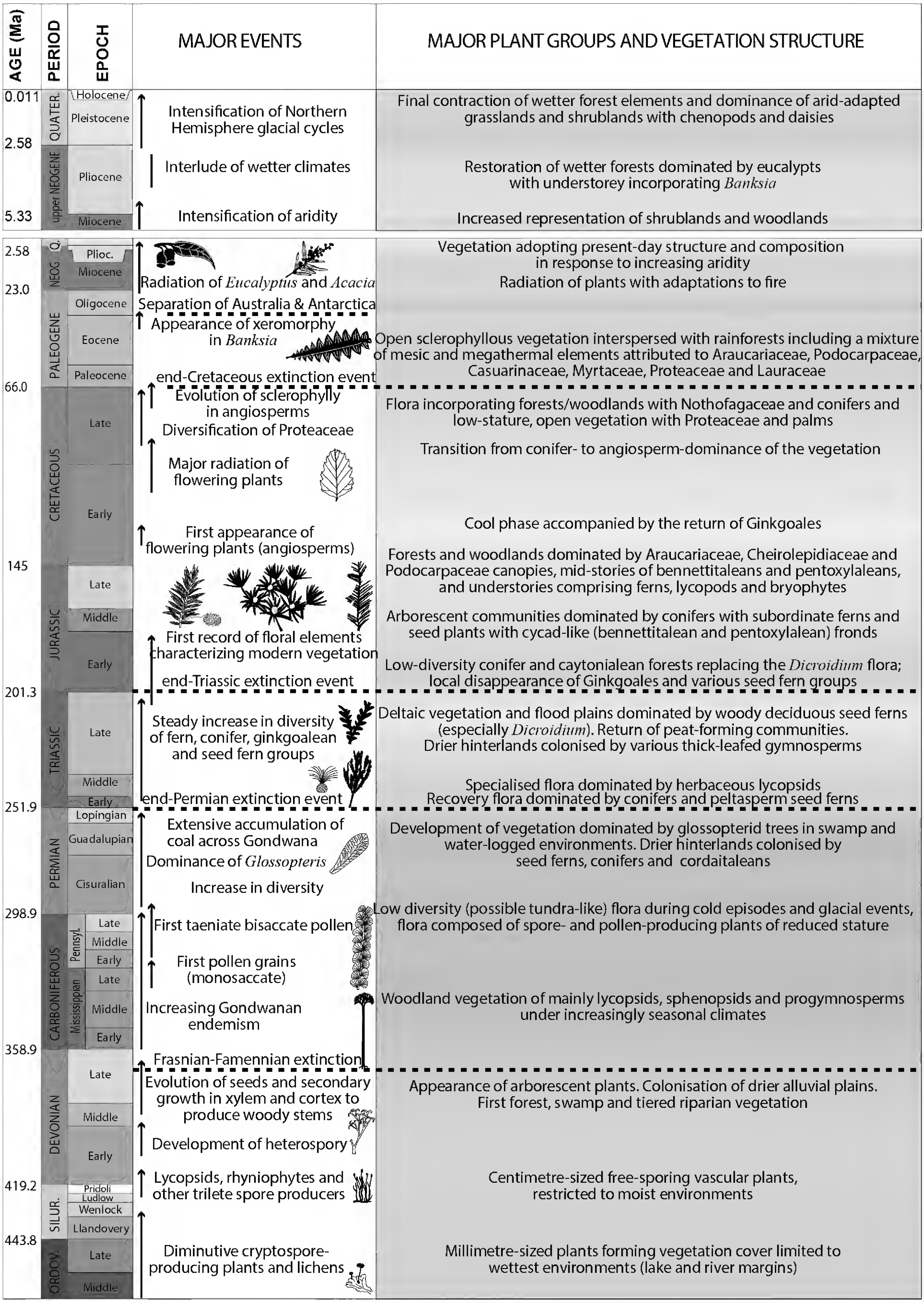

**Figure 9.** Major plant-evolutionary events and vegetation changes in Western Australia. The blue and red backgrounds represent cooler and warmer episodes, respectively.

fire-tolerant grasslands and shrublands replaced the last stands of mesothermal forests dominated by Araucariaceae, Podocarpaceae and Nothofagaceae. In the mid-late Holocene, the vegetation of the South West developed into that which we know today: a mosaic of sclerophyll forests and woodlands, heath and wetlands.

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Repository abbreviations: AMF—Australian Museum, Sydney, AQ— Accession Queensland, Queensland Herbarium, GSWA—Geological Survey of Western Australia, NRM—Swedish Museum of Natural History, Stockholm, UWA—University of Western Australia, WAM—Western Australian Museum.

## Appendix 1.

Information (age, stratigraphy, location and source) relative to the localities and petroleum wells mentioned in the text.

### Table 1

Localities, stratigraphic units and ages for the figured specimens.

| Taxa | Figure | Locality | Depth (m) | Unit | Age | Reference (or location of specimen) |
|---|---|---|---|---|---|---|
| *Velatitetras laevigata* | 2A | Theia 1 | 1217.67–17.7 | Goldwyer Fm | Early–Middle Ordovician | Spaak *et al.* (2017) |
| indeterminate cryptospore | 2B | Theia 1 | 1217.67–17.7 | Goldwyer Fm | Early–Middle Ordovician | Spaak *et al.* (2017) |
| *Geminospora lemurata* | 2C,D | | | Gneudna Fm | Frasnian (Late Devonian) | uncatalogued, at UWA |
| *Rhabdosporites langii* | 2E | BMR 2 Laurel Downs | 517.2–20.3 | Fairfield Group | late Famennian (Late Devonian) | Balme & Hassell (1962) |
| *Verrucosisporites scurrus* | 2F | | | Gneudna Fm | Frasnian (Late Devonian) | uncatalogued, Balme (1988) |
| *Emphanisporites annulatus* | 2G | | | Gneudna Fm | Frasnian (Late Devonian) | uncatalogued, at UWA |
| *Emphanisporites rotatus* | 2H | Uranerz CDH8 | | Gneudna Fm | Frasnian (Late Devonian) | Balme (1988) |
| *Gneudnaspora divellomedia* | 2I | Aquitaine DDH4 | | Gneudna Fm | Frasnian (Late Devonian) | Balme (1988) |
| *Ancyrospora langii* | 2J | | | Gneudna Fm | Frasnian (Late Devonian) | uncatalogued, at UWA |
| *Retispora lepidophyta* | 2K | Stumpy Soak 2 | 25.6 | Fairfield Group | late Famennian (Late Devonian) | Balme & Hassell (1962) |
| *Convolutispora fromensis*, holotype | 2L | Frome Rocks 2 | 1310.6–12.1 | Luluigui Fm | late Famennian (Late Devonian) | Balme & Hassell (1962) |
| *Granulatisporites frustulentus*, holotype | 2M | BMR 2 Laurel Downs | 514.4–17.2 | Fairfield Group | late Famennian (Late Devonian) | Balme & Hassell (1962) |
| *Claytonispora distincta* | 2N | Meda 1 | 1541–43 | Laurel Fm | Early Carboniferous (~Tournaisian) | Playford (1972) |
| *Diatomozonotriletes birkheadensis* | 2O | YCH 2 | 170.1 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Anapiculatisporites amplus* | 2P | YCH 2 | 118.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Raistrickia accincta* | 2Q | YCH 2 | 170.1 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Raistrickia corymbiata*, holotype | 2R | YCH 2 | 170.1 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Reticulatisporites magnidictyus* | 2S | Minderoo 1 | 607.2 | ?Quail Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Auroraspora solisorta* | 2T | Gnarloo 1 | 476.4 | ?Quail Fm | mid-Carboniferous | Playford & Mory (2017) |
| *Grandispora maculosa* | 3A | DDH CL5 | 179.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015) |
| *Psomospora detecta* | 3B | YCH 2 | 118.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Indotriradites daemonii* | 3C | DDH CL5 | 179.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015) |
| *Indotriradites kuttungensis* | 3D | YCH 2 | 231.5 | ?Nangetty Fm | mid-Carboniferous | Playford (2015), Playford & Mory (2017) |
| *Velamisporites cortaderensis* | 3E | DDH CL5 | 179.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015) |
| *Verrucosisporites quasigobbettii* | 3F | DDH CL5 | 179.8 | ?Nangetty Fm | mid-Carboniferous | Playford (2015) |
| *Spelaeotriletes ybertii* | 3G | Blackstone 1 | 1448.8–62.1 | Reeves Fm | mid-Carboniferous | slide held by GSWA (WAPIMS) |
| *Plicatipollenites* sp. | 3H | Scarpia 1 | 1459 | Anderson Fm | Early Carboniferous (~Visean) | slide held by GSWA (WAPIMS) |
| *Potonieisporites* sp. | 3I | Scarpia 1 | 1459 | Anderson Fm | Early Carboniferous (~Visean) | slide held by GSWA (WAPIMS) |
| *Calamospora* sp. | 3J | Scarpia 1 | 1459 | Anderson Fm | Early Carboniferous (~Visean) | slide held by GSWA (WAPIMS) |
| *Punctatisporites gretensis* | 3K | Hebburn No. 2 Colliery, NSW. | | Main Greta Seam | late Early Permian | rephotographed holotype<br>(slide held by UWA) |
| *Secarisporites* sp. | 3L | Blackstone 1 | 1448.8–62.1 | Reeves Fm | mid-Carboniferous | slide held by GSWA (WAPIMS) |
| *Protohaploxypinus samoilovichii* | 3M | outcrop | | Kockatea Shale | Early Triassic | Haig *et al.* (2015) |
| *Dulhuntyispora parvithola* | 3N | Pyramid Bore | undiff. cuttings | Hardman Fm | Middle–Late Permian | GSWA sample 185801 |
| *Horriditriletes tereteangulatus* | 3O | Fraser River 1 | 574.5 | Grant Group | Early Permian | slide held by GSWA (WAPIMS) |
| *Microbaculispora tentula* | 3P | Point Moody 1 | 838.2–51.2 | Grant Group | ~Early Permian | slide held by GSWA (WAPIMS) |
| *Lundbladispora willmotii* | 3Q | Lynher 1 | 2682–697.5 | Nome Fm | Late Triassic | slide held by GSWA (WAPIMS) |

**Table 1**. (cont.)

| Taxa | Figure | Locality | Depth (m) | Unit | Age | Reference (or location of specimen) |
|---|---|---|---|---|---|---|
| *Kraeuselisporites cuspidus* | 3R | Batavia 1 | 2565 m | Kockatea Shale | Early Triassic | Geoscience Australia, slide 1977430 |
| *Aratrisporites banksii* | 3S | ODP-760A | 380.6 | Mungaroo Fm | Late Triassic | slide held by Chevron Australia |
| *Falcisporites australis* | 3T | Roc 1 | 3360–70 m | Keraudren Fm | Early Triassic | slide held by GSWA (WAPIMS) |
| Lepidodendroid lycopsid trunk | 4A | outcrop | – | Kellys Knob Ss | Frasnian (Late Devonian) | Mory & Beere (1988) |
| *Ottokaria bullata* | 4B | Irwin River (N Branch) | – | Irwin River CM | Early Permian | McLoughlin (1995) |
| *Raniganjia minima* | 4C | Muja pit, Collie | – | Muja CM | Middle Permian | McLoughlin (1992) |
| *Paracalamites australis* | 4D | Stockton pit, Collie | – | Ewington CM | Early Permian | specimen held by NRM |
| *Glossopteris* sp. | 4E | Stockton pit, Collie | – | Ewington CM | Early Permian | specimen held by NRM |
| *Sphenophyllum morganae* | 4F | Irwin River (N Branch) | – | Irwin River CM | Early Permian | McLoughlin (1992) |
| *Liknopetalon* sp. | 4G | Irwin River (N Branch) | – | Irwin River CM | Early Permian | Adendorff *et al.* (2003) |
| *Gondwanophyton daymondii* | 4H | Irwin River (N Branch) | – | Irwin River CM | Early Permian | McLoughlin (1992) |
| *Noeggerathiopsis* sp. | 4I | Muja pit, Collie | – | Muja CM | Middle Permian | McLoughlin & McNamara (2001) |
| *Vertebraria australis* | 4J | Mount Talbot | – | Condren Ss | Middle Permian | specimen held by NRM |
| *Bergiopteris* sp. cf. *B. archangelskyi* | 4K | Irwin River (S Branch) | – | Wagina Ss | Late Permian | McLoughlin (1995) |
| *Sphenophyllum rhodesii* | 4L | Irwin River (N Branch) | – | Irwin River CM | Early Permian | McLoughlin (1992) |
| *Ephedripites macistriatus* | 5A | ODP-760A | 241 | Mungaroo Fm | Late Triassic | slide held by Chevron Australia |
| *Minutosaccus crenulatus* | 5B | ODP-760A | 241 | Mungaroo Fm | Late Triassic | slide held by Chevron Australia |
| *Samaropollenites speciosus* | 5C | ODP-760A | 94.13 | Mungaroo Fm | Late Triassic | slide held by Chevron Australia |
| *Aulisporites astigmosus* | 5D | ODP-760B | 380.6 | Mungaroo Fm | Late Triassic | slide held by Chevron Australia |
| *Classopollis* sp | 5E, F | Badaminna 1 | 1543.8 | Cattamarra CM | Early Jurassic | slide held by UWA |
| *Callialasporites turbatus* | 5G | Badaminna 1 | 1148.3 | Cadda Fm | Middle Jurassic | slide held by UWA |
| *Callialasporites dampieri* | 5H | Badaminna 1 | 1413.9 | Cattamarra CM | Early–Middle Jurassic | slide held by UWA |
| *Araucariacites australis* | 5I | Gingin 1 | 1412 | Yarragadee Fm | Late Jurassic | slide held by UWA |
| *Ischyosporites marburgensis* | 5J, K | Badaminna 1 | 1303.6 | Cattamarra CM | Early–Middle Jurassic | slide held by UWA |
| *Matonisporites crassiangulatus* | 5L | Hill River 2A | 80.9 | Cattamarra CM | Early–Middle Jurassic | slide held by UWA |
| *Cyathidites minor* | 5M | Badaminna 1 | 694.9 | Yarragadee Fm | Late Jurassic | slide held by UWA |
| *Osmundacidites welmanii* | 5N | Badaminna 1 | 1543.8 | Cattamarra CM | Early Jurassic | slide held by UWA |
| *Microcachryidites antarcticus* | 5O | BH16 | 27.07 | Warnbro Group | Early Cretaceous | slide to be submitted to GSWA |
| *Staplinisporites caminus* | 5P | Investigator 1 | 1635 | Barrow Group | Early Cretaceous | slide held by GSWA (WAPIMS) |
| *Foveosporites subtriangularis* | 5Q | Harvey 1 | 165–180 | Leederville Fm | Early Cretaceous | slide held by GSWA (WAPIMS) |
| *Retitriletes circolumenus* | 5R, S | Investigator 1 | 1513 | Barrow Group | Early Cretaceous | slide held by GSWA (WAPIMS) |
| *Retitriletes clavatoides* | 5T | Investigator 1 | 1513 | Barrow Group | Early Cretaceous | slide held by GSWA (WAPIMS) |
| cf. *Nymboidiantum multilobatum* | 6A | Glengarry near Geraldton | | Kockatea Shale | Early Triassic | Haig *et al.* (2015) |
| *Sphenopteris* sp. | 6B | 5 km N of Mingenew | – | Yarragadee Fm | Late Jurassic | McLoughlin & Pott (2009) |
| *Pagiophyllum amanguanus* | 6C | 6 km N of Mingenew | – | Yarragadee Fm | Late Jurassic | McLoughlin & Pott (2009) |
| *Otozamites linearis* | 6D | 7 km N of Mingenew | – | Yarragadee Fm | Late Jurassic | McLoughlin & Pott (2009) |
| *Elatocladus confertus* | 6E | 8 km N of Mingenew | – | Yarragadee Fm | Late Jurassic | McLoughlin & Pott (2009) |
| *Ptilophyllum cutchense* | 6F | 9 km N of Mingenew | – | Yarragadee Fm | Late Jurassic | McLoughlin & Pott (2009) |
| *Isoetites elegans* | 6G | near Gingin | – | Leederville Fm | Early Cretaceous | Walkom (1944) |
| *Hausmannia* sp. | 6H | near Gingin | – | Leederville Fm | Early Cretaceous | Walkom (1944) |
| megaspores associated with *Isoetites elegans* | 6I | Gantheaume Point | – | Broome Ss | Early Cretaceous | McLoughlin (1996) |
| *Ptilophyllum cutchense* | 6J | near Gingin | – | Leederville Fm | Early Cretaceous | McLoughlin (1996) |
| *Taeniopteris daintreei* | 6K | WAPET outcrop NH3 | – | Nanutarra Fm | Early Cretaceous | not previously illustrated |

**Table 1**. (cont.)

| Taxa | Figure | Locality | Depth (m) | Unit | Age | Reference (or location of specimen) |
|---|---|---|---|---|---|---|
| *Cladophlebis* sp. cf. *C. oblonga* | 6L | Gantheaume Point | – | Broome Ss | Early Cretaceous | McLoughlin (1996) |
| *Ptilophyllum acutifolium* | 6M | Jubrico Creek | | Nanutarra Fm | Early Cretaceous | McLoughlin (1996) |
| *Nathorstianella babbagensis* | 6N | Gantheaume Point | – | Broome Ss | Early Cretaceous | McLoughlin (1996) |
| *Komlopteris* sp. cf. *K. indica* | 6O | near Gingin | – | Leederville Fm | Early Cretaceous | McLoughlin (1996) |
| *Proteacidites carobelindiae* | 7A–C | Balladonia 15 | 63 | ?Pallinup Fm | late Eocene | Milne (1998) |
| *Proteacidittes carobelindiae* | 7D | Zanthus 11 | 39 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Proteacidites palisadus* | 7E, F | Mullalo Production Bore 02/13 | 33–36 | Kings Park Fm | late Paleocene | Milne (2018) |
| *Proteacidites annularis* | 7G | Zanthus 11 | 37 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Proteacidites adenanthoides* | 7H | Mullalo Production Bore 02/13 | 156–159 | ?Poison Hill Gs | Late Cretaceous | Milne (2018) |
| *Clavifera triplex* | 7I | Mullalo Production Bore 02/13 | 156–160 | ?Poison Hill Gs | Late Cretaceous | Milne (2018) |
| *Phyllocladidites mawsonii* | 7J | Zanthus 11 | 41 | ?Pallinup Fm | late Eocene | Carpenter & Milne (in press) |
| *Lygistepollenites florinii* | 7K | Mulga Rock | 53.9 | unamed | late Eocene | Mack (2016) |
| *Nothofagidites* cf. *emarcidus* | 7L | Lake Wells | 123.8–124 | unamed | Miocene – lower Pliocene | sample held by Curtin |
| *Haloragacidites harrisii* | 7M | Lake Wells | 119.9–112 | unamed | Miocene – lower Pliocene | sample held by Curtin |
| *Anacolosidites acutullus* | 7N | Zanthus 11 | 39 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Proteacidites punctiporus* | 7O | Zanthus 11 | 37 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Proteacidites cumulus* | 7P | Zanthus 11 | 41 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Proteacidites reticulatus* | 7Q | Zanthus 11 | 38 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Milfordia homeopunctata* | 7R | Zanthus 11 | 41 | ?Pallinup Fm | late Eocene | sample held by Curtin |
| *Myrtaceidites eucalyptoides* | 7S | Lake Wells | 119.9–112 | unamed | Miocene – lower Pliocene | sample held by Curtin |
| *Eucalyptus marginata* | 7T | South West | | unamed | Holocene | sample held by Curtin |
| probably *Agathis* | 8A | Muir-Unicup core MU11 | 22.19–22.23 | unnamed | Cenozoic (late Eocene) | Al-Shawareb (2009) |
| *Dacrycarpus vieillardii* | 8B | New Caledonia | | | modern | NA |
| *Dacrycarpus* sp. | 8C | Muir-Unicup core MU11 | 72.8–72.9 | Werillup Fm | Cenozoic (late Eocene) | Al-Shawareb (2009) |
| *Dacrydium* sp. | 8D | Muir-Unicup core MU11 | 22.6–22.63 | Werillup Fm | Cenozoic (late Eocene) | Al-Shawareb (2009) |
| *Nothofagus plicata* | 8E | Walebing | | Kojonup Ss | Cenozoic (late Eocene) | uncatalogued |
| *Nothofagus alpina* | 8F | southern South America | | | modern | NA |
| *Bowenia spectabilis* | 8G | Daintree rainforest, Queensland | | | modern | NA |
| *Bowenia* sp. | 8H | Muir-Unicup core MU11 | 22.19–22.23 | Werillup Fm | Cenozoic (late Eocene) | Al-Shawareb (2009) |
| Persoonieae | 8I | Muir-Unicup core MU11 | 22.88–22.97 | Werillup Fm | Cenozoic (late Eocene) | Al-Shawareb (2009) |
| *Banksia*-like foliage | 8J | Muradup | | Kojonup Ss | Cenozoic (late Eocene) | specimen held by UWA |
| *B. candolleana* | 8K | Southwestern Australia | | | modern | NA |
| *B. paleocrypta* | 8L | Walebing | | Kojonup Ss | Cenozoic (late Eocene) | unregistered, Carpenter *et al.* (2014) |
| *B. menziesii* | 8M | Southwestern Australia | | | modern | NA |

| | |
|---|---|
| CM - coal measures | Curtin - Curtin University |
| Fm - Formation | GSWA - Geological Survey of Western Australia http://dmp.wa.gov.au/Petroleum-and-Geothermal-1497.aspx |
| Gs - Greensand | NRM - Swedish Museum of Natural History |
| Ss - Sandstone | UWA - E. de C.C. Earth Science Museum, The University of Western Australia |

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**Table 2**.
Locations mentioned in text and Table 1 arranged by basin.

| Basin | Petroleum well, mineral drillhole or locality | Sub-basin | Latitude (°S) | Longitude (°E) |
|---|---|---|---|---|
| Bonaparte | outcrop near Cockatoo Fault | Burt Range Sub-basin | 15.916556 | 129.087528 |
| Browse | Lynher 1 | Barcoo Sub-basin | 15.938714 | 121.084352 |
| Canning | Blackstone 1 | Lennard Shelf | 17.585533 | 124.353049 |
| Canning | BMR 2 Laurel Downs | Lennard Shelf | 18.1183 | 125.3347 |
| Canning | Culvida Soak | Gregory Sub-basin | ~20.227 | ~126.929 |
| Canning | Fraser River 1 | Fitzroy Trough | 17.416157 | 123.163617 |
| Canning | Frome Rocks 2 | Jurgurra Terrace | 18.253879 | 123.661253 |
| Canning | Gantheaume Point | Jurgurra Terrace | 17.974300 | 122.177098 |
| Canning | Meda 1 | Lennard Shelf | 17.397533 | 124.193587 |
| Canning | Mount Talbot | Fitzroy Trough | 18.85548 | 126.09332 |
| Canning | Point Moody 1 | Gregory Sub-basin | 21.259444 | 127.806111 |
| Canning | Pyramid Bore | Fitzroy Trough | 18.359333 | 124.659333 |
| Canning | Scarpia 1 | Fitzroy Trough | 18.052141 | 124.844624 |
| Canning | Stumpy Soak 2 (water bore) | Lennard Shelf | ~17.8 | ~125.1 |
| Canning | Theia 1 | Broome Platform | 18.901072 | 123.293867 |
| ?Eucla | Mulga Rock | NA | ~29.985 | ~123.81 |
| Eucla | Zanthus 11 | Balladonia Shelf | 31.9371 | 123.4942 |
| Northern Carnarvon | Investigator 1 | Exmouth Plateau | 20.350531 | 112.96841 |
| Northern Carnarvon | Jubrico Creek | Peedamullah Shelf | 22.5256 | 115.3202 |
| Northern Carnarvon | Long Island 1 | Barrow Sub-basin | 21.619527 | 114.68939 |
| Northern Carnarvon | Minderoo 1 | Peedamullah Shelf | 21.845944 | 115.079793 |
| Northern Carnarvon | ODP 122-760A | Wombat Plateau | 16.9220 | 115.5413 |
| Northern Carnarvon | ODP 122-760B | Wombat Plateau | 19.9207 | 112.2540 |
| Northern Carnarvon | Onslow 1 | Barrow Sub-basin | 21.765225 | 114.875997 |
| Northern Carnarvon | WAPET NH3 | Peedamullah Shelf | 22.14861 | 115.45694 |
| overlies Yilgarn Craton | Lake Wells | NA | 27.2339 | 122.9922 |
| overlies Yilgarn Craton | Muir-Unicup core MU11 | NA | 34.339013 | 116.824689 |
| overlies Yilgarn Craton | Muradup | NA | 33.91 | 116.91 |
| overlies Yilgarn Craton | Walebing | NA | 30.69 | 116.225 |
| overlies Yilgarn Craton | West Dale | NA | 32.227 | 116.603 |
| Perth | Badaminna 1 | Dandaragan Trough | 31.340721 | 115.668695 |
| Perth | Batavia 1 | Abrolhos Sub-basin | 28.898403 | 114.261554 |
| Perth | CRA Coolcalalaya YCH2 | Coolcalalaya Sub-basin | 27.731861 | 115.109067 |
| Perth | DDH CL5 | Irwin Terrace | 28.369 | 115.411 |
| Perth | Ewington open cut mine | Collie Sub-basin | 33.21731 | 116.15039 |
| Perth | Gingin 1 | Beermullah Trough | 31.143056 | 115.827222 |
| Perth | Gingin, 3 km NNE of town | Beermullah Trough | 31.324 | 115.9217 |
| Perth | Glengarry, near Geraldton | Greenough Shelf | 28.83 | 114.79 |
| Perth | Harvey 1 | Mandurah Terrace | 32.991886 | 115.774489 |
| Perth | Hill River 2A | Dandaragan Trough | 30.182535 | 115.247214 |
| Perth | Irwin R (N Branch) | Irwin Terrace | 28.9386 | 115.5484 |
| Perth | Irwin R (S Branch) | Irwin Terrace | 28.9587 | 115.5545 |
| Perth | Lanco Bunbury Port Engineering BH16 | Bunbury Trough | 33.4451389 | 115.685167 |
| Perth | Mingenew, road cutting 5 km N of town | Wicherina Terrace | 29.1454 | 115.4414 |
| Perth | Muja Pit, Collie | Collie Sub-basin | 33.25564 | 116.18788 |
| Perth | Mullaloo Production Bore 02/13 | Mandurah Terrace | 31.99366 | 115.88298 |
| Perth | Stockdale Pit, Collie | Collie Sub-basin | 33.21731 | 116.15039 |
| Perth | YCH 2 | Coolcalalaya Sub-basin | 27.718194 | 114.995917 |
| Roebuck | Roc 1 | Bedout Sub-basin | 18.8807 | 118.8225 |
| Southern Carnarvon | Aquitaine & Uranerz boreholes | Merlinleigh Sub-basin | 23.6 – 24.1 | 115.1 – 115.2 |
| Southern Carnarvon | Coburn 1 | Gascoyne Platform | 26.4203 | 114.1331 |
| Southern Carnarvon | Gnaraloo 1 | Gascoyne Platform | 23.675645 | 113.786241 |
| Southern Carnarvon | Yaringa 1 | Gascoyne Platform | 26.064852 | 114.36111 |

**Appendix 2**. Taxa cited in the main text and in explanations of figures 2–8. Megascopic remains are preceded by #, extant species or genera by ♦, and marine cysts by ◊.

♦ *Adenanthos* Labillardière, 1805
*Anacolosidites acutullus* Cookson & Pike, 1954
# *Agathis* Salisbury, 1807
♦ *Anacolosa* (Blume, 1826) Blume, 1850
*Anapiculatisporites amplus* Playford & Powis, 1979
*Anapiculatisporites concinnus* Playford, 1962
*Ancyrospora langii* (Taugourdeau-Lantz, 1960) Allen, 1965
*Aratrisporites banksii* Playford, 1965
# *Araucaria* Jussieu, 1789
*Araucariacites australis* Cookson, 1947 ex Couper, 1953
# *Araucarioxylon* Kraus, 1870
# *Arberia* White, 1908
*Aulisporites astigmosus* (Leschik, 1956) Klaus, 1960
*Auroraspora solisorta* Hoffmeister, Staplin & Malloy, 1955
*Baculatisporites* Pflug & Thomson, 1953
♦ *Banksia candolleana* Meissner, 1855
♦ *Banksia menziesii* R. Brown, 1830
♦ *Banksia nutans* R. Brown, 1810
# *Banksia paleocrypta* Carpenter, McLoughlin, Hill, McNamara & Jordan, 2014
♦ *Banksia tricuspis* Meissner, 1855
*Banksieaeidites* Cookson, 1950
# *Baragwanathia longifolia* Lang & Cookson, 1935
♦ *Beauprea spathulaefolia* Virot, 1968.
*Beaupreaidites diversiformis* Milne, 1998
*Beaupreaidites elegansiformis* Cookson, 1950 emend. Milne, 1998.
# *Bergiopteris* sp. cf. *B. archangelskyi* Rigby, 1991
♦ *Bowenia spectabilis* W. Hooker ex J. Hooker, 1863
*Calamospora* Schopf, Wilson & Bentall, 1944
*Callialasporites dampieri* (Balme, 1957) Sukh Dev, 1961
*Callialasporites turbatus* (Balme, 1957) Schultz, 1967
♦ *Callitris preissii* Miquel, 1845
*Calyptosporites proximocavatus* Balme, 1988
*Camerosporites* Leschik, 1956
*Classopollis* Pflug, 1953
# *Cladophlebis* sp. cf. C. oblonga Halle, 1913
*Clavifera triplex* (Bolkhovitina, 1953) Bolkhovitina, 1966
*Claytonispora distincta* (Clayton, 1971) Playford & Melo, 2012
*Convolutispora fromensis* Balme & Hassell, 1962
♦ *Corymbia calophylla* (Lindley, 1841) K.D.Hill & L.A.S. Johnson, 1995
*Cristatisporites triangulatus* (Allen, 1965) McGregor & Camfield, 1982
*Cyathidites minor* Couper, 1953
*Cyclogranisporites* R. Potonié & Kremp, 1954
*Cymbosporites hormiscoides* Balme, 1988
# *Dacrydium* Solander, 1786 ex Lambert, 1807
# *Dacrycarpus vieillardii* (Parlatore, 1868) de Laubenfels, 1969
*Densoisporites* Weyland & Krieger, 1953
*Diatomozonotriletes birkheadensis* Powis, 1984
# *Dicroidium* Gothan, 1912
♦ *Doryanthes* Corrêa, 1802
*Dulhuntyispora parvithola* (Balme & Hennelly, 1956) Potonié, 1960
*Elatocladus confertus* (Oldham & Morris, 1863) Halle, 1913
♦ *Eucalyptus gomphocephala* de Candolle, 1828
♦ *Eucalyptus marginata* Smith, 1802
# *Glossopteris* Brongniart, 1828 ex Brongniart, 1831
# *Gondwanophyton daymondii* Rigby, 1993
*Grandispora maculosa* Playford & Helby, 1968
*Granulatisporites frustulentus* Balme & Hassell, 1962
♦ *Grevillea* R. Brown ex Knight, 1810
*Haloragacidites harrisii* (Couper, 1953) Harris, 1971
# *Hausmannia* Dunker, 1846
♦ *Helicia* Loureiro, 1790
*Horriditriletes tereteangulatus* (Balme & Hennelly, 1956) Backhouse, 1991
*Indotriradites daemonii* Loboziak, Melo, Playford & Streel, 1999
*Indotriradites kuttungensis* (Playford & Helby, 1968) Playford, 1991
*Infernopollenites* Scheuring, 1970
*Ischyosporites marburgensis* de Jersey, 1963
# *Isoetites elegans* Walkom, 1944
*Kraeuselisporites cuspidus* Balme, 1963
# *Komlopteris* sp. cf. *K. indica* (Feistmantel, 1877) Barbacka, 1994
# *Lepidodendron* Sternberg, 1820
# *Libocedrus* Endlicher, 1847
# *Liknopetalon* Smithies, 1985 emend. Adendorff, Bamford & McLoughlin, 2003
*Lundbladispora willmotti* Balme, 1963
*Lygistepollenites florinii* (Cookson & Pike, 1954) Stover & Evans, 1973
*Matonisporites crassiangulatus* (Balme, 1957) Dettmann, 1963
♦ *Macadamia* F. Mueller, 1857
♦ *Melaleuca* Linnaeus, 1767
*Microbaculispora tentula* Tiwari, 1965
*Microcachryidites antarcticus* Cookson, 1947
*Minutosaccus crenulatus* Dolby & Balme, 1976
◊ *Micrhystridium* Deflandre, 1937
*Milfordia homeopunctata* (McIntyre, 1965) Partridge, 1973
*Myrtaceidites eucalyptoides* Cookson & Pike, 1954
# *Nathorstianella babbagensis* (Woodward, 1895) Glaessner & Rao, 1955

# cf. *Nymboidiantum multilobatum* Holmes, 2003

# *Noeggerathiopsis* Feistmantel, 1879

*Nothofagidites* sp. cf. *N. emarcidus* (Cookson, 1958) Harris, 1964

# *Nothofagus plicata* Scriven, McLoughlin & Hill, 1995

♦ *Nothofagus alpina* (Poepping & Endlicher, 1838) A.S. Ørsted, 1871

# *Nothorhacopteris argentinica* (Geinitz, 1876) Archangelsky, 1983

*Osmundacidites wellmanii* Couper, 1953

# *Ottokaria bullata* McLoughlin, 1995

# *Otozamites linearis* Halle, 1913

*Ovalipollis* Krutzsch, 1955

# *Pagiophyllum amanguanus* McLoughlin & Pott, 2009

# *Paracalamites australis* Rigby, 1966

♦ *Persoonia* Smith, 1798

♦ *Petrophile* R. Brown ex Knight, 1810

*Phyllocladidites mawsonii* Cookson, 1947 ex Couper, 1953

*Plicatipollenites* Lele, 1964

*Potonieisporites* Bhardwaj, 1954

*Proteacidites adenanthoides* Cookson, 1950

*Proteacidites annularis* Cookson, 1950

*Proteacidites carobelindiae* Milne, 1998

*Proteacidites cirritulus* Milne, 1998

*Proteacidites concretus* Harris, 1972

*Proteacidites cumulus* Stover & Partridge, 1982

*Proteacidites palisadus* Couper, 1953

*Proteacidites punctiporus* Macphail, Truswell & Partridge, 1993

*Proteacidites reticulatus* Cookson, 1950

*Protohaploxypinus samoilovichii* (Jansonius, 1962) Hart, 1964

*Psomospora detecta* Playford & Helby, 1968

# *Ptilophyllum acutifolium* Morris (in Grant, 1840)

# *Ptilophyllum cutchense* Morris (in Grant, 1840) emend. Bose & Kasat, 1972

*Punctatisporites gretensis* Balme & Hennelly, 1956

*Raistrickia accincta* Playford & Helby, 1968

*Raistrickia corymbiata* Playford in Playford & Mory, 2017

# *Raniganjia minima* Rigby, 1966

*Reticulatisporites magnidictyus* Playford & Helby, 1968 emend. Playford, 2017

*Retispora lepidophyta* (Kedo, 1957) Playford, 1976

*Retitriletes circolumenus* (Cookson & Dettmann, 1958) Backhouse, 1978

*Retitriletes clavatoides* (Couper, 1958) Döring, Krutzsch, Mai & Schulz, 1963

*Rimaesporites* Leschik, 1956

*Rhabdosporites langii* (Eisenack, 1944) Richardson, 1960

*Samaropollenites speciosus* Goubin, 1965

*Secarisporites* Neves, 1961

*Spelaeotriletes ybertii* (Marques-Toigo, 1970) Playford & Powis, 1979

# *Sphenophyllum morganae* McLoughlin, 1992

# *Sphenophyllum rhodesii* Rigby, 1966

# *Sphenopteris* Sternberg, 1825

*Staplinisporites caminus* (Balme, 1957) Pocock, 1962

# *Taeniopteris daintreei* McCoy, 1874

*Tetrahedraletes medinensis* Strother & Traverse, 1979 emend. Wellman & Richardson, 1993

*Velamisporites cortaderensis* (Césari & Limarino, 1987) Playford, 2015

*Velatitetras laevigata* Burgess, 1991

# *Vertebraria australis* McCoy, 1847 emend. Schopf, 1982

*Verrucosisporites quasigobbettii* Jones & Truswell, 1992

*Verrucosisporites scurrus* (Naumova, 1953) McGregor & Camfield, 1982

◊ *Veryhachium* Deunff, 1954

♦ *Welwitschia mirabilis* Hooker, 1862

♦ *Xylomelum occidentale* R. Brown, 1830

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# Sea level controls on the geomorphic evolution of Geographe Bay, south-west Australia

**GIADA BUFARALE** [1*], **MICHAEL J O'LEARY** [2] **& JULIEN BOURGET** [2]

[1] *Department of Applied Geology, Curtin University, GPO Box U1987, Perth, WA 6845, Australia*

[2] *School of Earth Sciences, University of Western Australia, Crawley, WA 6009, Australia*

* *Corresponding author:* ✉ *giada.bufarale@postgrad.curtin.edu.au*

## Abstract

High-resolution shallow seismic profiles collected along the inner shelf in Geographe Bay (south-west Australia) illustrate a highly-variable buried architecture. Three main acoustic units, separated by unconformities, correspond to different geological facies, deposited under various sea-level conditions. The acoustic basement (Unit B) belongs to the Lower Cretaceous Leederville Formation; the middle unit is attributable to the Tamala Limestone (Unit P, Mid- to Late Pleistocene) and the top unit (Unit H) is Holocene. Combining the seismic data with high-resolution bathymetry and sediment grabs, several surficial and buried morphological features are revealed, including sandbars, palaeochannels and ridges.

The shore-oblique sandbars have been directly influenced by local hydrodynamics including mean wave direction and currents, benthic habitats such as seagrass, and sediment grain size. The palaeochannels (buried and surficial) are the expression of previous sea-level lowstands. Two sets of shore-parallel, low-relief ridges, at depths of ~7 m and ~20 m, are relict landforms that are most likely regressive beach ridges and sub-littoral deposits, belonging to the Tamala Limestone. These structures were formed during Late Pleistocene relatively high sea-level stages (late Marine Isotope Stages 5e and 5c, respectively, between 120 and 100 thousand years ago), cemented when the sea level was lower and subsequently subject to transgressive erosion.

The newly acquired seismic datasets shows that the inner shelf is mostly covered by a veneer of sediment (with average thickness of 50 cm) above the Pleistocene hard surface, whereas sandbars can be up to 6 m thick.

**Keywords: Geographe Bay, Sandbars, Palaeochannels, Low-relief ridges, Sea level oscillations**

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## INTRODUCTION

Geographe Bay, between Cape Naturaliste and the city of Bunbury, in the south-western corner of Western Australia, lacks major fluvial sediment input and is considered sediment starved like much of the state's coastline (McMahon & Finlayson 2003; Brooke *et al.* 2017). Consequently, much of the sediment available for shoreline nourishment is sourced by the remobilisation of relict siliciclastic sediments deposited on the inner shelf during sea-level lowstands, and from carbonate organisms (such as coralline algae, molluscs, foraminifera and bryozoans), which are produced in and around the extensive seagrass banks that characterise Geographe Bay (James & Bones 2010; Brooke *et al.* 2014). The relict siliciclastic grains within the inner shelf are a finite resource as the volume of sediment available for transport onshore is limited by wave energy, water depth and grain size (Whitehouse 2007). In contrast, carbonate grains are continually being produced and can potentially provide a sediment resource for coastal nourishment. However, the supply of carbonate sediment to the coast is limited by the rates of carbonate production, which can be influenced by changing environmental parameters such as sea-surface temperature, nutrient availability and habitat change (James & Bone 2010), as well as hydrodynamic processes.

The Geographe Bay coastline is fringed by a series of low-relief coastal eolianites and dunes (Brooke *et al.* 2014), with sections of the coast presently experiencing coastal erosion, the cause of which is still poorly understood (Geographe Catchment Council 2008; Barr & Eliot 2011, Barr *et al.* 2017). Thus there is a need to better characterise the marine-sediment resources, particularly in a context of shoreline behaviour within a sediment-starved coastal environment, under rising sea levels and changing wave climate.

The aim of this study was to better understand local coastal evolution, the sediment resource potential of Geographe Bay, and the influence that geomorphology, hydrodynamics and habitat have on sediment mobility and onshore transport. An integrated approach was adopted, combining high-resolution bathymetry, sedimentological analysis, hydrodynamic data and high-resolution reflection-seismic images, conducted between Busselton and Port Geographe (Geographe Bay, Rottnest Shelf, south-west Western Australia).

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The lithology and age of inner shelf deposits were inferred from previous investigations from Geographe Bay to Rottnest Island (including the Swan Coastal Plain; e.g., Probert 1967; Playford *et al.* 1976; Wharton 1981, 1982; Commander 1982; Hirschberg 1988, 1989; Deeney 1989; Collins and Baxter 1984; Hamilton & Collins 1997; Schafer *et al.* 2008; Brooke *et al.* 2010, 2014) because coring and dating was not part of the present study. Interpretation of the geomorphological features is supported by the findings of Brooke *et al.* (2010, 2014) who carried out an extensive morphostratigraphic investigation of shore-parallel, relict barriers and ridges between Hillarys (30 km north of Rottnest Island) and Cockburn Sound (up to 34 km south of Rottnest Island), using bathymetric and topographic digital relief models and previously acquired dating (from Price *et al.* 2001 and Hearty 2003). Several shallow cores (up to 6 m long) cut within Cockburn Sound (about 100 km north of the survey area) by Skene *et al.* (2005) provide valuable insights into the sub-seafloor deposits of south-west Australia and were used to support the interpretation of the shallow stratigraphy proposed in this study. Of fundamental importance for the inferred chronostratigraphy of the survey area, are the geotechnical, sedimentological and palynological data obtained through the 'Quindalup borehole line project' (Wharton 1981, 1982) and the 'Busselton shallow-drilling project', (Hirschberg 1988, 1989) on the Swan Coastal Plain between Dunsborough and Capel (Fig. 1), as part of an assessment of the groundwater resources of the Perth Basin. Although the majority of these studies were investigating groundwater aquifers, the findings derived by collecting terrestrial borehole sediment can be extended to the nearshore marine area, due to proximity of the boreholes to the coastline.

## REGIONAL SETTING

### Coastal physiography

Geographe Bay is a 90 km long, J-shaped bay with a west-northwest aspect in the north and north-west through to north-east in the south (Fig. 1). The nearshore bathymetry is relatively simple with a shallow-dipping seabed reaching 30 m depth about 15 km from the coast. However, the south-westernmost section between Dunsborough and Cape Naturaliste is characterised by a steeper bathymetric gradient with water depths reaching 40 m within 1 km of the coast (Fig. 1).

The region is characterised by a Mediterranean climate, warm and dry between November and March (summer) and cool and wet in winter (Bureau of Meteorology - Australia 2011). There is only one permanent river (Capel River; Fig. 1, no. 16) that discharges directly into the ocean (mean annual flow of 39.9 Gigalitres (Department of Water 2008), the other waterways are ephemeral or seasonal and flow

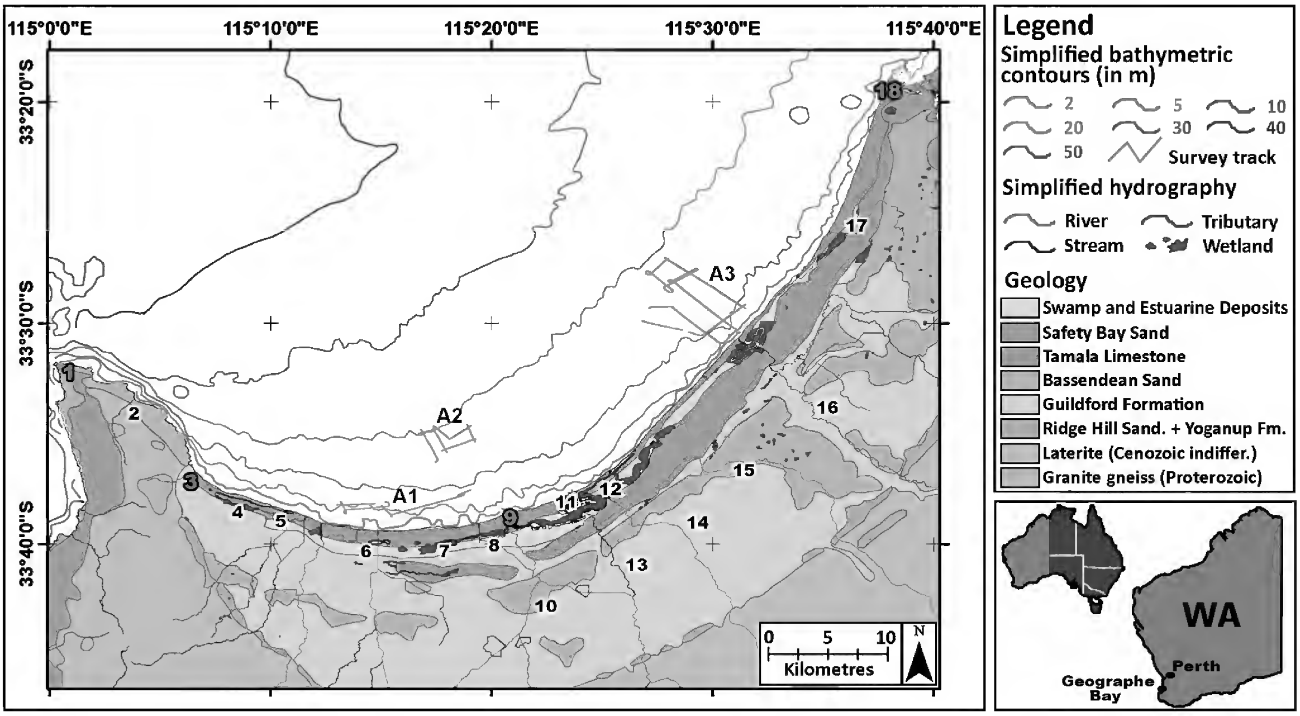

**Figure 1.** Geographe Bay map showing simplified surface geology (redrawn after Playford *et al.* 1976), localities (red labels) and bodies of water (black labels). 1 Cape Naturaliste, 2 Jingarmup Creek, 3 Dunsborough, 4 Toby Inlet, 5 Toby drain, 6 Quindalup, 7 Broadwater–New River, 8 Vasse-Diversion drain, 9 Busselton and Busselton Jetty, 10 Vasse River, 11 Port Geographe Marina, 12 Vasse–Wonnerup Estuary, 13 Sabina River, 14 Abba River, 15 Lundlow River, 16 Capel River, 17 Mile Brook diversion, 18 Point Casuarina (Bunbury). A1, A2 and A3 are the seismic survey locations. The geophysical survey track plot is also marked (in pink). Hydrography: Linear (Hierarchy; Department of Water DOW-029; 29-10-2008 12:18:04) from Shared Location Information Platform (SLIP; WMS Server: https://www2.landgate.wa.gov.au/ows/wmspublic?; Service Name: SLIP Public Web Map Service (ISO 19115 Categories). Simplified bathymetric contours are shown (source: Department of Transport).

mainly into drains (White & Comer 1999). Extensive seagrass meadows (*Posidonia sinuosa* and *Amphibolis antarctica*) represent the major benthic habitat within the bay, covering more than 90% of the seabed down to 10 m below sea level (Van Niel *et al.* 2009). The seagrass coverage decreases progressively northward and with depth, down to 30 m below mean sea level (BSL; Oldham *et al.* 2010).

Geographe Bay, like in the rest of south-western Australia, experiences a diurnal microtidal regime with a spring tidal amplitude on the order of 0.6 m (CSIRO 2015). Winds are mainly seasonal: the summer period is dominated by relatively light to moderate south to south-westerly offshore sea breezes (up to 15 m/s, in the afternoon) while strong south-westerly to north-westerly winds (up to 25–30 m/s), associated with cold fronts, occur periodically during the winter months (Fahrner & Pattiaratchi 1994; Oldham *et al.* 2010). The wave regime is mostly dominated by the seasonal winds, with waves typically reaching heights of up to 2 m in winter and less than 1 m in summer (Fahrner & Pattiaratchi 1994; Oldham *et al.* 2010). Surface waves are also influenced by an oceanic southwest swell, with Cape Naturaliste refracting waves into Geographe Bay, protecting the coast from the prevailing long-period ground swell (Fahrner & Pattiaratchi 1994; Oldham *et al.* 2010).

Coastal currents and water-circulation patterns are mainly wind driven, including storm waves, sea breezes and local bathymetry (Fahrner & Pattiaratchi 1994; Oldham *et al.* 2010). These metocean processes generate eastward to north-eastward longshore currents that influence sediment transport, control the seafloor sediment characteristics and are ultimately reflected in the sedimentary record (Paul & Searle 1978; Hamilton & Collins 1997; Oldham *et al.* 2010). Seagrass meadows also have a significant role in the overall hydrodynamic conditions of the bay, attenuating wave and current energy and sediment particle transport (McMahon *et al.* 1997; Oldham *et al.* 2010).

### Coastal Geology and Geomorphology

Geographe Bay lies on the south-western Australian continental shelf margin (Fairbridge 1961; Baker *et al.* 2005) within the southern Perth Basin—a Phanerozoic, intensely faulted half-graben, infilled with about 15 km of Paleozoic – Lower Cretaceous clastic strata and Lower Cretaceous – Holocene carbonate sediment (Collins & Baxter 1984). The area has been relatively tectonically stable since the Mid-Pleistocene (Playford *et al.* 1976, Szabo 1979; Kendrick *et al.* 1991; Stirling *et al.* 1995; Baker *et al.* 2005; Brooke *et al.* 2014).

The Lower Cretaceous Leederville Formation, which consists of fine- to medium-grained quartz sandstone interbedded with shale, is inferred to be mostly non-marine, with minor shallow-water near-shore marine horizons (Playford *et al.* 1976; Deeney 1989; Hirschberg 1989; Schafer *et al.* 2008). The formation is unconformably overlain by Quaternary superficial units, predominantly sand and limestone in the west, and lacustrine clay in the east (Deeney 1989; Hirschberg 1989). The superficial deposits, collectively known as the Kwinana Group, form the Swan Coastal Plain, a narrow strip (10–15 km wide) of reworked Quaternary sediment that comprises shallow marine and littoral deposits, and associated fossil eolian dunes aligned sub-parallel to the coastline (Collins 1988; Commander 2003). Fluvial, alluvial and lacustrine deposits are also present (Playford *et al.* 1976; Hirschberg 1989). The shoreline successions become progressively younger and decrease in elevation westward. These comprises the Ridge Hill Shelf (possibly Lower Pleistocene Ridge Hill Sandstone); Yoganup Shoreline deposits (possibly Middle Pleistocene Yoganup Formation), the Bassendean, Spearwood and Quindalup Dune Systems, respectively the Middle–Upper Pleistocene Bassendean Sand, eolian limestone and yellow sand of Tamala Limestone; and Holocene marine and eolian parabolic dunes and the Safety Bay Sand (Playford *et al.* 1976; Commander 2003; Fig. 1).

The Rottnest Shelf, defined by Carrigy & Fairbridge (1954), can be subdivided into three main bathymetric provinces: (1) the Inner Shelf, which extends from 0 to 100 m in depth, where submerged terraces and ridges formed during past periods of low sea level (Fig. 1); (2) the Outer Shelf that ends with the shelf–slope break at 170 m; and (3) the Upper Continental Slope (Collins 1988). Traces of subaerial erosion are recognisable in remnant subaqueous features such as reefs, shore-parallel ridges and barrier-dune systems (Collins 1988; Playford 1997; Brooke *et al.* 2010).

## METHODS

### Seafloor mapping

In 2016, the Western Australian Department of Transport (DoT) acquired and processed bathymetric datasets, during multiple LiDAR (Light Detection and Ranging), multibeam and Laser surveys (Coastal Information, DoT 2016). The high-resolution data have a horizontal sounding density of 5 x 5 m and cover the nearshore seafloor up to about 30 m water depth (Coastal Information, DoT 2016).

A map of the main seafloor features was produced through a visual interpretation of the bathymetry, using ESRI's ArcGIS Desktop 10.5. The surficial geomorphological features were manually outlined at a 1:10 000 scale and include sandbars, palaeochannels and ridges.

The morphological information was used to determine which areas within the bay to carry out the following seismic survey. Three distinct areas (A1–3; Fig. 1) were selected for detailed seismic investigation and sediment sampling: (1) A1 in the westernmost portion of the investigation area is characterised by a high concentration of sandbars, oblique to the shoreline; (2) A2, 6 km seaward from Busselton Jetty, has numerous deep-water (~20 m) ridges and palaeochannels; and (3) A3, in front of the Capel River mouth, is distinguished by several shallow-water (<10 m) ridges and palaeochannels.

### High-resolution shallow-seismic data acquisition

A total of 71 km of high-resolution reflection seismic profiles were acquired between the mouths of Buayanup drain and Capel River (A1, A2 and A3, Fig. 1). The main track orientations were parallel and perpendicular to the coastline, to capture most elements of the seafloor morphology. In A1, the seismic survey covered 16 km, mainly oriented north-northeasterly to south-southwesterly, in water depths of 5–10 m. A total of 15 km of seismic profiles were collected within A2, in relatively deep waters (~15–22 m). A3 comprises 40 km of seismic tracks, mostly orthogonal to the coastline, between ~8 and 22 m water depth.

The seismic survey was undertaken using an Applied Acoustic Boomer System, comprising an energy source (CSP-P 300) and a sound source (AA201 boomer plate), mounted on a surface-tow catamaran. An 8-element hydrophone streamer was employed as receiver. A GNSS (Global Navigation Satellite System) receiver Trimble NetR9 was interfaced to the acquisition workstation, broadcasting NMEA string to the geophysical software (SonarWiz 6 V6.01.0024, Chesapeake Technology Inc.). Data was digitally recorded in Seg-Y format and real-time quality control was done during data collection.

SonarWiz 6 software was also employed for data processing. The first step of post processing was bottom tracking, which is used to digitise the seafloor reflector. In the second step, standard signal processing procedures, such as application of Time Varying Gain (TVG) and enhancing the contrast, were applied to improve the signal to noise ratio. In the final step, sub-bottom horizons were digitised with manual picking. Based on the local geology and the speed of sound in sediments (see Whiteley & Stewart 2008; Duncan *et al.* 2009; Duncan & Gavrilov 2012), the depth below the seafloor and the sediment thickness values were depth converted using an estimated propagation velocity of 2000 m/s. Given a margin of error of about ±50 m/s, the vertical error is ~0.5 m.

### Sediment sampling and analysis

A pipe dredge was used to collect 17 unconsolidated surficial sediment samples along areas A1 (10 samples) and A2 (7 samples). Sampling location coordinates were recorded directly into SonarWiz 6, using the same positioning system used for the seismic survey.

The samples were dried and sieved using a mechanical shaker, over 63 µm, 125 µm, 250 µm, 500 µm, 1 mm and 2 mm meshes, and examined using a stereoscopic light microscope. Analysis of the sediment included an evaluation of colour using the Munsell Soil Chart (Munsell 1954), estimation of shape (roundness/sphericity of individual grains) and identification of the mineral and biogenic components.

## RESULTS

### Shallow stratigraphy

The shallow seismic survey allowed the characterisation of the internal architecture of the sub-surface reflectors and identification of stratigraphic features, down to a depth of approximately 30–40 m below the seafloor. The sub-surface reflectors TB (top Unit B) and TP (top Unit P) bound three discrete seismic units (from bottom to top: B, P and H, respectively; Fig. 2). Two minor reflectors (TP1 and TP2) also have been detected within Unit P along the survey area.

UNIT B

TB (green in the seismic interpretation; Fig. 2) is the deepest reflector recognised in the study area, ranging between ~15 m and 30 m below sea floor (~27 m BSL in A2 and ~47 m BSL in A3). Where detected, TB appears to be mostly relatively flat and laterally continuous. In A2 and A3, where profiles orthogonal to the coastline are longer (2.5–6 km), TB is clearly seen deepening offshore, lying sub-parallel to the modern seafloor. In several coastal-parallel profiles, irregular incisions can occasionally be recognised.. The TB reflector caps a low amplitude and seismically chaotic unit (Unit B), No other main seismic reflectors can be recognised below TB, for this reason, TB can be considered the top boundary of the acoustic basement.

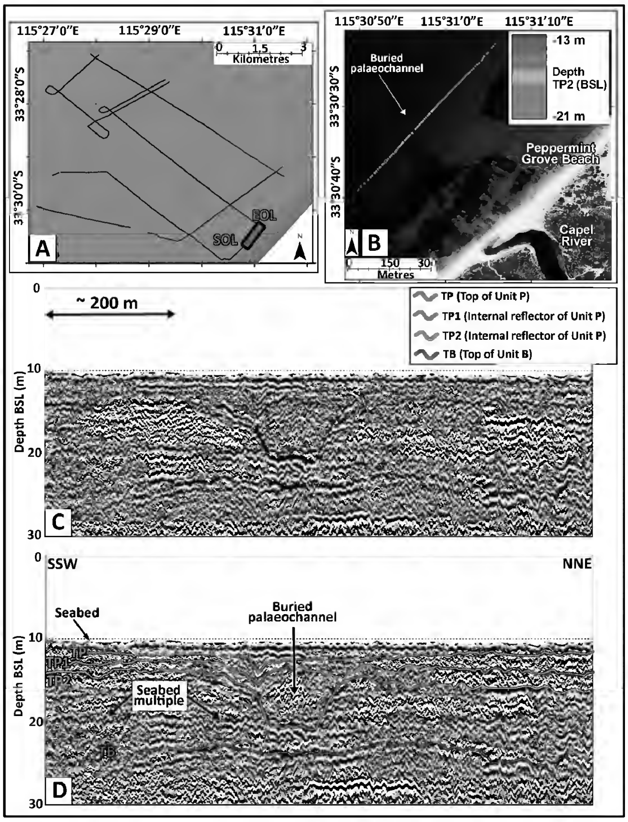

**Figure 2.** Example of seismic profile, showing the two main seismic reflectors depicted in the survey area (TP and TB) and two secondary reflectors (TP1 and TP2). A: Seismic tracks for Area 3. The location of the profile reported in C, D is highlighted in green (SOL: start of line, EOL: end of line). B: Orthophoto from SLIP (Shared Land Information Platform; Enabler portal, Landgate Imagery Bunbury 2031 Oct–Nov 2010 Mosaic). The buried palaeochannel is clearly visible when plotting the depth of the reflector TP2 (from sea level). C, D: uninterpreted and interpreted seismic profile. Note the well-defined buried palaeochannel. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediments is equivalent to ~2000 m/s. The horizontal axis represents the distance covered by the vessel and the scale is in metres.

### UNIT P

Reflector TP (shown in orange, Fig. 2) is well resolved in area A1 and in the profiles close to shore in A3. This sharp reflector is undulated to irregular, with several depressions and incisions and marks the top of Unit P, which is bounded between TP and TB. The internal reflection character of Unit P varies across the survey area and ranges from chaotic or reflection-free, to poorly or moderately stratified. Two minor reflectors can occasionally be recognised within this unit (TP1 and TP2). TP1 is mostly recognisable near shore, especially in A3 (depicted in yellow in the seismic interpretation, Fig. 2). This secondary reflector is generally flat, with some channel-like depressions, up to 250 m wide and 11 m deep. TP2 is normally present in A2 and A3 (2) and, as with TP1, it appears relatively flat, with intermittent depressions up to 7 m deep (Fig. 2C).

### UNIT H

Unit H is bounded between the seafloor and the reflector TP. Where TP is detected, the thickness of this surficial unit ranges from less than 50 cm to about 6 m and averages 1–3 m. In some areas, a strong return signal of the seafloor, seabed multiples and local poor imaging mask this unit (and consequently the ability to detect the underlying horizons TP and TB). In addition, it is likely that in some places, especially in the offshore profiles, Unit H is too thin to be detected with the equipment used (vertical resolution of the boomer is approximately 30 cm) or is absent; these uncertainties made the interpretation of Unit H potentially ambiguous. Some parallel stratified reflections can be identified within Unit H.

## Seabed features

High-resolution bathymetry highlights three main geomorphic features that characterise the seabed morphology in Geographe Bay, these are sandbars, palaeochannels and ridges (Fig. 3).

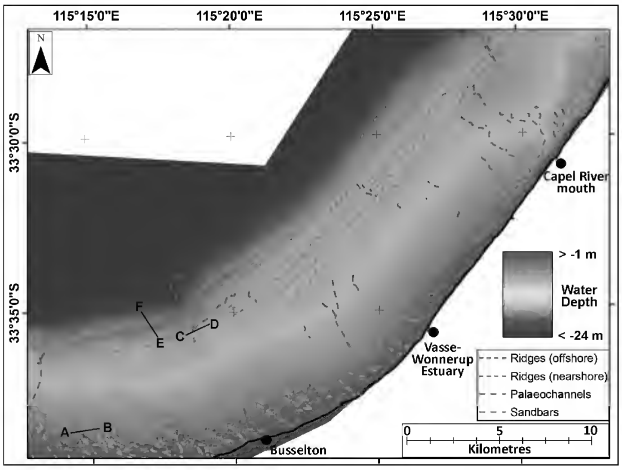

**Figure 3.** Composite bathymetric data (from Department of Transport) overlaid by seabed features. White areas: no data. Profile A–B: see Figure 4. Profile C–D: see Figure 5. Profile E–F: see Figure 6.

### SANDBARS

The sandbars and associated swales are near-continuous linear features that extend obliquely (at an acute angle to the shoreline of 15–30°) from nearshore, up to ~6 km seaward (between Geographe and West Busselton), to a water depth of 10 m. They mainly lie in the south-western portion of the bay, with the easternmost sandbar lying in front of the northern tip of Vasse–Wonnerup Estuary (location 12 in Figs 1, 3). The distance between successive sandbar crests increases to the north-east, ranging from about 250 m to more than 1.5 km. These sandbars vary greatly in size from about 100–300 m wide with the dune crest up to ~3 m above the seabed, and thin seaward. They are generally asymmetrical, with an almost bare stoss flank and a vegetated lee side (Fig. 4).

### PALAEOCHANNELS

The high-resolution bathymetric and seismic images revealed the presence of several partially buried and surficial palaeochannels, assembled predominantly around Area 1 and Area 3, respectively (see surficial palaeochannels marked in light blue in Figs 3, 5).

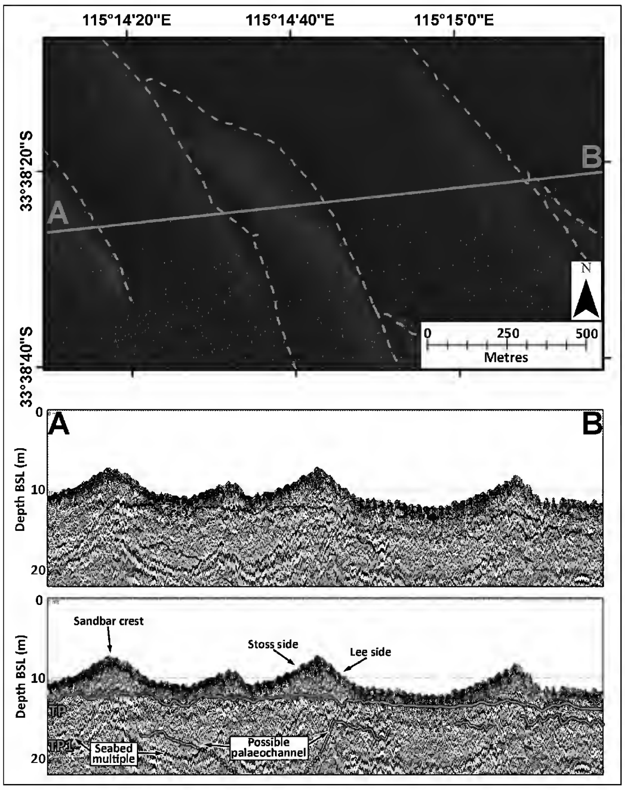

**Figure 4.** Profile A–B: sandbars, for location refer to Figure 3. Length: ~1755 m. Top: orthophoto from SLIP Enabler portal (Landgate Imagery). Darker colours represent areas covered with seagrass meadows. Pink dash line depicts the crest of the sandbars. Bottom: uninterpreted and interpreted seismic profile showing the buried architecture below the sandbars. The reflector TP is almost flat; conversely, reflector TP1 is irregular with a possible palaeochannel, marked with dash line. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediments is equivalent to ~2000 m/s.

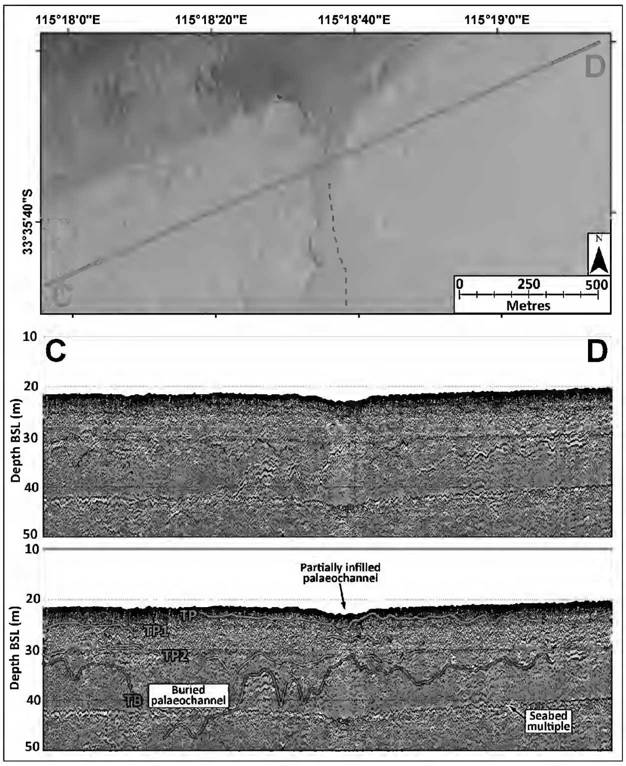

**Figure 5.** Profile C–D: palaeochannels, for location refer to Figure 3. Length: ~2175 m. Top: composite bathymetric data (from DoT) through the offshore channel. The light blue dash line depicts the thalweg of the surficial channel. Bottom: uninterpreted and interpreted seismic profile revealing a deeper buried palaeochannel. The palaeochannel is almost entirely infilled with sediment belonging to Unit H. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediments is equivalent to ~2000 m/s.

The surficial features have a variable length, from a few hundred metres to ~6 km, and are generally perpendicular to the coastline and quite shallow, with an average depth ~1 m below the surrounding seabed.

LOW-RELIEF RIDGES

Further significant geomorphic features that characterise the seabed in Geographe Bay are the linear, shore-parallel, low-relief ridges (Fig. 6).

Two distinct groups are observed: (1) the deep-water ridges that lie 6–9.5 km from the shoreline at depths of ~15–20 m; and (2) the shallow-water ridges, which are found only in the north-eastern portion of the bay and are within 1 km from the coast in water depths <7 m (Fig. 3). Cross-section transects indicate that the ridges have an uneven profile, with an almost flat top, a steep stoss end landward and a gentle lee slope seaward (Fig. 6), with a relief of less than 3 m. The deep-water ridge crests are sub-parallel and between 200 and 900 m apart, whereas the shallow-water ridges are more closely spaced, and their crests are between 100 and 500 m apart.

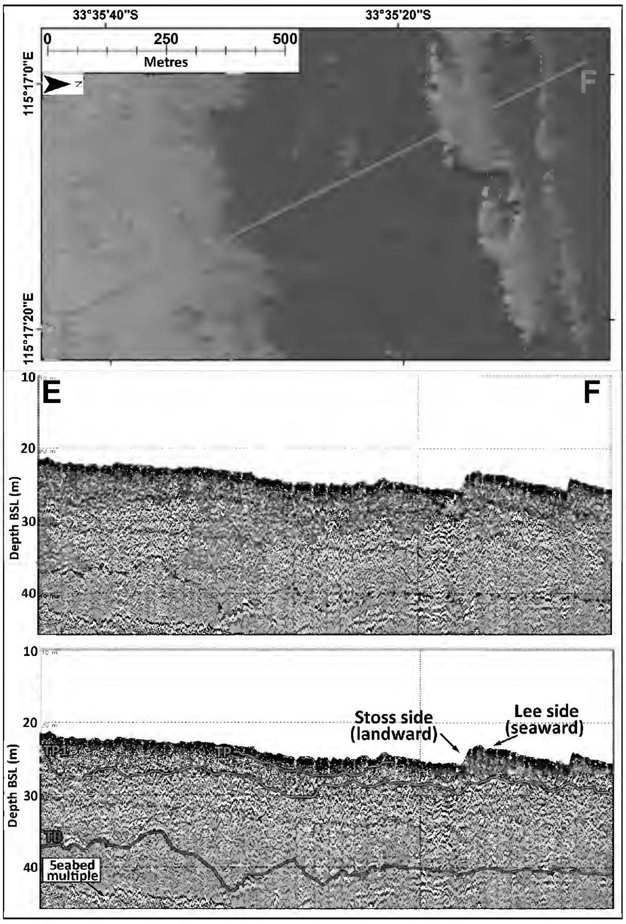

**Figure 6.** Profile E–F: ridges, for location refer to Figure 3. Length: 1215 m. Top: composite bathymetric data (from DoT). Yellow dash line depicts the crest of the ridges. Note: the layout of the map has been rotated by 270° to match the orientation of the seismic profile. The north arrow has been adjusted accordingly. Bottom: uninterpreted and interpreted seismic profile displaying the sub-surficial architecture; note Units P and H are not clearly discernible. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediments is equivalent to ~2000 m/s.

### Sediment distribution

In A1, the samples collected along the sandbars range mainly from coarse sand (0.5–1 mm, in green) to medium sand (0.25–0.5 mm; purple fraction in Fig. 7). Very coarse material (>2 mm) is entirely made up of biogenic skeletal grains that are highly variable in size (up to 3.5 cm in diameter) and consists mostly of fragmented or whole gastropods, but also includes bivalves, foraminifera and scaphopods. Overall, the sediment is pale yellow (Munsell colour, 10YR, 8/3 to 7/4). The mineral composition is mixed carbonate–silicate sand, dominated by quartz, which reaches ~60% of each bulk sample. In the finer fraction, quartz is dominant, representing about 85–90% of the sediment having grain dimensions <1 mm. The quartz grains generally display a medium to low sphericity and are predominantly sub-angular to rounded. They are mainly clear, translucent

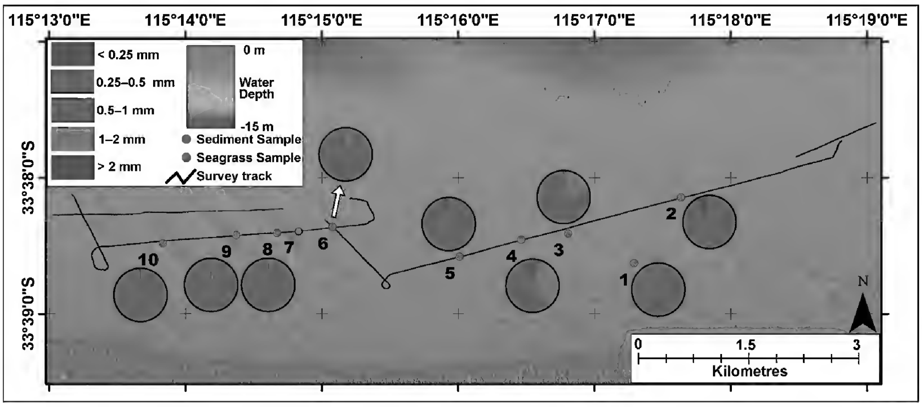

**Figure 7.** Surficial sediment distribution superimposed on composite bathymetric data (from DoT). Each pie chart illustrates different grain size distribution in the sediment collected in Area 1. Sediment typically ranges from medium sands (0.25–0.5 mm, in purple) and coarse sands (0.5–1 mm, in green). Note: sample 7 contained only seagrass debris.

to frosted, generally with crescentic impact marks, but occasionally, they appear frosted and yellow, orange to light brown. The remaining sediment comprises bioclasts (especially in samples 3, 4 and 6), minor feldspar, rock fragments, possible red/brown garnet and black heavy minerals, particularly in finer grains. Finer siliciclastic sediments (medium to fine sand) are more dominant on sandbar crests. Coarse and very coarse material, generally bioclastic in origin, tends to accumulate in the troughs between sandbars, such as in samples 3, 4 and 6 (Fig. 7).

In A2, the sediment sampled from the top of the deep-water ridges is coarser and contains a larger amount of quartz than along the sandbars (Fig. 8) in which finer particles are also present. The quartz grains are colourless, yellow or red to brown, generally translucent to transparent, sub- to well-rounded, with variable sphericity. The biogenic fragments include broken mollusc shells, foraminifera and coralline algae. Bryozoans and larger lithified fragments are also present; the latter consist of a mixture of detrital quartz and sand-sized biogenic fragments, with carbonate cement (calcite), indicating the calcarenite origin of the hard surface close to the seafloor. The biggest piece of this calcarenite (10 x 6 x 1.5 cm) was collected in sample 14.

Grain size of sediment around the deep-water ridges decreases seaward, where the medium-sand content increases (for instance, sample 11, Fig. 8). The availability of unconsolidated sediment also diminishes farther offshore. At some sites, several attempts at sediment sampling were unsuccessful, due to the indurated nature of the seafloor. As on the sandbars, coarser material is found in depressions (samples 12, 15, 16 and 17) and finer material on crests (i.e. sample 14).

## STRATIGRAPHIC INTERPRETATION

In several places, no reflectors could be identified beyond the seafloor due to a combination of factors that significantly reduced the quality of the seismic imaging. Hard bottoms and lack of velocity contrast between the buried lithologies are inferred to be the main causes of signal attenuation and limited acoustic penetration. In addition, dense seagrass is likely to have affected

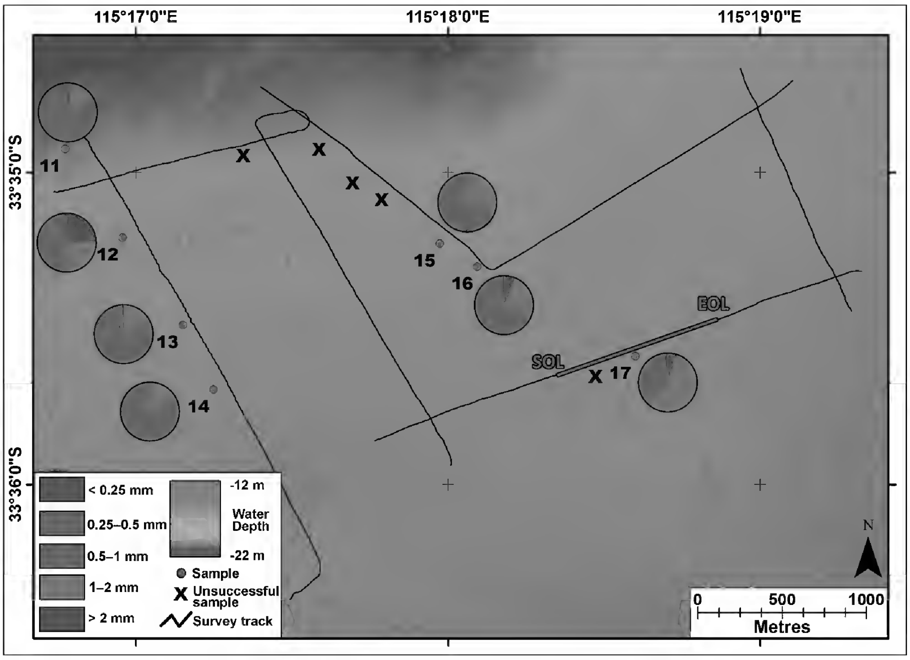

**Figure 8.** Surficial sediment distribution superimposed on composite bathymetric data (from DoT). As in Figure 7, each pie chart illustrates different grain size distribution in the sediment. In Area 2, sediment ranges mainly from coarse sands (0.5–1 mm, in green) and very coarse sands (1–2 mm, in red). The black cross symbols represent stations where sampling was unsuccessful due to the hard substrate. The green line marks the location of the seismic profile in Figure 12. SOL: Start of Line; EOL: End of Line.

the propagation of the signal, causing scattering and consequent deterioration of the quality in the acquired profiles. Acoustic multiples and ringing also were additional issues in some profiles as the reflections mask the deep reflectors (refer to Kearey *et al.* 2002).

The following chronostratigraphic interpretation is based on the findings of previous investigations carried out by the Geological Survey of Western Australia (Wharton 1981, 1982; Hirschberg 1988, 1989; Deeney 1989). During these studies, which aimed to define the lateral and vertical extent of the local aquifer systems, three clusters of boreholes were drilled near the shoreline adjacent to Area 1 (just west of Busselton, Figs 1, 9). The bore completion reports (Hirschberg 1988) showed that the shallow stratigraphy, up to 50 m below the Australian Height Datum (AHD) includes three successive units): (1) the Lower Cretaceous Leederville Formation (Unit B, basement); (2) the Pleistocene Tamala Limestone (up to 15 m thick); and (3) Holocene deposits (maximum thickness of 10 m; Fig. 9).

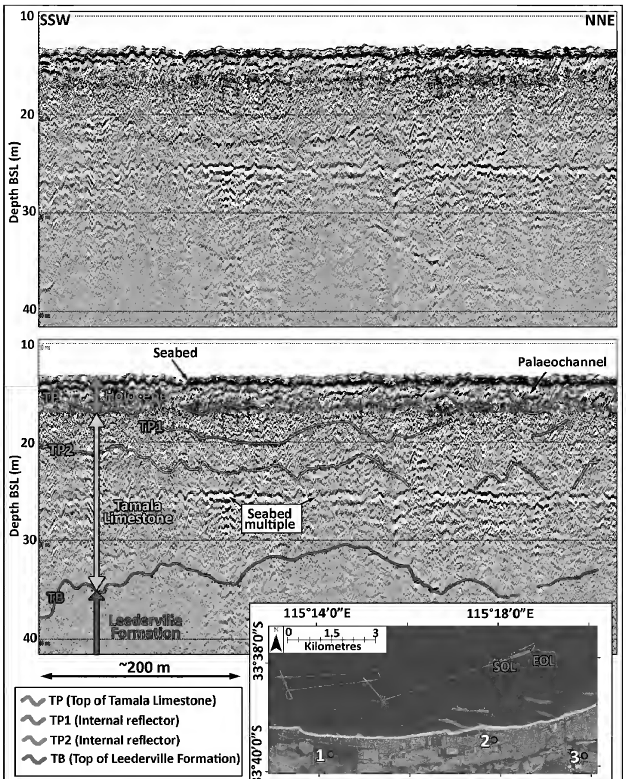

**Figure 9.** Top: uninterpreted seismic profile. Bottom: interpreted seismic profile. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediment is equivalent to 2000 m/s. The horizontal axis represents the distance covered by the vessel and the scale is in metres; in the insert location of the line, recorded in Area 1. The dots represent the boreholes collected by Wharton (1981, 1982) and Hirschberg (1989). Orthophoto section from SLIP (Shared Land Information Platform) Enabler portal, Landgate Imagery (Busselton Shire Jan 2016 Mosaic).

### Unit B: Leederville Formation

Based on the sedimentological records, the newly acquired seismic data and the available literature (e.g. Probert 1967; Wharton 1981, 1982; Deeney 1989; Hirschberg 1989; Collins & Baxter 1984; Hamilton & Collins 1997), the intensely scoured Unit B is interpreted as the Leederville Formation, a Lower Cretaceous succession of interbedded sandstone with siltstone and claystone (Cockbain & Playford 1973; Playford *et al.* 1976). Wharton (1982) and Hirschberg (1989) described the formation as weakly consolidated, fine- to coarse-grained sandstone interbedded with silty dark carbonaceous shales (Fig, 9). Accessory minerals, including heavy minerals, feldspar and pyrite, are common (Wharton 1981, 1982; Hirschberg 1989). It is likely that the heavy minerals found in the surficial sediments, collected in Area 1 and Area 2, are derived from erosion of the Leederville Formation, during the Plio-Pleistocene, when several cycles of sea-level variation controlled the deposition and reworking of these minerals, especially along the shoreline (Collins & Baxter 1984). The borehole logs also show that the Leederville Formation is unconformably overlain by the Pleistocene Tamala Limestone (Wharton 1981, 1982; Hirschberg 1989).

### Unit P: Tamala Limestone

Based on the findings of Wharton (1981, 1982) and Hirschberg (1989), it is possible to assume that Unit P corresponds to the Tamala Limestone. These authors described the formation as light-brown to orange, fine to coarse, bioclastic sand and limestone. Several other studies that have investigated the sub-surficial geology of Geographe Bay and adjacent areas, support the proposed interpretation of Unit P, including Paul & Searle (1978), Collins (1988) and Skene *et al.* (2005). The latter carried out an extensive coring program in Cockburn Sound and intersected the top of Tamala Limestone in several cores.

The Tamala Limestone forms a coastal strip, roughly parallel to the present shoreline, extending up to 10 km inland and 30 km offshore (inner shelf, Brooke *et al.* 2010) and stretches along the state's coast for more than 1000 km, from the South West to Shark Bay in the north (Fig. 1, right bottom corner). The formation represents a series of shoreline deposits and associated eolianite build-ups (cemented dunes), composed of coastal carbonate sediment and quartzose sand (Brooke *et al.* 2010), deposited during Pleistocene marine transgressive events (Brooke *et al.* 2014).

Since the Tamala Limestone is strongly diachronous, with a deposition spanning the Mid–Late Pleistocene to Early Holocene (Murray-Wallace & Kimber 1989; Brooke *et al.* 2014; Gozzard 2007), the minor reflectors within Unit P (TP1 and TP2) likely represent different periods of deposition, diagenesis and erosion of the formation, and reflect different stages of sea level. Palaeochannels are the confirmation of these oscillations. Palaeochannels that were incised during lowering sea level and successively infilled by more recent sediment are common within Unit P (Fig. 2).

### Unit H: Holocene unit

It can be assumed that the sediments belonging to Unit H are a thin blanket of Holocene deposits, over the Tamala

Limestone. Several authors have investigated the marine Holocene deposits along the Western Australian coast, in order to understand the timing of marine inundations. For instance, Baker *et al.* (2005) dated relict formations of inter-tidal serpulid tubeworms (vertical resolution as sea-level indicators: ±25 cm, following Baker & Haworth 1997; Baker & Haworth 2000 and Baker *et al.* 2001) from 21 locations along southern Western Australia, from Rottnest Island to Esperance (Fig. 1). Their research demonstrated that sea level peaked about 2.0 m above present between 6600 and 6800 years Before Present (BP), followed by an uneven fall to the present. Notably, a similar timing and elevation of the peak Holocene sea level was identified by Jahnert & Collins (2013) and Bufarale & Collins (2015) in Shark Bay. According to the composite Holocene sea-level curve for the Houtman Abrolhos Islands (Collins *et al.* 2006), it is likely that the sea inundated the inner shelf in Geographe Bay during the early Holocene, around 10 thousand years (ky) ago, when the base (sea) level reached the modern isobath of 20 m.

From the sediment analysis, the deposits are a mixture of relict siliciclastic grains, with a variable component of bioclasts. The thin ferruginous coating on the siliciclastic grains in Area 2 suggests that the sediment is reworked material of the Cooloongup Sand, a unit derived from the residual deposits left from Tamala Limestone dissolution (Lipar & Webb 2014). The light yellow to cream quartzose sediments in Area 1 may have originated from the reworking of the Burragenup Member, a Holocene unit of the Safety Bay Sand, composed of remnants of cemented dunes (Lipar & Webb 2014). In contrast, the carbonate grains are more recent and linked with the development of \seagrass meadows.

Unit H cannot be clearly recognised in deeper water (in A2 and part of A3, between 15 and 20 m BSL), using a seismic device. This is an important observation suggesting a very limited Holocene cover. In an essentially sediment-starved environment like Geographe Bay, where the riverine input of siliciclastic sediment is limited, it is possible to credit the importance of seagrass as a key-feature in sediment production and deposition. Seagrasses in fact not only produce *in situ* biogenic deposits, but also represent significant trapping and binding agents of the unconsolidated sediment (Hendriks *et al.* 2008; Gibbes *et al.* 2014; Bufarale & Collins 2015). This remark is in apparent contrast with the results of the sediment analysis, which show quartz as the dominant component. In this area, it is likely that hydrodynamic sorting also affects the lithological distribution. Bioclasts and quartz have in fact, significant hydrodynamic differences: carbonates are less dense, platy and have a greater surface area, therefore are easily subject to hydrodynamic sorting, whereas quartz grains are denser and less prone to be transported (Longhitano 2011; Chiarella *et al.* 2012). As a result, the carbonate sediment is reworked and transported onshore by waves (Brooke *et al.* 2014), and siliciclastic grains remain trapped within the sandbars, which act as a sediment sink, on the inner continental shelf.

## GEOMORPHOLOGICAL FEATURES

The end of the Marine Isotope Stage 5e (MIS) climatic optimum (~118 ky BP) was characterised by a rapid marine regression, coinciding with an insolation minimum and cooler global temperatures (Lambeck & Chappell 2001; Lambeck *et al.* 2002; Bianchi & Gersonde 2002; Hearty *et al.* 2007). For the following ~110–7 ky BP, the sea level was lower than at present (Collins *et al.* 2006; Jahnert & Collins 2013; Bufarale *et al.* 2017). During this time, the Capel River and other river systems in the region deposited siliciclastic sediment on the shelf, and waves and currents mobilised terrigenous grains longshore, trapping some in Geographe Bay (Collins 1988). Coarser grains are mostly confined to palaeochannels or topographic lows whereas finer sediments were deposited on the palaeo-shoreface and then transported along the coast. During the late Pleistocene – early Holocene sea-level oscillations siliciclastic material was intensively reworked (and rounded) and transported seaward by fluvial and eolian processes under falling sea level and landward by waves and currents under rising sea level (Collins 1988).

Around 10 ky BP, a marine transgression led to significant changes to sediment erosion, transport and deposition in Geographe Bay. The inner shelf became submerged and waves and currents started to mobilise the unconsolidated siliciclastic grains, forming longitudinal sandbars, which are presently aligned with

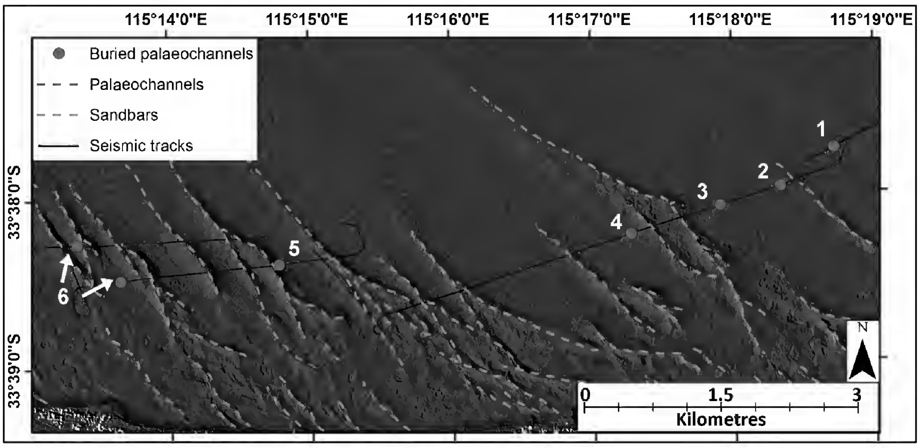

**Figure 10.** Location of sandbars (pink dashed line) and buried palaeochannels (identified with the seismic profiles, marked in light blue dots) in area A1. Surficial palaeochannel incisions are also delineated (light blue dashed line).

prevailing wave direction and partially covered with seagrass. In contrast to the ridges, these features are likely to have a quartz-dominated core, with a veneer of carbonate material (Paul & Saerle 1978). Although the sediment directly beneath the seagrasses was not sampled, samples from the exposed stoss side showed that the bar is quartz-dominated, supporting this interpretation.

### Sandbars

In Geographe Bay, the oblique sandbars, first described by Paul & Searle (1978), are all subparallel (Fig. 10). Superimposing the sandbar map distribution (from Fig. 10) to the mean wave direction chart (Fig. 11), the interaction between these elements is highlighted, with the sandbars positioned perpendicular to the mean wave direction. The mean wave direction chart shows how the south-westerly storm waves are refracted around Cape Naturaliste toward Geographe Bay coast (Pattiaratchi & Wijeratne 2011), clearly playing a significant role in mobilising the sediment and creating the sandbars. These observations have been investigated by Pattiaratchi *et al.* (2011, 2015, 2017) who reviewed the impact that the construction of Port Geographe had on the local shoreline evolution. Using a computer program simulating waves, water flow and sediment transport, coupled with bathymetric and LiDAR data, these researchers confirmed that storm-wave action and currents have a strong control on sand-bar formation.

Because the shelf is sediment starved, medium to coarse sand only dominates in nearshore sediments (as revealed from the sediment analysis; Figs 7, 8). Farther north (i.e. in front of Capel River mouth) it is likely that finer sediment is kept in suspension above the seabed where waves and currents sweep it towards the southern part of the bay. Here, due to a combination of coastal morphology, seagrass and hydrodynamic controls, the sediment is rearranged in linear sandbars, oblique to the coastline. This phenomenon has been described from several regions around the world, including North Carolina (United States of America. Murray & Thieler 2004) and New Zealand (Green *et al.* 2004) where longshore currents and large waves deposit coarse material on the seafloor.

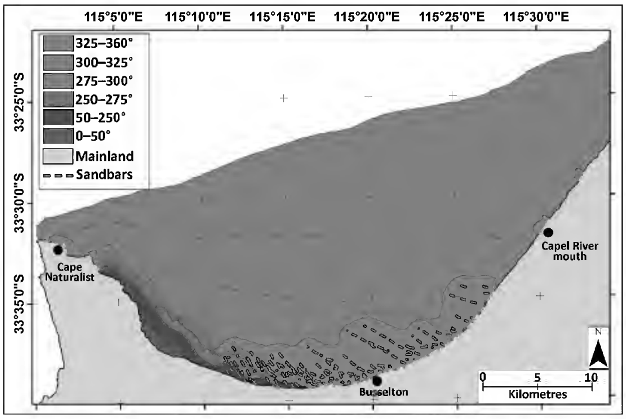

**Figure 11.** Predicted mean wave direction during storm events (redrawn after Pattiaratchi & Wijeratne 2011) with superimposed sandbar tracks. Note that the sandbar crests rotate according to the prevalent wave direction.

### Palaeochannels

Surficial and buried incisions have been described in detail in several studies worldwide, using different methods, including bathymetric and seismic data. Ryan *et al.* (2007), for example, employed various bathymetric datasets to detect several palaeochannels between the Burdekin and Fitzroy Rivers (north-eastern Australia). Bufarale *et al.* (2017) mapped three sets of palaeochannels under the modern Swan River (adjacent to Perth central business district, Western Australia) using a boomer system. Similarly, underwater seismic refraction was employed by Whiteley & Stewart (2008) to identify a major palaeochannel under the modern Lane Cove River (Sydney, New South Wales). McNinch and collaborators (McNinch 2004; Browder & McNinch 2006; Schupp *et al.* 2006; McNinch & Miselis 2012; Thieler *et al.* 2014) have described buried palaeochannels and oblique sandbars, along North Carolina and Virginia (U.S. central Atlantic coast) using seismic profiles, combined with swath bathymetry and side-scan sonar images.

Within the study area, several surficial and buried palaeochannels have been detected through high-resolution bathymetric and seismic datasets. Buried palaeochannels are mainly found in A1, where six incisions can be depicted in the seismic profiles (Fig. 10). In A2 and A3, four and three main buried palaeochannels can be recognised, respectively. In area A2, the westernmost buried palaeochannels appear to be the prolongation of channel 1 and 2 (Fig. 10) seaward. In Area 3, a deep incision is clearly observed in the seismic profiles close to the shoreline (Fig. 2). The palaeochannel is directly in line with the modern mouth of the Capel River, evidence that an ancient Capel River was active also in the past. At present, the incision is ~5 m deep, but considering that erosion of the upper part of the unit is likely to have happened, this channel and related palaeoriver might have been more significant, in terms of dimensions, discharge and flow than the modern one. The buried and surficial palaeochannels typically follow the same course, indicating that the pre-existing topography may have shaped and influenced successive morphological features (Fig. 12).

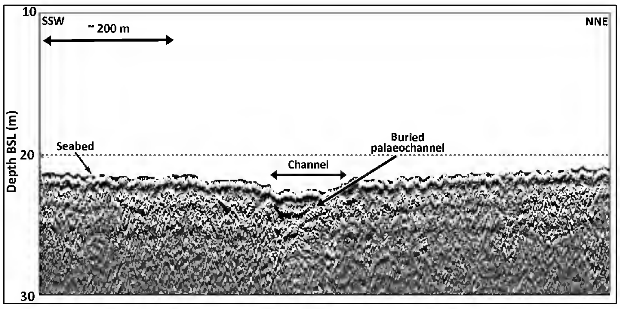

**Figure 12.** Seismic profile in A2 (for location see Figure 8) showing an underlying seafloor palaeochannel that is the surficial expression of a buried incision. The vertical axis corresponds to the depth below sea level (BSL) and the scale is in metres. The sound velocity in the sediments is equivalent to ~2000 m/s.

Surficial incisions, recognisable in the high-resolution bathymetric composite images, are more numerous in Area 3. The discrepancy is attributable to different Holocene thicknesses between the north-eastern A3 and the south-western A1. In the latter, where the Holocene unit is well-developed and a large amount of sediment is trapped along the sandbars, the palaeochannels have been infilled and covered up, and hence not recognisable within the bathymetric data, only in seismic profiles (Fig. 13). In A3, on the other hand, strong coastal currents (Fahrner & Pattiaratchi 1994) and the lack of seagrass meadows (McMahon *et al.* 1997; Oldham *et al.* 2010) have limited the deposition of sediment that instead has been transported and deposited farther south, leaving the surficial incisions more evident in the bathymetric data.

In central-western Geographe Bay (near study area A1), similar to along the coasts of North Carolina and Virginia (U.S.A.; Browder & McNinch 2006) and Paraná inner shelf (southern Brazil; Oliveira 2015), buried palaeochannels and oblique sandbars are found adjacent (Fig. 13). However, unlike coastal U.S.A. and Brazil, where palaeochannels have been argued to influence the development of shore-oblique sandbars (McNinch 2004), in Geographe Bay this relationship is not significant as hydrodynamic conditions (waves and currents) are the main process involved in the formation of bottom geomorphology (Paul & Searle 1978; Hamilton & Collins 1997; Oldham *et al.* 2010; Pattiaratchi & Wijeratne 2011).

### Submerged low-relief ridges

As noted using the high-resolution bathymetric composite images, and also from the seismic profiles, small ridges can be recognised, corrugating the seafloor, near the coastline and into deeper water. The ridge complexes are topped by a veneer of Holocene deposits (especially thin in deep-water and toward the northern portion of the study area, near A2 and A3, respectively). The cores of the ridges are inferred to be composed of Tamala Limestone (Ramsey *et al.* 2016).

Shore parallel ridges are common structures along the Western Australian coast, both onshore (Commander 2003) and submerged on the shelf (James *et al.* 1999; Twiggs & Collins 2010; Brooke *et al.* 2010, 2014; Nichol & Brooke 2011), recording major past sea level changes. These geomorphological structures are relict landforms, like shoreface palaeodunes or beach ridges, which are commonly found in carbonate-dominated, sediment-starved coasts (Reading 2009; Brooke *et al.* 2010) and record relatively stable episodes of regressive shoreline conditions, followed by transgressive erosion. Because of their low relief above the seabed and discontinuity, it is unlikely that these ridges have acted as a barrier inhibiting or trapping onshore sediment transport.

Similar to the onshore Swan Coastal Plain, where sub-aerial coastal dune ridges become progressively younger from east to west (Commander 2003), the submerged ridges also young in the same direction, recording Late Pleistocene relatively high sea level stages. The schematic cross sections illustrating the Late Quaternary geomorphological evolution (Fig. 14) show how shallow-water ridges in the south (area A1 in Fig. 1) might have been eroded completely or covered by Holocene sediments, whereas they are preserved in the north (area A3 in Fig. 1).The shallow-water ridges in the south (area A1) might have been eroded completely or covered by Holocene sediments.

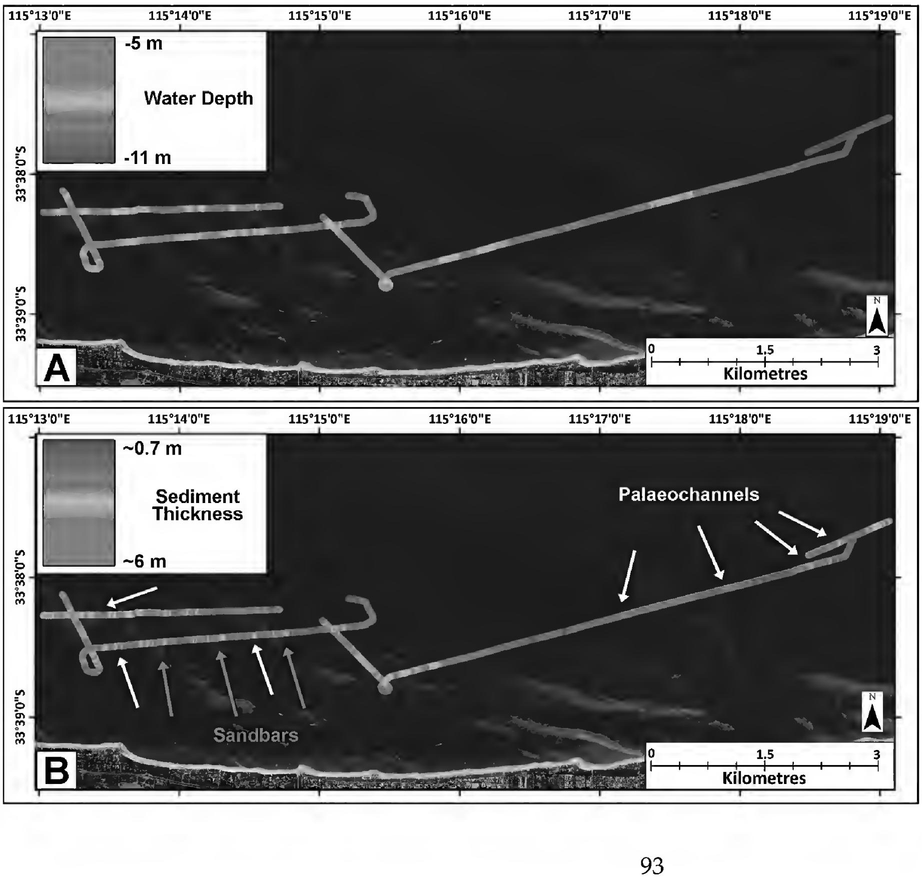

**Figure 13.** Water depth and Unit H sediment thickness in Area 1. Orthophoto is from SLIP Enabler portal, Landgate Imagery (Busselton Shire Jan 2016 Mosaic). A) The water depth is shallower along the oblique sand bars and deepens eastward. The water depth is in metres and calculated approximating the sound velocity of 1500 m/s. B). The Holocene unit is very thin in deeper water and between the sandbars. The sediment thickness values are expressed in metres, calculated approximating the sound velocity of 2000 m/s. The thickest sediment is found along the sandbars (red arrows) and palaeochannels (white arrows).

The shallow-water ridges were the first ridge complex to form. At the termination of MIS 5e, when the sea level was about 8 to 10 m lower than the present (Chappell *et al.* 1996), these barriers started their development, close to the innermost palaeo shoreline (Fig. 14, ~120 ka). When the sea level further dropped, stranding these features, cementation commenced. Similarly, the second ridge complex (deep-water ridges) established its shape in an analogous manner, when the sea level was 20–30 m below present (Chappell *et al.* 1996; Creveling *et al.* 2017; Fig. 14, ~100 ky). Until ~10 ky BP, most of the inner shelf was exposed, favouring the cementation of the ridges. When the sea level inundated the shelf (early Holocene), erosion took place, leaving the lithified ridges asymmetric, with a flat top (Fig. 14, present).

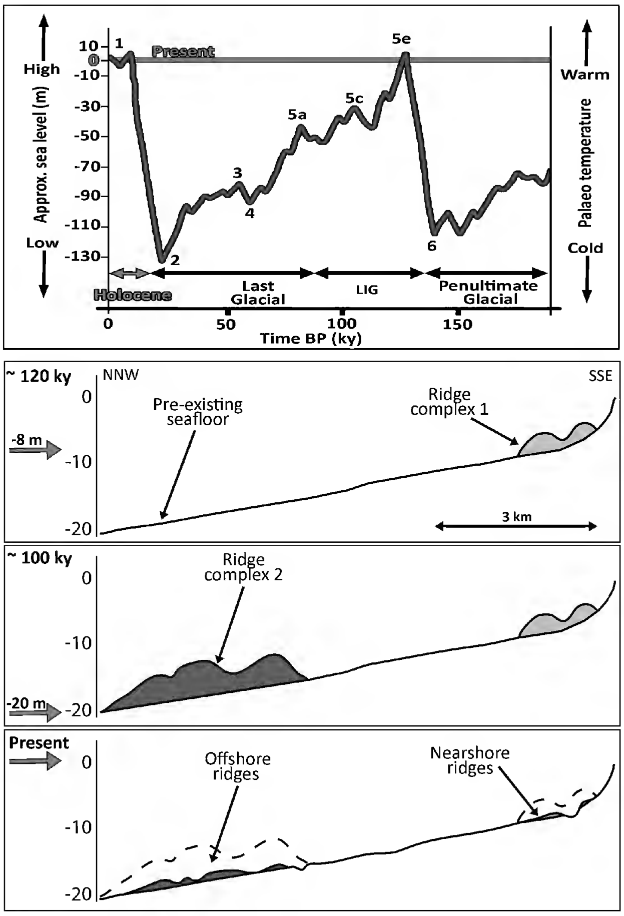

**Figure 14.** Top: Sea level curve since ~200 ky. Odd numbers refer to Interglacial Marine Isotope Stages (MIS) and even numbers indicate the Glacial MIS. The curve is based on oxygen isotope ratio $\delta^{18}O$ (modified after Saqab & Bourget 2015 and Bufarale *et al.* 2017). Bottom: Schematic model showing the onset and evolution of regressive beach ridges and, possibly sub-littoral deposits. The profile is a simplified cross section, near A3 in the northern portion of the study area. Horizontal axis: ~9 km; vertical axis: depth values are in metres, referred to the present sea level (where 0 corresponds to modern mean sea level). The arrows represent the stage of sea level, in different time; red: falling sea level, blue: rising sea level. The figure has been drawn based on the data from this study and the conceptual model proposed by Brooke *et al.* (2010) and Brooke *et al.* (2014).

The chronostratigraphic interpretation of these geomorphic features is supported by several studies carried out on similar structures along the state's coast, in particular in the South West (notably Brooke *et al.* 2010, 2014). These studies describe the chronology and the nature of three submerged ridge sets, between Rottnest Island and Cockburn Sound, from nearshore up to 50–60 m of depth BSL. In the present study the two shallow ridges are equivalent to the shallow-water and deep-water features and the third set, not included in this investigation, is more recent (MIS 5a). Nevertheless, additional coring and dating of both the ridge complexes could help to confirm this interpretation, and also provide a better assessment of the late Pleistocene evolution of the South West coast.

## CONCLUSIONS

Reflection seismic data, combined with high-resolution composite bathymetric datasets and sedimentological analysis, provided the following new insights into the inner continental shelf in Geographe Bay:

1) Shallow architecture and stratigraphy is revealed for the first time. The seismic profiles show three main sedimentary units, separated by unconformities and deposited under various sea level conditions, which include:
   - An acoustic basement (TB, Leederville Formation), dated as Early Cretaceous;
   - One intermediate unit (TP), belonging to Tamala Limestone, of mid- to late Pleistocene age;
   - A surficial unit (TH), deposited since the early Holocene, at around 10 ky.
2) The surficial sediment of the Holocene unit is dominated by quartz but also include a percentage of carbonates and other accessory minerals and rock fragments. Finer siliciclastic sediment is more dominant on top of topographic highs and sandbars. Coarse and very coarse material, mainly carbonate, tends to accumulate in the swales and depressions. These Holocene deposits are hence the result of a combination of erosion of older formations (mainly Tamala Limestone, although heavy minerals derive from the erosion of the Leederville Formation) and *in situ* accumulation of carbonate sediment from seagrass and other benthic communities.
3) Three main features that characterise the seabed are:
   - Several palaeochannels (buried and surficial) that are an expression of previous sea-level lowstands.
   - Near-continuous, asymmetrical sandbars and associated swales, that extend obliquely from nearshore to ~6 km seaward. These linear features mostly lie in the south-western portion of the bay, and generally have an almost bare stoss flank and a lee side intensely colonised by seagrass. The sandbars result from (a) local hydrodynamics, causing the sandbars to be primary sediment sinks of siliciclastic grains, with waves and currents (including longshore)

influencing the geomorphology in the inner continental shelf; (b) grain size and (c) the influence of seagrass meadows.

- Two sets of shore-parallel, low-relief ridges, at depths of <10 m and ~20 m, represent relict landforms, probably regressive beach ridges and sub-littoral deposits (paleo-dunes), belonging to the Tamala Limestone. These late Pleistocene geomorphological structures formed during relatively high sea-level stages (end of MIS 5e – start of MIS 5d and 5c, respectively). The ridges were subsequently cemented and subject to successive marine (transgressive) erosion. Based on the morphology of these submerged strand plains, an abrasion surface characterises the top of the ridges, where the top has been cut out, exposing the core or the base of the ridges.

The data confirm that the shelf is essentially sediment-starved and the very limited Holocene deposits produced along the shelf, have then been reworked and transported onshore by waves. In terms of sediment-resource potential, the sandbars are a reservoir of the sediment on the shelf, with the core likely to be quartz sand.

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# The conservation significance of the biota of Barrow Island, Western Australia

A. JASMYN J. LYNCH [1*], ROBERT J.S. BEETON [2] & PENELOPE GREENSLADE [3,4]

[1] *Molonglo Conservation Group, Fyshwick ACT 2609, Australia*

[2] *School of Earth and Environmental Sciences, University of Queensland, St Lucia Qld 4072, Australia*

[3] *Centre for Environmental Management, School of Health and Life Sciences, Federation University, Ballarat Vic. 3353, Australia*

[4] *Research School of Biology, Australian National University, Acton ACT 2601, Australia*

* *Corresponding author: ✉ jasmyn.lynch@molonglo.org.au; ajj.lynch@gmail.com*

## Abstract

Offshore islands are often important in conservation because of the presence of locally endemic species and for acting as refuges for native wildlife from the impacts of invasive species and inappropriate development. Barrow Island, a small, semi-arid island off the Pilbara coast of north-western Australia, has maintained the integrity of its terrestrial and aquatic biota despite sporadic incursions by invasive species and the operation of commercial oil extraction and liquified natural gas processing for over 50 years. We collate information from a wide range of sources to provide a framework to inform the ongoing management of the terrestrial and aquatic fauna and flora species that have conservation significance on the island. These include endemic flora and fauna; species listed as threatened by state, national and international authorities; species that are rare or extinct in other parts of their original range; species of biogeographic significance; and migratory birds and marine fauna of national and international significance. In addition, Barrow Island has been of value in acting as a source area for translocations of vulnerable and endangered mammal species that have been eradicated in other parts of their range. The many species with conservation significance and their use in successful translocation programs demonstrates the island's national and international importance for conservation. In addition, Barrow Island provides exemplary opportunities for research on effective co-management of development and conservation, on mitigation and prevention of the invasion and impacts of exotic species, and on the influence of historical biogeographic processes on the distributions and evolution of biota.

**Keywords: island conservation, endemism, rarity, migratory fauna, invasive species, biogeography**

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## INTRODUCTION

Barrow Island (20°47′52.8″S, 115 24′21.6″E; Fig. 1) off the coast of north-west Western Australia is one of Australia's most important island sanctuaries. Its significance has long been recognised with its declaration in 1910 as a 'Class A' Nature Reserve, the highest level of protection available under Western Australian legislation. Although this small, semi-arid continental island covers just 236 km$^2$ and is located 56 km offshore, it has many resident and migratory taxa of conservation significance, and a relatively high diversity of terrestrial fauna and flora. Only 11 (2%) of 512 Australian islands contain more mammal species than Barrow Island and most (9) of those 11 islands are larger in area (Abbott & Burbidge 1995; Burbidge & Abbott 2017; Tables 1, 2). Three smaller islands with the same or more native mammals than Barrow Island are located much closer to the mainland. Of these, Augustus Island (Fig. 1) lies within 6 km of Western Australia's mainland, whereas the other two (Phillip Island, Victoria; Burrup, Western Australia; Fig. 1) are connected to the mainland by artificial causeways. During periods of lower sea-levels, they were separated from the mainland by coastal plains, mudflats or swamps (Kirkwood & Johnston 2006; Stankowski & Johnson 2014). Likewise, there are more plant species on Barrow Island than on various other offshore arid or semi-arid islands of similar size (Main & Yadav, 1971; Table 3). Endemic species, subspecies and forms have developed on the island (Buckley 1983; Driskell *et al.* 2002) but inbreeding depression has been detected in some taxa (Eldridge *et al.* 2004).

Conservation and development co-exist on Barrow Island. Commercial oil-production industry began on the island in 1964 and in 2009 liquefied natural gas (LNG) processing facilities were established to process gas from the Gorgon reservoir, 70 km to the north-west of the island (Fig. 1). Ongoing expansion of sub-sea gas drilling and transfer infrastructure from the Gorgon gas fields will sustain the LNG project for a lifespan of 40 years (Chevron 2018). Multi-purpose land-use on the island has been enabled by a strict quarantine and environmental management programme with regular surveillance and monitoring for invasive species (Burbidge 1999; Burbidge

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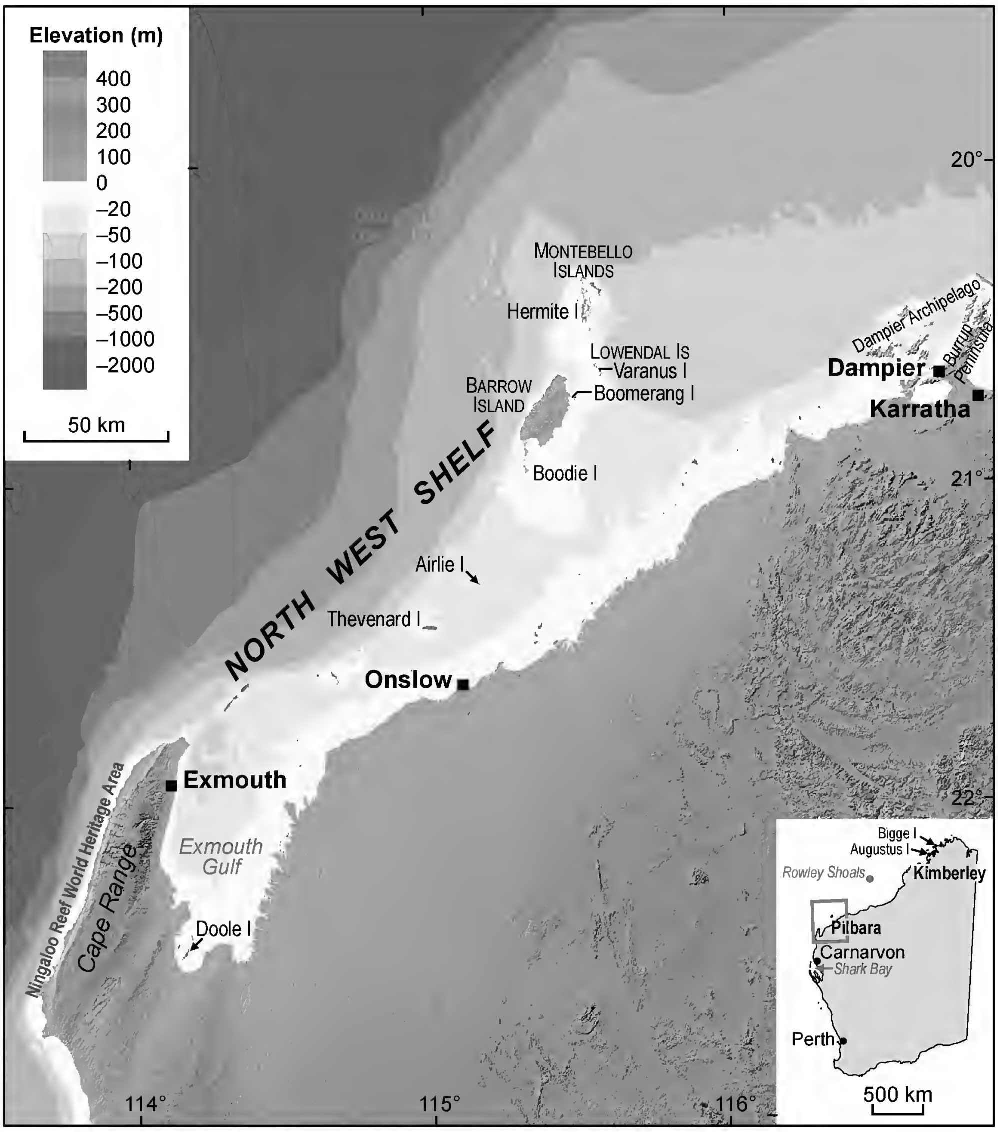

**Figure 1**. The location of Barrow Island within Western Australia.

& Manly 2002; Greenslade *et al.* 2013a, 2013b; Scott *et al.* 2017). The recent opening of a university science centre on the island will support further research into environmental protection and industrial development in fragile ecosystems (Perera 2018).

Like Barrow Island, other areas of Western Australia are subject to rapid development for extraction and export of mineral and gas resources. For example, several major offshore LNG projects have commenced in recent years (Environmental Protection Authority 2007; Government of Western Australia 2017). The petroleum industry is the state's second-most economically valuable industry and offshore LNG is the most valuable petroleum product, accounting in 2017 for $14.9 billion (Government of Western Australia 2017). The North West Shelf, where Barrow lsland is located, produces approximately 59% of the state's oil and 93% of its gas (Department of Environment and Conservation 2006).

The establishment of LNG processing facilities on Barrow Island required approval from the Western Australian and Australian governments. Approvals were granted in 2007 and 2009, despite opposition from the state authority in which the nature reserve is vested (Conservation Commission of Western Australia 2003), the Western Australian Environmental Protection Authority (2009), and a former senior state government scientist (ABC Radio National 2009). Stringent environmental conditions were imposed on the developers (Chevron, ExxonMobil and Shell), including quarantine controls on all materials and personnel travelling to the island, regular surveillance for exotic species, and a requirement for compliance with over 20 environmental management plans. Additional commitments from the developers included conservation undertakings worth approximately AUD$150 million and funding to enable Department of Environment and Conservation staff to be based on the island for management of any impacts on marine conservation over the life of the project (Department of State Development 2009).

The agreement of the consortium reflects the high economic value of the regional LNG reserves but also Barrow Island's high national and international conservation significance. The flora and fauna (except for some invertebrate groups) were well known because

**Table 1**

Australian islands with equivalent or greater number of extant (and extinct) native and exotic or introduced mammals compared to Barrow Island, ranked by area (data from Abbott & Burbidge 1995; Burbidge & Abbott 2017).

| Island | Area (ha) | No. native species | No. non-native species |
|---|---|---|---|
| Phillip Island, Vic* | 10 116 | 16 (+1 extinct) | 10 (1 now absent) |
| Burrup (Murujuga, Dampier Is), WA* | 11 804 | 15 (+1 extinct) | 5 |
| Moreton Island, Qld | 17 021 | 10 | 5 |
| Bigge Island, WA | 17 128 | 9 | 0 |
| Bribie Island, Qld | 17 500 | 12 | 2 |
| Augustus Island, WA | 18 929 | 13 | 0 |
| **Barrow Island, WA** | **23 569** | **13** | **2 (2 eradicated)** |
| North Stradbroke Island, Qld | 26 344 | 17 | 3 |
| Vanderlin Island, NT | 27 690 | 11 | 5 |
| Hinchinbrook Island, Qld | 31 756 | 18 | 4 (2 now absent) |
| Bruny Island, Tas | 36 735 | 15 | 8 (1 now absent) |
| Cape Barren, Tas | 46 220 | 9 (+2 extinct) | 5 |
| King Island, Tas | 109 100 | 13 (+4 extinct) | 9 |
| Flinders Island, Tas | 135 900 | 15 (+2 extinct) | 8 (1 now absent) |
| Bathurst Island, NT | 169 300 | 14 | 3 |
| Fraser Island, Qld | 165 280 | 2 | 3 (1 now absent) |
| Groote Eylandt, NT | 228 500 | 28 | 1 |
| Kangaroo Island, SA | 442 000 | 18 (+4 extinct) | 13 (3 now absent) |
| Melville Island, NT | 578 000 | 21 | 4 |
| Tasmania | 6 452 000 | 33 (+1 extinct) | 12 |

*Burrup and Phillip Island are coastal islands linked to the mainland by causeways. Burrup is also connected at low tide. Bigge Island is about 6 km offshore

of sponsorship from the Western Australian Petroleum Exploration Company, which has operated oil wells over the southern part of the island since 1964. However, intermittent surveys of fauna have been undertaken only since 1991; e.g. sampling of the stygofauna (aquatic fauna living within groundwater systems) and troglobitic fauna (air-breathing subterranean fauna living in caves, cavities and fractured rock; Humphreys *et al.* 2013). The government response to Chevron Australia's (2005) draft environmental impact statement was that extensive surveys would be undertaken and they should include invertebrates. This has led to over 2000 new records of species and new taxa being described.

Broader inventories of the natural resources of the island, assembled as part of the Gorgon LNG development approval process, contributed to the Environmental Impact Statement (EIS) and Environmental Review and Management Programme (Draft EIS/ERMP; see Chevron Australia, 2005) prepared for the federal Department of the Environment and Heritage and the Western Australian Environmental Protection Authority. The EIS documented the known biological and physical resources of the island, including the vegetation, floristics, vertebrate fauna, cave fauna (troglophytes and stygofauna), invertebrates, and marine flora and fauna.

This article provides an updated evaluation of the conservation significance and management approach implemented for Barrow Island and its nearshore environments based on the species present and their state and national conservation status. Our objective is to collate information from a wide range of sources

**Table 2**

The number of native and exotic mammals on islands in north and north-western Australia of similar size (10 000–60 000 ha) to Barrow Island (NT and WA data from Abbott & Burbidge 1995; WA data also from Burbidge & Abbott 2017).

| Island | Area (ha) | No. native species | No. exotic species |
|---|---|---|---|
| Burrup (Murujuga, Dampier Is), WA* | 11 804 | 15 (+1 extinct) | 5 |
| West Sir Ed Pellow, NT | 13 373 | 5 | 0 |
| Bigge Island, WA | 17 128 | 9 | 0 |
| Augustus Island, WA | 18 929 | 13 | 0 |
| Marchinbar Island, NT | 21 190 | 9 | 0 |
| **Barrow Island, WA** | **23 569** | **13** | **2 (eradicated)** |
| Elcho Island, NT | 26 950 | 8 | 3 |
| Vanderlin Island, NT | 27 690 | 11 | 5 |
| Croker Island, NT | 31 000 | 1 | 6 |
| Dirk Hartog Island, WA | 58 640 | 5 (+10 extinct) | 6 (2 now absent) |

*Burrup is a coastal island in the Dampier Archipelago connected to the mainland at low tide and by a road and rail causeway built in the mid-1960s

**Table 3**
Numbers of native and endemic plant taxa on various islands with arid or semi-arid vegetation.

| Island | Region | Area (km²) | No. native taxa (no. endemic) | Reference |
|---|---|---|---|---|
| St Helena | Angola–Namibian coast, Africa | 122 | 70 (49) | Rowlands (no date) |
| Isla Santa Maria | Galapagos Islands | 171 | 258 | van der Werff (1983) |
| Sal | Cape Verde Islands | 216 | 147 | Duarte *et al.* (2008) |
| São Vicente | Cape Verde Islands (Macaronesia) | 227 | 296 | Duarte *et al.* (2008) |
| **Barrow** | **North-western Australia** | **234** | **406 (2)** | **Chevron Australia (2005)** |
| Maio | Cape Verde Islands | 269 | 220 | Duarte *et al.* (2008) |
| El Hierro | Canary Islands (Macaronesia) | 269 | 426 | Fernández-Palacios & Andersson (2000) |
| Dirk Hartog | North-western Australia | 596 | 300 | Abbott (1978) |
| Isla San Cristóbal | Galapagos Islands | 552 | 291 | van der Werff (1983) |

as a reference for ongoing management of this and other Australian islands that require multi-purpose management for conservation and development. Other small island nature reserves in north-western Australia (i.e. Thevenard Island, Airlie Island, Varanus Island; Fig. 1) also support oil and gas production facilities, and drilling for gas has been approved only 50 km from the Ningaloo Reef World Heritage Area (Fig. 1; ‘Shell drilling permit for Ningaloo Reef approved’ 2011). Successful management of industry within environmentally important areas depends on comprehensive, current knowledge of environmental values and management of the risks and potential impacts on these values within a precautionary scientific approach (Greenslade *et al.* 2013a). We further comment on the importance of the island as a resource for research on co-management of development and conservation, mitigation and prevention of the invasion and impacts of exotic species, and the influence of historical biogeographic processes on the distribution patterns and evolution of regional biotic assemblages.

## METHODS

The available literature on the terrestrial, subterranean and nearshore marine biota of Barrow Island was reviewed. This included the Gorgon development EIS (Chevron Australia 2005) and published scientific literature. The NatureMap database[1] (Western Australian Department of Parks and Wildlife) also was used to identify species present on Barrow Island. Lists of taxa were compared to their status as rare, threatened or protected taxa (as of 21–24 August 2018) under current biodiversity conservation legislation and conventions. These were the Western Australian *Wildlife Conservation Act 1950* and the Department of Environment and Conservation’s Threatened Flora Rankings for rare or priority plants; the Australian *Environment Protection and Biodiversity Conservation Act 1999* (EPBC Act) using the SPRAT database[2] for taxa listed as threatened, as protected migratory species (i.e. under the Bonn Convention, the Japan–Australia Migratory Bird Agreement, the China–Australia Migratory Bird Agreement, and the Republic of Korea–Australia Migratory Bird Agreement), or as protected marine or cetacean species; the International Union for Conservation of Nature (IUCN) Red List of threatened species; and the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES). Comparison was also made (on 31 August 2018) with protected fish listed on the Western Australian *Fish Resources Management Regulations 1995* Schedule 2 Parts 1–3, which is under the *Fish Resources Management Act 1994*.

## OVERVIEW OF THE ISLAND’S GEOGRAPHY AND BIOTA

Barrow Island is a continental island situated 56 km offshore. It is located near the edge of the continental shelf, regionally (115–122°E) termed the North West Shelf (Fig. 1). This broad submarine limestone shelf has chains of islands emerging roughly parallel to the mainland coast. Of these, Barrow Island, the Montebello Islands and nearby Lowendal Islands are the largest and farthest offshore (Chevron Australia 2005). This island complex includes over 315 low islands, islets and rocky stacks composed of limestone and cross-bedded sandstones (Department of Environment and Conservation 2006). During Quaternary high sea-level phases, such as at present, the islands are isolated from the mainland by a shallow (0–20 m deep) intervening ocean. However, during periods of lower sea levels, the islands are connected to the mainland across an exposed swampy coastal plain (Veth *et al.* 2017). Archaeological evidence indicates that Indigenous people lived on Barrow Island from around 51–46 ka until about 7 ka, when rising sea-levels caused the ultimate isolation of the island from the mainland (Veth *et al.* 2017). The first evidence of European awareness of the island is its inclusion on a Dutch navigational chart from 1628 (Moro & Lagdon 2013).

Barrow Island is 25 km long and 10 km wide, and rises to a maximum of 62 m above sea level (Department of Environment and Conservation 2006). It is composed primarily of limestone outcrops and deposits overlain by sands and gravels, with extensive rock platforms and rocky headlands on the west and east coasts (Chevron Australia 2005). The local climate is semi-arid and seasonally wet, with a mean annual rainfall of 306 mm but high inter-annual variability (Bureau of Meteorology 2011).

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[1] https://naturemap.dbca.wa.gov.au/

[2] http://www.environment.gov.au/cgi-bin/sprat/public/sprat.pl

There are 34 vegetation types on the island (Mattiske & Associates 1993), comprised primarily of coastal and inland arid zone plants (Buckley 1983). These include 406 native vascular plant species and 14 introduced vascular plants (Chevron Australia 2005). The marine flora includes mangroves and seagrasses, macro- and micro-algae, and samphire plants in isolated, sheltered pockets in the upper intertidal zone (Department of Environment and Conservation 2006).

The terrestrial fauna includes 14 land mammals (including two bats), 128 terrestrial and migratory bird species, 43 terrestrial reptile species, one frog species, 37 subterranean vertebrates and invertebrates, and over 2200 terrestrial invertebrates (Chevron Australia 2005; Callan *et al.* 2011; Moro & Lagdon 2013; Burbidge & Abbott 2017). The marine fauna includes mammals (e.g. whales, dolphins, dugong), waterbirds, sea turtles, sea snakes, fishes, and a diversity of lesser known vertebrate and invertebrate species (Department of Environment and Conservation 2006).

There are 22 confirmed or putative non-indigenous invertebrates recorded from the island but currently no non-indigenous vertebrates (Chevron Australia 2005; Callan *et al.* 2011). Barrow Island has been invaded in the past by mice (*Mus musculus*; at least four times) and Black rats (*Rattus rattus*) but both species were eradicated (Burbidge and Abbott 2017, suppl. material). The absence of exotic vertebrates means that several mammal species are present that have been predated or out-competed on the mainland and some other offshore islands (Main & Yadav 1971; Burbidge & Abbott 2017).

Barrow Island lies within the Montebello–Barrow Island marine conservation reserve, comprising the Montebello Islands Marine Park (58 331 ha), Barrow Island Marine Park (4169 ha) and Barrow Island Marine Management Area (114 693 ha). The reserve is in the Pilbara Offshore marine bioregion (Department of Environment and Conservation 2006).

Barrow Island Nature Reserve was listed on Australia's Register of the National Estate in 1978 followed by the marine area in 2000. However, the Register of the National Estate was removed from the *Environment Protection and Biodiversity Conservation Act 1999* on 19 February 2012 and neither the island nor the marine area is on Australia's current Commonwealth Heritage List[3]. However, the island retains its Western Australian status and is subject to an intensive protection regime implemented by the State and petroleum interests.

## CONSERVATION VALUES

### Terrestrial vertebrate fauna

Barrow Island is one of Australia's most important mammal refuges and conservation areas. Four mammal subspecies and one island form are endemic to the island; six species are listed as threatened under state or national legislation or both; and one species is on the state list of priority species (Appendix 1, Table 1; see Appendix 2 for a full list of taxa referred to in this paper). The island has been an important source for repopulating mammal species that have declined or become extinct elsewhere. As part of the environmental offset programs, a few threatened mammal species and two bird species have been translocated from Barrow Island to other Western Australian islands (Table 4). *Bettongia lesueur* was translocated to the Montebello Island group and Faure Island in Shark Bay, and also reintroduced to Boodie Island near Barrow Island (Burbidge & Abbott 2017). Similarly, there have been two conservation translocations of *Isoodon auratus* from Barrow Island (reintroduction to Hermite Island, Montebello Island group; translocation to Doole Island, Exmouth Gulf; Fig. 1) and a reinvasion of the nearby Boomerang Island (Fig. 1) after the species was eliminated during the eradication of Black rats in 1983. *Lagorchestes conspicillatus* was reintroduced from Barrow Island to Hermite Island after its local extinction (Burbidge & Abbott 2017, suppl. material; Table 4). Three species (*I. auratus, B. lesueur, Trichosurus vulpecula* subsp. *arnhemensis*) have been translocated to the mainland, with Water rats (*Hydromys chrysogaster*) under consideration (Department of Environment and Conservation 2010, 2011; Table 4). Chevron's Threatened Species Translocation and Reintroduction Program was valued at $10 million over 12 years (Department of Environment and Conservation 2011).

Many of the island's reptiles and birds are of conservation significance. There are distinct races or evolutionary significant units in some reptile species and the non-migratory avifauna that may have developed with the isolation of the island (Chevron Australia 2005). A subspecies of skink and a blind snake appear to be endemic to the island, and the blind snake is listed as a priority species (Appendix 1, Table 1; see 'Subterranean fauna'). There is also an endemic subspecies of bird (*Malurus leucopterus edouardi,* White-winged fairy wren) which is the most genetically distinct race within the species (Driskell *et al.* 2002), and which is listed as vulnerable nationally and in Western Australia. The land bird assemblage is depauperate, with only 16 of the 51 land bird species being residents or regular migrants. However, non-migratory birds on the island (e.g. Bar-shouldered dove *Geopelia humeralis*, Singing honeyeater *Gavicalis virescens*, Spinifexbird *Eremiornis carteri*) are assumed to have diverged genetically from mainland populations (Chevron Australia 2005).

Twelve of the island's birds are classified as threatened in Western Australia; two as endangered, nine as vulnerable and one as a priority species. Nine of these state-listed birds are also classified as threatened under the federal EPBC Act although only with partial overlap between the state and national classifications. Four birds are classified nationally as critically endangered, two as endangered, and three as vulnerable species. A total of 43 birds are categorised under the EPBC Act as migratory taxa and 63 as protected marine species, with some of these birds also being listed as threatened at state or national level. In relation to international conservation listings and conventions, five birds are classified as threatened (four endangered, one vulnerable) and seven as near threatened by the IUCN, with three birds listed on CITES schedule 2 (Appendix 1, Table 1).

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[3] http://www.environment.gov.au/heritage/places/commonwealth-heritage-list (viewed 15 September 2018)

**Table 4**

Conservation translocations of mammals and birds from Barrow Island to other WA islands and the mainland (from Burbidge & Abbott 2017, suppl. material; DEC 2010, 2011).

| Animal | Translocation site | Region | Intervention |
|---|---|---|---|
| *Bettongia lesueur* (Barrow Island burrowing bettong) | Alpha Island | Montebello Islands | 40 animals translocated in 2011 |
| *B. lesueur* | Faure Island | Shark Bay | 36 animals translocated in 1993 and 17 in 2002 |
| *B. lesueur* | Boodie Island | Barrow Island group | 36 animals reintroduced in 1993 after eradication in 1985–88 probably due to poisoning from rodenticide. Now common |
| *B. lesueur* | Lorna Glen | Northern Goldfields | 65 animals translocated in 2010 |
| *Isoodon auratus* (Barrow Island golden bandicoot) | Hermite Island | Montebello Islands | 161 animals reintroduced in 2010 after their local eradication between 1912 and 1950 |
| *I. auratus* | Doole Island | Exmouth Gulf | 92 animals translocated in 2010 and 2011 |
| *I. auratus* | Boomerang Island | Barrow Island group | Reinvasion from Barrow Island |
| *I. auratus* | Lorna Glen | Northern Goldfields | 164 animals translocated in 2010 |
| *Lagorchestes conspicillatus* (Barrow Island spectacled hare-wallaby) | Hermite Island | Montebello Islands | 111 animals reintroduced in 2010 after local extinction between 1912 and 1950 |
| *Trichosurus vulpecula* ssp. *arnhemensis* (Northern brushtail possum) | Cape Range National Park | South of Exmouth, Pilbara | 104 animals translocated in 2010 |
| *Eremiornis carteri* (Spinifex bird) | Hermite Island | Montebello Islands | Reintroduction in 2010 with 35 birds and restocking in 2011 with 12 birds |
| *Malurus leucopterus edouardi* (Barrow Island black and white fairy wren) | Hermite Island | Montebello Islands | Reintroduction in 2010 with 27 birds and restocking in 2011 with 10 birds |

Barrow Island is a significant staging post for southward migrating birds, a destination site, and a staging site for many migratory species (Chevron Australia 2005). Some migrant species rest on the island in the non-breeding summer season whereas other birds 'over-winter' on the island (Chevron Australia 2005). The island supports large numbers of waders and waterbirds, including some species such as the Ruddy turnstone (*Arenaria interpres*) and Bar-tailed godwit (*Limosa lapponica*) that have declined over the last 30 years (Bamford & Moro 2011). There are 50 species of marine littoral avifauna on the island (Chevron Australia 2005).

The island has been designated an Important Bird Area (IBA) under the Birdlife International programme due to its importance to migratory waders traversing via the East Asian–Australasian Flyway (EAAF; Chevron Australia 2005 appendix C3; Bamford & Moro 2011). Because of its importance for seven migratory waders, the island ranks equal tenth among the 147 significant sites in Australia for migratory waders, the fifth most important for the Grey-tailed tattler (*Tringa brevipes*) and fourth most important for the Ruddy turnstone (Bamford & Moro 2011).

The island also qualifies as an internationally significant migratory wader site under the Ramsar Convention. It meets the 1% of EAAF population threshold for five species, the staging threshold of supporting 0.25% of populations for eight species during seasonal migrations, and a 1% of global population threshold for one species (Chevron Australia 2005 appendix C3; Bamford & Moro 2011; Appendix 1, Table 1). Barrow Island supports over 1% of the species' population in the EAAF for the trans-equatorial migratory waders: Grey-tailed tattler, Ruddy turnstone, Red-necked stint (*Calidris ruficollis*), Greater sand plover (*Charadrius leschenaultii*) and Lesser sand plover (*C. mongolus*). It meets the staging criterion of at least 0.25% of a species' population during southward or northward seasonal migrations for eight migratory waders: Red-necked stint, Bar-tailed Godwit, Grey-tailed tattler, Ruddy turnstone, Greater sand plover, Common greenshank (*Tringa nebularia*), Lesser sand plover and Sanderling (*Calidris alba*) (Chevron Australia 2005; Bamford & Moro 2011).

The island is regionally significant for containing 2.4 – 6.6% of the known populations of three migratory species (Grey-tailed tattler, Ruddy turnstone, Red-necked stint) and at least 1% of the global population of the Red-necked stint (Chevron Australia 2005, appendix C3; Bamford & Moro 2011; Appendix 1, Table 1). There are also significant populations of two non-migratory birds: the Fairy tern (*Sterna nereis*) which moves only locally, and the northern race (*opthalmicus*) of the Sooty oystercatcher (*Haematopus fuliginosus*) which is an island resident (Chevron Australia 2005; Appendix 1, Table 1).

### Marine vertebrate fauna

Marine vertebrates of conservation significance found on or near Barrow Island include cetaceans, sea turtles, sharks and sygnathids (seahorses, sea-dragons and pipefish). All 40 species of cetaceans likely to be present in the area (Appendix 1, Table 1) are protected under the EPBC Act. Three species of turtle regularly nest on Barrow Island (Green turtles *Chelonia mydas;* Flatback turtles *Natator depressus*, Hawksbill turtles *Eretmochelys imbricata*), whereas occasional nesting by Loggerhead turtles (*Caretta caretta*) has been recorded and another three species are likely to be present near the island (Appendix 1, Table 1; Department of Environment and Conservation 2006). The Western Australian Hawksbill population is the largest remaining in the Indian Ocean.

All Australian sea turtles are protected under state and national conservation legislation, by the Bonn Convention for the protection of migratory animals and under CITES Schedule 1 (Appendix 1, Table 1). All waters within a 20 km radius of Barrow Island were identified in the National Recovery Plan for Marine Turtles in Australia (Environment Australia 2003) as critical habitat for the survival of Green turtles. Sharks are protected under state and national conservation legislation; species that visit the Barrow Island area include the Whale shark (*Rhincodon typus*), Grey nurse shark (*Carcharias taurus*) and Great white shark (*Carcharodon carcharias*). Two species of seahorse recorded near the island are protected under national legislation: Spiny seahorse (*Hippocampus histrix*) and Yellow seahorse (*H. kuda*) whereas two others are protected in Western Australia: Leafy seadragon (*Phycodurus eques*) and Common seadragon (*Phyllopteryx taeniolatus*).

In relation to Western Australia's conservation legislation, five marine vertebrates found near Barrow Island are listed as endangered, eight as vulnerable, four as priority taxa, one as conservation dependent, and two as other specially protected fauna. Five species are listed as protected fish (Appendix 1, Table 1). Most of these taxa are also considered to be threatened nationally; two marine vertebrates are listed as critically endangered nationally, five as endangered nationally, and nine as vulnerable nationally. Four of the marine vertebrates have also been classified by the IUCN as threatened: one as critically endangered (Leaf-scaled sea snake *Aipysurus foliosquama*), one as endangered (Whale shark), and 11 as vulnerable; with 24 identified as data deficient. Twenty-two marine vertebrates potentially present in the area are protected migratory species, 47 are protected marine species, and 52 are listed under CITES.

### Terrestrial invertebrates

The invertebrate taxa of Barrow Island are an important component of the fauna of the island because of their high species richness and contribution to ecosystem processes (Chevron Australia 2005). However, their conservation significance cannot be evaluated because a high proportion are yet to be described. Based on an intensive survey of terrestrial invertebrates on Barrow Island from 2005 to 2009, Callan *et al.* (2011) recorded 1873 species and morphospecies from 321 families and 27 orders, of which only 292 are named species. Majer *et al.* (2013) estimated 2481 invertebrates are present while noting that the fauna varied considerably between seasons, years and even weeks, and with recent rainfall as well as with distance from the coast. Further descriptions and reporting on these surveys were collated in Gunawardene *et al.* (2013).

A few well-studied taxa, generally few in species, vagile or of possible economic importance, are relatively well known. For instance, all species of the Odonata (four species), Embiidina (one species) and Isoptera (27 species) can be named and are widespread (Callan *et al.* 2011; Jones 2013). However, in some groups, the percentage of described species is low and the knowledge of endemism and conservation status is poor. This reflects the species richness of these groups, a paucity of older and more regionally extensive surveys, and limited taxonomic expertise.

The Gorgon development EIS (Chevron Australia 2005) identified 22 terrestrial invertebrate taxa as endemic to Barrow Island and one marine invertebrate as restricted to sand bars in the Montebello–Lowendal–Barrow Island region (Appendix 1, Table 2). These taxa are considered to be 'short range endemics' (SRE; i.e. invertebrates restricted in range by poor dispersal abilities or opportunities that are restricted to areas of less than 10 000 km$^2$; Harvey 2002). Surveys on Barrow Island have found over 40 potential SRE taxa, including species of spider, pseudoscorpions, centipedes, millipede, scorpions and land snails (Chevron Australia 2005). For example, there are eight species of arachnid and two terrestrial millipedes that are endemic to the island based on current records (Appendix 1, Table 2). Three species of camaenid land snails (*Quistrachia montebelloensis, Rhagada barrowensis, R. plicata*) found on Barrow Island and nearby islands have maximum ranges of only 22–70 km (Johnson *et al.* 2013).

Less conclusively, there is a terrestrial mollusc that, on current records, is an endemic whereas one pseudoscorpion is probably endemic (J. Majer pers. comm. 2011) and seven species of Collembola may be endemic (Greenslade 2013; see below). Several new species of silverfish (*Heterolepisma parva, Qantelsella maculosa, Q. aurantia, Hemitelsella transpectinata* (syn. *Acrotelsella transpectinata*), *Xenolepisma perexiguum*) were described from specimens collected on Barrow Island by Smith (2013, 2015), but he noted that further work is needed on the group. Similarly, Mound (2013) referred to a few thrip (Thysanoptera) species only known from Barrow Island (*Desmothrips barrowi, Gynaikothrips* sp., *Podothrips barrowi*) but reasoned that the poor knowledge of the mainland fauna meant that these species could not be considered yet as endemic to the island. The booklouse species *Lithoseopsis humphreysi* (Psocodea: Amphientomidae) is currently known only from Barrow Island and Cape Range (Taylor 2013). In the terrestrial isopods (Crustacea: Oniscidea), Judd & Perina (2013) indicated that at least six of the 18 described species are potential SREs.

More taxonomic studies as well as surveys in the Pilbara and Cape Range are required to clarify the true level of invertebrate endemism. Using the Collembola as an example, they have been intensively collected over a period of four years in all the island's habitats, including the intertidal zone and subterranean habitats. Sampling used pitfall traps, sweeping, extraction of soil cores, leaf litter samples, emergence traps and yellow pans. Collembola abundance is largely dependent on rainfall and at least one species was only detected after a heavy rainfall. Seventy-one species have been distinguished including 14 species from the marine littoral zone, one new generic record (*Calx,* family Entomobryidae) for Australia, and two possibly three exotic species (Greenslade 2013). The level of island endemism is low with most species probably also present elsewhere in northern Australia (Greenslade 2013). However, only 25% of the taxa had been described or were from a known species group (Greenslade 2013). Some taxa (e.g. *Calx* sp. and two intertidal species cf. *Kenyura* sp. and *Caufrenyllodes* sp.) are only known from one location. Two species of *Drepanura* (family Entomobryidae) are endemic to Barrow Island based on current records (Ma *et al.* 2015; P. Greenslade pers. comm. 2019). At least one, and possibly more, subterranean Collembola is endemic (see 'Subterranean fauna' below).

Endemism is also low in the ants (Hymenoptera) from Barrow Island. Of the approximately 117 species with 76 named, five may be endemic with four of these being un-named taxa (Heterick 2013). Similarly, only one of 11 species of parasitoid wasps in the genus *Elasmus* is potentially endemic but again further work is needed on the wasp fauna of Barrow Island and the Pilbara (Stevens *et al.* 2013).

### Subterranean fauna

The north-western Australian region may contain one of the more systematically diverse subterranean faunas globally, with many relict obligate stygofauna and a considerable level of regional endemism (Eberhard *et al.* 2005; Humphreys *et al.* 2013). Sixty-three species of stygofauna and 19 troglobitic fauna have been documented for Barrow Island (Humphreys *et al.* 2013). However, there are likely to be more species on the island as many areas have not been surveyed (Humphreys *et al.* 2013). In the Collembola, one endemic species *Acanthocyrtus barrowensis* which lacks pigmentation is known but further investigation is needed to assess whether this is due to the taxon occupying a subterranean habitat or just developing in low light intensity (Greenslade unpubl. report). Three other subterranean species (*Pseudosinella* sp., *Megalothorax* sp., *Cyphoda* sp.) also may be island endemics (Greenslade 2013).

Most of the stygofauna are invertebrates, primarily of the phyla Arthropoda and Annelida. The anchialine amphipod fauna (inhabiting underground waters with marine influence) is particularly notable for endemicity with 12 species described from Barrow Island specimens (Bradbury & Williams 1996a, 1996b; Bradbury 2002).

There are two vertebrate stygial taxa (order Chordata): the endemic Blind Cave Gudgeon *Milyeringa justitia* that has been only recorded from three bores on Barrow Island, and a cave synbranchid (Swamp eel) *Ophisternon* sp. which was photographed at one site but not collected (Larson *et al.* 2013). The Swamp eel is presumed, at the moment, to be *O. candidum*, which is widely distributed on Cape Range peninsula and in the west Pilbara region (Humphreys *et al.* 2013).

The most common troglobite on Barrow Island is the schizomid *Draculoides bramstokeri,* which is also known from Cape Range (Chevron Australia 2005; Humphreys *et al.* 2013). Other troglobitic or stygobitic fauna of the island include species of arachnid, pseudoscorpion, cockroach, isopod, hexapod, millipede and a blind snake (Aplin 1998; Car *et al.* 2013; Humphreys *et al.* 2013; Appendix 1, Table 2).

A subterranean blind snake (*Anilios longissimus* syn. *Ramphotyphlops longissimus*) was collected in 1995 when it emerged with well casing that may have punched through a deep cavern (Aplin 1998). The blind snake is known from only one specimen but is extremely distinctive and not obviously allied to any other known taxon (Aplin 1998). It may be the only known troglobitic reptile globally (Chevron Australia 2005) and is on the state priority species list. Similarly, the millipede *Speleostrophus nesiotes* is the first known troglobitic spiroboloid millipede and is likely to be a short range endemic restricted to Barrow Island (Chevron Australia 2005; Car *et al.* 2013). Car *et al.* (2013) also reported a new species of Haplodesmidae millipede endemic to Barrow Island that is probably troglobitic and likely to be a new genus, and an endemic epigean millipede *Boreohesperus dubitalis*. Another notable endemic of Barrow Island is the troglobitic scorpion *Aops oncodactylus*; it is the only known troglobitic urodacid, the only one known from continental Australia, and its ancestor appears to represent an early branch in the family Urodacidae (Volschenk & Prendini 2008). Eleven of the stygofauna and two other troglobites on Barrow Island are listed under Western Australian legislation as vulnerable species, while the Blind cave gudgeon and Blind cave eel are also recorded as nationally vulnerable under the EPBC Act (Appendix 1, Table 1).

### Terrestrial flora

With 406 native plant species (Chevron Australia 2005), Barrow Island has a relatively high level of species richness compared to other islands of similar size and vegetation type (Table 3). In contrast, tropical islands in north-eastern Australia have higher rainfall and more plant species: Whitsunday Island, Qld (20°15′S 148°58′E, 109 km$^2$) has 495 species and Hinchinbrook Island, Qld (18°20′S 146°14′E, 399 km$^2$) has 600 plant species (Batianoff & Dillewaard 1997).

The Barrow Island flora does not display as high a level of endemism as the vertebrate fauna but is regionally significant because of rare and priority taxa, other taxa that may be restricted to the island, and many that are at their limit of range (Chevron Australia 2005). There are two plant forms or variants that are endemic to the island (Appendix 1, Table 3). These are a variant of *Cucumis variabilis* (Telford *et al.* 2011) and a dwarf form of *Acacia trudgeniana* (Maslin & van Leeuwen 2008). There are also two priority plant taxa on the island (Appendix 1, Table 3): *Helichrysum oligochaetum* and *Corchorus congener*. The island has 50 species at the northern limit for plants of Cape Range and southwards, 122 at the southern limit of range for plants of the Kimberley region, and 193 at the western limit for plants of the Pilbara region (Chevron Australia 2005, appendix C1 p7 – attachment A). In addition, Chevron Australia (2005) referred to five plant taxa that are of conservation significance on Barrow Island as they are restricted to creek beds and gullies—habitats that have been reduced locally through human disturbance (Appendix 1, Table 3).

### Marine flora and invertebrate fauna

The marine flora generally is widespread, being connected with assemblages in the Dampier Archipelago and the Rowley Shoals to the north by the Leeuwin

Current (Department of Environment and Conservation 2006; Fig. 1). Most marine flora (and fauna) species in the bioregion are tropical and widely distributed throughout the Indo-West Pacific region due to natural oceanographic links.

Nevertheless, there may be many endemic and undescribed species because of habitat diversity (Department of Environment and Conservation 2006). Even at a small scale, habitat differentiation (e.g. from wave energy) has been shown to influence benthic species distributions across the region and specifically between offshore and nearshore assemblages; some intertidal molluscan genera (e.g. *Conus, Modiolus, Rhinoclavis*) demonstrate this with some species restricted to the west coast of Barrow Island with congenerics along the east coast (Department of Environment and Conservation 2006). Six species of macro-algae have only been recorded from near Barrow Island but the region has not been systematically surveyed.

A recent study of scleractinian corals found 15 species not recorded elsewhere in Western Australia and assessed the diversity of corals in the Pilbara vicinity of Barrow Island to be significant at regional, national and international scales (Richards & Rosser 2012). Thirty-nine coral species in the Barrow–Montebello Island assemblage are listed by the IUCN as vulnerable to extinction, including one of the locally dominant species, *Pectinia lactuca* (Richards & Rosser 2012; Appendix 1, Table 4). The area may provide a high latitude refuge for these and other coral species from climate change (Richards & Rosser 2012).

## BIOGEOGRAPHIC AFFINITIES

The composition of the biota of Barrow Island reflects several biogeographic patterns and the disparate evolutionary pathways of its constituent species through the Quaternary. On a geological timescale, Barrow Island is more typically a land-bridge island and an extremity of the Australian mainland rather than a remote offshore continental island (Fig. 1). The last 2.4 Ma of the Quaternary have encompassed over 20 major climatic fluctuations with the continental shelves exposed at least eight times (Galloway & Kemp 1981; Colhoun & Peterson 1986). Based on modelling of sea levels, Barrow Island may have been geographically isolated from the Australian mainland (i.e. sea levels were up to 20 m lower than present) for only about 25% of the last 500 ka (Bintanja *et al.* 2005) or about 14% of the last 150 ka (Grant *et al.* 2012). The biogeographic patterns reflect at least three types of species history (see Appendix 1, Table 5).

### Endemic species with close relationships to onshore conspecifics or congeners

Many subterranean taxa are endemic to Barrow Island and have close relationships with conspecifics or congeners at Cape Range and to a lesser degree the Pilbara coastal plain (Eberhard *et al.* 2005, table 1). The subterranean fauna of the Barrow Island – Cape Range – Pilbara coastal region is one of the most biodiverse globally, which Bradbury and Williams (1997) attributed to the stranding of ancestral founder populations in small discrete subterranean basins followed by regressive evolution. Barrow Island and Cape Range occur in geologically similar sub-basins within the Northern Carnarvon geologic basin. Their thick Mesozoic sequences of limestone, claystone, sandstone and calcarenite differ from the adjacent onshore parts of the Carnarvon Basin which are dominated by Palaeozoic strata with a veneer of Mesozoic and Cainozoic sediments (Hocking *et al.* 1987). These differ substantially from the volcanic and metamorphic rocks of the Precambrian Pilbara Craton farther east and north-east on the mainland (Hocking *et al.* 1987).

Stygobionts have endured in this semi-arid region because the subsurface habitats provide lower temperatures and relatively stable environmental conditions (Bradbury & Williams 1997). Some of the amphipod stygofauna on Barrow Island live in waters with marine influence and are derived from closely allied marine ancestors (thalassostygobionts e.g. the anchialine troglobite *Liagoceradocus*). Others occupy subterranean freshwater habitats but are derived from marine ancestors and their ranges overlap with areas of marine transgressions during the Cretaceous (e.g. many hadzioids such as Barrow Island's *Nedsia* species and *Bogidomma* genus; Bradbury & Williams 1996a, 1997). The biogeography of the stygofauna, anchialine fauna and troglofauna is strongly linked with Gondwana, the Tethys and rainforests, respectively (Humphreys *et al.* 2013). The antiquity of elements of the biota is further indicated by the presence of endemic genera (e.g. *Bogidomma*) and a relict scorpion (*Aops oncodactylus*), whose ancestor is believed to belong to an early branch of the family Urodacidae.

### Resident terrestrial taxa closely related to Pilbara biota

This biogeographic pattern is shown by resident terrestrial taxa, a few of which have a low level of subspecific variation from mainland taxa in the Pilbara and broader region. The fauna, including invertebrates such as ants for example, is generally a subset of the Pilbara biota, has low endemism and, in the case of birds, is depauperate in species with only 16 of the 51 species of terrestrial avifauna being residents or regular migrants to the island (Main & Yadav 1971; Chevron Australia 2005; Heterick 2013). Nevertheless, there are four endemic subspecies and one island form amongst the resident small mammals, and one endemic subspecies of an epigean (i.e. not subterranean) reptile and of a non-migratory bird. In addition, two forms or variants of vascular plants are endemic to the island, and about 30 terrestrial invertebrate taxa are short-range or island endemics. Notably, two closely related species of the highly vagile fly family Dolichopodidae (Diptera) have been recorded, one that is endemic to Barrow Island and the other to Cape Range (Bickel 2013). Forty-one species of this family are known from the Pilbara. Bickel (2013) surmised that some of the Dolichopodidae distributions reflect a sweepstake effect of progressive species impoverishment towards the Pilbara of tropical and monsoonal taxa that are able to persist in protected mesic sites, but also that a widespread richer mid-Tertiary biota has since fragmented into isolated pockets.

Overall, the level of endemism amongst the terrestrial taxa of Barrow Island indicates selective pressure on resident taxa from intermittent isolation with sea-level and climatic changes through the Quaternary. Amongst the birds for example, the subspecific divergence evident in the White-winged fairy wren relates to their localised distribution and lack of genetic interchange between populations on Barrow Island and other parts of the species' range. There has been persistence of habitats for these taxa even with higher past sea levels—for example, at 128 ka, the sea level has been estimated to have been about 7 m higher than today, which may have caused the inundation of about one-fifth of the island (Appendix 1, Table 6). However, storm surges would have further reduced the available habitats, as would intermittent disturbance of habitats from cyclones. Barrow Island is located in an area of comparatively high cyclone frequency and intensity (Jaffrés *et al.* 2018, fig. 15) and has experienced the strongest winds recorded globally (408 km/h) during the passage of Cyclone Olivia in 1996 (Bureau of Meteorology 2018). Many non-vagile species are likely to be highly vulnerable to extirpation by such events on Barrow Island, although some of these taxa, like Aboriginal people, would have traversed the coastal plain environments exposed during lower sea levels.

### Taxa generally lacking localised variation

The third biogeographic pattern is evident in the many currently vagile or widespread species that have been recorded for Barrow Island and is reflective of their dispersive abilities. These taxa generally lack any localised variation related to their presence on or close to Barrow Island. This group includes migratory and migrant taxa, aquatic taxa and vagile taxa with flying capability at some stage of their life cycle. For example, most of the bird assemblage are migrants that regularly travel between the Pilbara mainland and offshore islands or are trans-equatorial migrants (Chevron Australia 2005).

This group also includes most of the plant species. Phytogeographically, Barrow Island is complex and particularly notable for having plants that are at their western, southern or northern limits of range. The flora is somewhat typical of the adjacent mainland in having 23% of the Pilbara region's taxa, but there are also floral affinities with the Cape Range (particularly in coastal areas) and affinities with the Kimberley region (Chevron Australia 2005; Eberhard *et al.* 2005). The only indigenous *Eucalyptus* on the island, *E. xerothermica,* is widespread across the Pilbara to Cape Range region. Some of these taxa may have persisted through glacial cycles on the island whereas others experienced a more recent influx.

## CONCLUSIONS

Our comprehensive compilation of the available data on the taxa of conservation significance of Barrow Island demonstrates the very high regional, national and international significance of the biota and the ongoing importance of the island for conservation. It is commendable that the integrity of the terrestrial and aquatic biota has been maintained despite the operation of commercial oil extraction and liquified natural gas processing for over 50 years. Partly this is due to effective quarantine protocols, inspections, regular monitoring, and eradication of invasive species that have intruded sporadically.

The biota of Barrow Island is significant for the many taxa that are endemic, threatened, diminished elsewhere in their range, protected under national or international conventions, or of biogeographic interest. As such, the island represents an important conservation and scientific resource. Some of the small mammals from the island have been used to re-establish populations in other parts of their range where they have been eliminated through predation by invasive feral animals. The number of animals translocated and their successful establishment elsewhere (Table 4) suggests that these species have been stable or increasing on the island and that there has been careful assessment of animals suitable for relocation.

We described three main biogeographic patterns for the biota of the island, although these could be further delineated. There are clear biological signals of the geological, geographic and climatological history of the area through the Quaternary, and of taxonomic links dating back to the Tertiary. Changing sea levels and climatic regimes are likely to have affected local species assemblages and divergence from mainland taxa. This provides opportunities to investigate biogeographic and evolutionary processes given the overlay of these patterns and the level of endemism represented in the island's biota. The drivers and refined understanding of these patterns could be explored through additional genetic studies.

In terms of conservation co-existing with development, it is clear that the conservation program since 1910 with industrial development since the 1960s has been a success. Although the economic efficiency of the management regime has been debated in the scientific literature (Moore *et al.* 2010, 2012; Greenslade *et al.* 2013a, 2013b), the core criticism was more general as it related to appropriate use of decision modelling, with Barrow Island used as one example. Moore *et al.* (2012) conceded that there had been no contention that the management strategy for the island had been 'wrong'. Nevertheless, the island's management also has attracted media criticism and political objections (e.g. Toohey 2015), so the recent establishment of an in situ research centre along with enhanced transparency may assist in alleviating or addressing such concerns.

The extensive period of effective operation of island 'arks' such as Barrow Island is relevant to conservation management on the mainland. An increasing number of predator proof reserves are being established to protect fauna from invasive species, but the intensive management strategy imposed on Barrow Island is unlikely to be economically or logistically affordable by many other organisations. Furthermore, there is evidence of inbreeding depression in some island populations (Eldridge *et al.* 2004), a factor that requires consideration if island populations are to be utilised for translocations or for maintaining viable, genetically diverse populations on the mainland in predator- (and small-mammal) proof, enclosed reserves over the long-term. Species in enclosed protected areas will still require intensive population management including genetic evaluation and manipulation. Society should be informed of the opportunity costs or tradeoffs and limitations of conservation choices focused on ecosystems, species, populations or DNA. Preservation of genetic diversity, behavioural characteristics and species interactions requires not only captive individuals but conservation of populations, habitats and viable ecosystems (Godden & Skellern 2006). An integrated framework with collaborative partnerships across government, research, industry and conservation organisations will be essential to achieve this.

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## APPENDIX 1 TABLES

**Table 1**

Fauna species on Barrow Island of conservation significance (from Sedgwick 1978; Chevron Australia 2005; Humphreys *et al.* 2013; EPBC Act list 21–24 August 2018; NatureMap (WA Department of Parks and Wildlife) search 22/2018.

| Scientific name (Common name) | Significant bird population | Island endemic subspecies | State threatened/ priortiy | Nationally threatened | IUCN Red List | Migratory - EPBC | Migratory - Bonn | Migratory - CAMBA | Migratory - JAMBA | Migratory - ROKAMBA | Marine/ Cetacean | CITES Schedule |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **MAMMALS** | | | | | | | | | | | | |
| **Dasyuridae** | | | | | | | | | | | | |
| *Planigale* sp. 1 (Westermans *et al.* 2016) | | | | | | | | | | | | |
| **Macropodidae** | | | | | | | | | | | | |
| *Lagorchestes conspicillatus conspicillatus* (Barrow Island Spectacled hare-wallaby) | | subsp. | VU | VU | | | | | | | | |
| *Osphranter robustus isabellinus* / syn. *Macropus robustus isabellinus* (Barrow Island Euro) | | subsp. | VU | VU | | | | | | | | |
| *Petrogale lateralis lateralis* (Black-flanked rock-wallaby) | | | EN | EN | EN | | | | | | | |
| **Muridae** | | | | | | | | | | | | |
| *Hydromys chrysogaster* (Water rat) | | | P4 | | LC | | | | | | | |
| *Pseudomys nanus* (Western chestnut mouse) | | Island form | | | LC | | | | | | | |
| **Peramelidae** | | | | | | | | | | | | |
| *Isoodon auratus barrowensis* (Barrow Island Golden bandicoot) | | subsp. | VU | VU | VU | | | | | | | |
| **Phalangeridae** | | | | | | | | | | | | |
| *Trichosurus vulpecula arnhemensis* (Northern brushtail possum; Kimberley) | | | VU | | | | | | | | | |
| **Potoroidae** | | | | | | | | | | | | |
| *Bettongia lesueur* (Barrow and Boodie Islands subspecies; Barrow Island Burrowing bettong) | | subsp. | CD | VU | NT | | | | | | | 1 |
| **REPTILES** | | | | | | | | | | | | |
| **Scincidae** | | | | | | | | | | | | |
| *Ctenotus pantherinus acripes* (Barrow Island leopard skink) | | subsp. | | | | | | | | | | |
| **Typhlopidae** | | | | | | | | | | | | |
| *Anilios longissimus* (Barrow Island blind snake; stygofauna) | | sp. | P2 | | | | | | | | | |

**Table 1**. (cont.)

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **BIRDS** | | | | | | | | | | | |
| **Accipitridae** | | | | | | | | | | | |
| *Haliaeetus (Pontoaetus) leucogaster* (White-bellied sea-eagle) | | | | LC | | | | | | M | 2 |
| *Haliastur indus* (Brahminy kite) | | | | LC | | | | | | M | |
| *Pandion cristatus* / syn. *Pandion haliaetus* (Osprey) | | IA | | LC | MI | X | | | | M | 2 |
| **Apodidae** | | | | | | | | | | | |
| *Apus (Apus) pacificus* (Fork-tailed swift) | | IA | | LC | MI | | X | X | X | M | |
| *Hirundapus caudacutus* (Spine-tailed swift, White-throated needletail) | | IA | | LC | MI | | X | X | X | M | |
| **Ardeidae** | | | | | | | | | | | |
| *Ardea modesta* / syn. *Ardea alba* (Great egret, Eastern great egret) | | | | LC | | | | | | M | |
| *Egretta garzetta* (Little egret) | | | | LC | | | | | | M | |
| *Egretta sacra* / syn. *Ardea sacra* (Eastern reef egret) | | | | LC | | | | | | M | |
| **Burhinidae** | | | | | | | | | | | |
| *Esacus magnirostris* / *E. neglectus* (Beach Stone-curlew) | | | | NT | | | | | | M | |
| **Campephagidae** | | | | | | | | | | | |
| *Coracina novaehollandiae* (Black-faced cuckoo-shrike) | | | | LC | | | | | | M | |
| **Charadriidae** | | | | | | | | | | | |
| *Charadrius (Charadrius) leschenaultii* (Greater sand plover) | b, c, i | IA, VU | VU | LC | MI | X | X | X | X | | |
| Vulnerable in WA at subsp. level | | | | | | | | | | | |
| *Charadrius (Charadrius) mongolus* (Lesser sand plover, Mongolian plover) | c, i | IA, EN | EN | LC | MI | X | X | X | X | M | |
| *Charadrius (Charadrius) ruficapillus* (Red-capped plover) | | | | LC | | | | | | M | |
| *Charadrius (Eupoda) veredus* (Oriental plover) | | IA | | LC | MI | X | X | X | X | M | |
| *Pluvialis fulva* (Pacific golden plover) | | IA | | LC | MI | X | X | X | X | M | |
| *Pluvialis squatarola* (Grey plover) | | IA | | LC | MI | X | X | X | X | M | |
| **Cuculidae** | | | | | | | | | | | |
| *Cacomantis pallidus* / syn. *Cuculus pallidus* (Pallid cuckoo) | | | | | | | | | | M | |
| *Cuculus optatus* / syn. *C. saturatus* (Oriental cuckoo) | | IA | | LC | MI | | | X | X | M | |
| **Diomedeidae** | | | | | | | | | | | |
| *Thalassarche chlororhynchos*/ syn. *Diomedea chlororhynchos* (Atlantic Yellow-nosed albatross) | | IA, VU | | EN | MI | X | | | | M | |
| **Falconidae** | | | | | | | | | | | |
| *Falco cenchroides* (Nankeen Kestrel) | | | | LC | | | | | | M | |
| **Fregatidae** | | | | | | | | | | | |
| *Fregata ariel* (Lesser frigatebird) | | IA | | LC | MI | | X | X | X | M | |
| **Glareolidae** | | | | | | | | | | | |
| *Glareola maldivarum* (Oriental pratincole) | | IA | | LC | MI | | X | X | X | M | |
| *Stiltia isabella* (Australian pratincole) | | | | LC | | | | | | M | |
| **Haematopodidae** | | | | | | | | | | | |
| *Haematopus fuliginosus* (Sooty oystercatcher) | j | | | LC | | | | | | | |

| | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| **Halcyonidae** | | | | | | | | | | | |
| *Todiramphus sanctus* (Sacred kingfisher) | | | | | LC | | | | | | M |
| **Hirundinidae** | | | | | | | | | | | |
| *Hirundo neoxena* (Welcome swallow) | | | | | LC | | | | | | M |
| *Hirundo rustica* (Barn swallow) | | | IA | | LC | MI | | X | X | X | M |
| *Petrochelidon nigricans* / syn. *Hirundo nigricans* (Tree martin) | | | | | LC | | | | | | M |
| **Hydrobatidae** | | | | | | | | | | | |
| *Oceanites oceanicus* (Wilson's storm petrel) | | | IA | | LC | MI | | | X | | M |
| **Laridae** | | | | | | | | | | | |
| *Anous tenuirostris* (Lesser noddy) | | | | | LC | | | | | | M |
| *Chlidonias leucopterus*/ syn. *Childonias leucoptera* (White-winged black tern) | | | IA | | LC | MI | | X | X | X | M |
| *Chroicocephalus novaehollandiae* / syn. *Larus novaehollandiae* (Silver Gull) | | | | | LC | | | | | | M |
| *Gelochelidon nilotica* (Gull-billed tern) | | | IA | | LC | MI | | X | | | M |
| *Hydroprogne caspia* / syn. *Sterna caspia* (Caspian tern) | | | IA | | LC | MI | | | X | | M |
| *Onychoprion anaethetus* / syn. *Sterna anaethetus* (Bridled tern) | i? | | IA | | LC | MI | | X | X | | M |
| *Sterna dougallii* (Roseate tern) | i? | | IA | | LC | MI | | X | X | | M |
| *Sterna hirundo* (Common tern) | | | IA | | LC | MI | | X | X | X | M |
| *Sternula albifrons* / syn. *Sterna albifrons* (Little tern) | | | IA | | LC | MI | X | X | X | X | M |
| *Sternula nereis* (Fairy tern) | h | | VU | VU | VU | | | | | | M |
| *Thalasseus bengalensis*/ syn. *Sterna bengalensis* (Lesser crested tern) | | | | | LC | | | | | | M |
| *Thalasseus bergii* / syn. *Sterna bergii* (Crested tern) | | | IA | | LC | MI | | | X | | M |
| **Maluridae** | | | | | | | | | | | |
| *Malurus leucopterus edouardi* (Barrow Island black and white fairy wren) | a | ssp. | VU | VU | | | | | | | |
| **Meropidae** | | | | | | | | | | | |
| *Merops ornatus* (Rainbow bee-eater) | | | | | LC | | | | | | M |
| **Motacillidae** | | | | | | | | | | | |
| *Anthus novaeseelandiae* / syn. *A. australis* (Australasian pipit, Richard's pipit, Australian pipit) | | | | | LC | | | | | | M |
| **Procellariidae** | | | | | | | | | | | |
| *Ardenna pacifica* / syn. *Puffinus pacificus* (Wedge-tailed shearwater) | | | IA | | LC | MI | | | X | | M |
| *Puffinus huttoni* (Hutton's shearwater) | | | EN | | EN | | | | | | M |
| **Scolopacidae** | | | | | | | | | | | |
| *Actitis hypoleucos*/ syn. *Tringa hypoleucos* (Common sandpiper) | | | IA | | LC | MI | X | X | X | X | M |
| *Arenaria interpres* (Ruddy turnstone) | b, c, f | | IA | | LC | MI | X | X | X | X | M |
| *Calidris acuminata* (Sharp-tailed sandpiper) | | | IA | | LC | MI | X | X | X | X | M |
| *Calidris alba* (Sanderling) | i | | IA | | LC | MI | X | X | X | X | M |
| *Calidris canutus* (Red knot; also vulnerable subsp. in WA) | | | IA, VU | EN | NT | MI | X | X | X | X | M |
| *Calidris ferruginea* (Curlew sandpiper) | | | IA, VU | CR | NT | MI | X | X | X | X | M |
| *Calidris ruficollis* (Red-necked stint) | b, c, d, e | | IA | | NT | MI | X | X | X | X | M |

**Table 1**. (cont.)

| | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Calidris tenuirostris* (Great knot) | | | IA, VU | CR | EN | MI | X | X | X | X | M | |
| *Limosa lapponica* (Bar-tailed godwit) | c | | IA | | NT | MI | X | X | X | X | M | |
| *Limosa lapponica menzbieri* is VU in WA and CR nationally | | | VU | CR | | | | | | | | |
| *Limosa limosa* (Black-tailed godwit) | | | IA | | NT | MI | X | X | X | X | M | |
| *Numenius madagascariensis* (Eastern curlew) | | | IA, VU | CR | EN | MI | X | X | X | X | M | |
| *Numenius minutus* (Little curlew) | | | IA | | LC | MI | X | X | X | X | M | |
| *Numenius phaeopus* (Whimbrel) | | | IA | | LC | MI | X | X | X | X | M | |
| *Tringa brevipes* (Grey-tailed tattler) | b, c, g | | IA, P4 | | NT | MI | X | X | X | X | M | |
| *Tringa glareola* (Wood sandpiper) | | | IA | | LC | MI | X | X | X | X | M | |
| *Tringa nebularia* (Common greenshank) | c | | IA | | LC | MI | X | X | X | X | M | |
| *Tringa stagnatilis* (Marsh sandpiper) | | | IA | | LC | MI | X | X | X | X | M | |
| *Xenus cinereus*/ syn. *Tringa terek* (Terek sandpiper) | | | IA | | LC | MI | X | X | X | X | M | |
| **Sulidae** | | | | | | | | | | | | |
| *Sula dactylatra* ssp. *bedouti* (Masked booby) | | | IA | | LC | MI | | | X | X | M | |
| *Sula leucogaster* (Brown booby) | | | IA | | LC | MI | | X | X | X | M | |
| **Otididae** | | | | | | | | | | | | |
| *Ardeotis australis* (Australian bustard) | | | | | LC | | | | | | | 2 |
| **FISH (STYGOFAUNA)** | | | | | | | | | | | | |
| **Eleotridae** | | | | | | | | | | | | |
| *Milyeringa justitia* (Barrow cave gudgeon)—listed nationally and internationally **as** *M. veritas* from which it was separated taxonomically in 2013 | | sp. | VU | VU | DD | | | | | | | |
| **Synbranchidae** | | | | | | | | | | | | |
| *Ophisternon candidum* (Blind cave eel) | | | VU | VU | DD | | | | | | | |
| **MARINE VERTEBRATES** | | | | | | | | | | | | |
| **Balaenidae** | | | | | | | | | | | | |
| *Eubalaena australis* (Southern right whale) | | | VU | EN | LC | MI | X | | | | C | 1 |
| **Balaenopteridae** | | | | | | | | | | | | |
| *Balaenoptera acutorostrata* (Minke whale) | | | | | LC | | | | | | C | 1, 2 |
| *Balaenoptera borealis* (Sei whale) | | | EN | VU | EN | MI | X | | | | C | 1 |
| *Balaenoptera edeni* (Bryde's whale) | | | | | LC | MI | X | | | | C | 1 |
| *Balaenoptera musculus* (Blue whale) | | | EN | EN | EN | MI | X | | | | C | 1 |
| *Balaenoptera physalus* (Fin whale) | | | EN | VU | EN | MI | X | | | | C | 1 |
| *Megaptera novaeangliae* (Humpback whale) | | | CD | VU | LC | MI | X | | | | C | 1 |
| **Cheloniidae** | | | | | | | | | | | | |
| *Caretta caretta* (Loggerhead turtle) | | | EN | EN | VU | MI | X | | | | M | 1 |
| *Chelonia mydas* (Green turtle) | | | VU | VU | EN | MI | X | | | | M | 1 |
| *Eretmochelys imbricata* (Hawksbill turtle) | | | VU | VU | CR | MI | X | | | | M | 1 |
| *Lepidochelys olivacea* (Olive ridley turtle, Pacific ridley turtle) | | | EN | EN | VU | MI | X | | | | M | 1 |
| *Natator depressus* (Flatback turtle) | | | VU | VU | DD | MI | X | | | | M | 1 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Delphinidae** | | | | | | | |
| *Delphinus delphis* (Common dolphin) | | | LC | | | C | 2 |
| *Feresa attenuata* (Pygmy killer whale) | | | DD | | | C | 2 |
| *Globicephala macrorhynchus* (Short-finned pilot whale) | | | DD | | | C | 2 |
| *Globicephala melas* (Long-finned pilot whale) | | | DD | | | C | 2 |
| *Grampus griseus* (Risso's dolphin) | | | LC | | | C | 2 |
| *Lagenodelphis hosei* (Fraser's dolphin) | | | LC | | | C | 2 |
| *Lagenorhynchus obscurus* (Dusky dolphin) | | | DD | MI | X | C | 2 |
| *Lissodelphis peronii* (Southern right whale dolphin) | | | DD | | | C | 2 |
| *Orcaella heinsohni* / syn. *O. brevirostris* (Australian Snubfin dolphin / Irrawaddy dolphin) | P4 | | VU | MI | X | C | 1 |
| *Orcinus orca* (Killer whale) | | | DD | MI | X | C | 2 |
| *Peponocephala electra* (Melon-headed whale) | | | LC | | | C | 2 |
| *Pseudorca crassidens* (False killer whale) | | | DD | | | C | 2 |
| *Sousa sahulensis* / syn. *S. chinensis* (Indo-Pacific humpback dolphin) | P4 | | VU | MI | X | C | 1 |
| *Stenella attenuata* (eastern tropical Pacific population, Southeast Asian populations; Pantropical spotted dolphin) | | | LC | MI | X | C | 2 |
| *Stenella coeruleoalba* (Striped dolphin) | | | LC | | | C | 2 |
| *Stenella longirostris* (Long-snouted Spinner dolphin) | P4 | | DD | | | C | 2 |
| *Steno bredanensis* (Rough-toothed dolphin) | | | LC | | | C | 2 |
| *Tursiops aduncus* (Spotted bottlenose dolphin, Indo-pacific Bottlenose Dolphin) | | | DD | MI | X | C | 2 |
| *Tursiops truncatus s. str.* (Bottlenose dolphin) | | | LC | | | C | 2 |
| **Dermochelyidae** | | | | | | | |
| *Dermochelys coriacea* (Leatherback turtle, Leathery turtle) | VU | EN | VU | MI | X | M | 1 |
| **Dugongidae** | | | | | | | |
| *Dugong dugon* (Dugong) | OS | | VU | MI | X | M | 1 |
| **Elapidae** (Sea snakes) | | | | | | | |
| *Aipysurus apraefrontalis* (Short-nosed sea snake) | CR | CR | CR | | | M | |
| *Aipysurus duboisii* (Dubois' seasnake, Reef Shallows Sea Snake) | | | LC | | | M | |
| *Aipysurus eydouxii* (Spine-tailed sea snake, Stagger-banded sea snake) | | | LC | | | M | |
| *Aipysurus foliosquama* (Leaf-scaled sea snake) | CR | CR | CR | | | M | |
| *Aipysurus laevis* (Olive sea snake, Golden sea snake) | | | LC | | | M | |
| *Emydocephalus annulatus* (Turtle-headed sea snake) | | | LC | | | M | |
| *Ephalophis greyi* (North-western mangrove sea snake) | | | LC | | | M | |
| *Hydrophis czeblukovi* (Fine-spined sea snake) | | | DD | | | M | |
| *Hydrophis elegans* (Elegant sea snake, Bar-bellied sea snake) | | | LC | | | M | |
| *Hydrophis kingii* / syn. *Disteira kingii* (Spectacled sea snake) | | | LC | | | M | |
| *Hydrophis major* / syn. *Disteira major* (Olive-headed sea snake) | | | LC | | | M | |
| *Hydrophis* sp. / syn. *H. ornatus* (Ornate reef sea snake) | | | LC | | | M | |
| *Hydrophis peronii* / syn. *Acalyptophis peronii* (Horned sea snake, Spiny-headed Sea snake) | | | LC | | | M | |
| *Hydrophis platurus* / syn. *Pelamis platurus* (Yellow-bellied sea snake) | | | LC | | | M | |
| *Hydrophis stokesii* / syn. *Astrotia stokesii* (Stokes' sea snake) | | | LC | | | M | |

**Table 1**. (cont.)

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **Lamnidae** | | | | | | | |
| *Carcharodon carcharias* (Great white shark) | VU, Prf | VU | VU | MI | X | | 2 |
| **Odontaspididae** | | | | | | | |
| *Carcharias taurus* (Grey nurse shark – west coast population) | VU | VU | VU | | | | |
| **Kogiidae** | | | | | | | |
| *Kogia breviceps* (Pygmy sperm whale) | | | DD | | | C | 2 |
| *Kogia sima* / syn. *K. simus* (Dwarf sperm whale) | | | DD | | | C | 2 |
| **Physeteridae** | | | | | | | |
| *Physeter macrocephalus* (Sperm whale) | VU | | VU | MI | X | C | 1 |
| **Rhincodontidae** | | | | | | | |
| *Rhincodon typus* (Whale shark) | OS, Prf | VU | EN | MI | X | | 2 |
| **Serranidae** | | | | | | | |
| *Epinephelus tukula* (Potato cod, Potato rockcod) | Prf | | LC | | | | |
| **Solenostomidae** (Ghost pipefish) | | | | | | | |
| *Solenostomus cyanopterus* (Blue-finned ghost pipefish, Robust ghost pipefish) | | | LC | | | M | |
| **Syngnathidae** | | | | | | | |
| *Bulbonaricus brauni* (Braun's pughead pipefish, Pug-headed pipefish) | | | LC | | | M | |
| *Campichthys tricarinatus* (Three-keel pipefish) | | | DD | | | M | |
| *Choeroichthys brachysoma* (Short-bodied pipefish) | | | LC | | | M | |
| *Choeroichthys latispinosus* (Murion Island pipefish) | | | DD | | | M | |
| *Choeroichthys suillus* (Pig-snouted pipefish) | | | LC | | | M | |
| *Doryrhamphus janssi* (Cleaner pipefish, Janss' pipefish) | | | LC | | | M | |
| *Festucalex scalaris* (Ladder pipefish) | | | LC | | | M | |
| *Filicampus tigris* (Tiger pipefish) | | | LC | | | M | |
| *Halicampus brocki* (Brock's pipefish) | | | LC | | | M | |
| *Halicampus grayi* (Mud pipefish) | | | LC | | | M | |
| *Halicampus nitidus* (Glittering pipefish) | | | LC | | | M | |
| *Halicampus spinirostris* (Spiny-snout pipefish) | | | LC | | | M | |
| *Haliichthys taeniophora* (Ribboned sea dragon) | | | LC | | | M | |
| *Hippichthys penicillus* (Beady pipefish, steep-nosed pipefish) | | | LC | | | M | |
| *Hippocampus angustus* (Narrow-bellied seahorse) | | | LC | | | M | 2 |
| *Hippocampus histrix* (Spiny seahorse) | | | VU | | | M | 2 |
| *Hippocampus kuda* (Spotted seahorse, Yellow seahorse, Estuary seahorse) | | | VU | | | M | 2 |
| *Micrognathus micronotopterus* (Tidepool pipefish) | | | LC | | | M | |
| *Phoxocampus belcheri* (Black rock pipefish) | | | LC | | | M | |
| *Phycodurus eques* (Leafy seadragon) | P2, Prf | | LC | | | M | |
| *Phyllopteryx taeniolatus* (Weedy or Common sea dragon) | Prf | | LC | | | M | |
| *Syngnathoides biaculeatus* (Double-ended pipehorse, Alligator pipefish) | | | LC | | | M | |
| *Trachyrhamphus bicoarctatus* (Bentstick pipefish, short-tailed pipefish) | | | LC | | | M | |
| *Trachyrhamphus longirostris* (Straight stick-pipefish) | | | LC | | | M | |

| | | | |
|---|---|---|---|
| **Ziphiidae** | | | |
| *Berardius arnuxii* (Arnoux's beaked whale) | DD | C | 1 |
| *Hyperoodon planifrons* (Southern bottlenose whale) | LC | C | 1 |
| *Indopacetus pacificus* / syn. *Mesoplodon pacificus* (Longman's beaked whale, Indo-pacific Beaked Whale) | DD | C | 2 |
| *Mesoplodon bowdoini* (Andrews' beaked whale) | DD | C | 2 |
| *Mesoplodon densirostris* (Blainville's beaked whale) | DD | C | 2 |
| *Mesoplodon grayi* (Gray's beaked whale) | DD | C | 2 |
| *Mesoplodon hectori* (Hector's beaked whale) | DD | C | 2 |
| *Mesoplodon layardii* (Strap-toothed beaked whale) | DD | C | 2 |
| *Mesoplodon mirus* (True's beaked whale) | DD | C | 2 |
| *Tasmacetus shepherdi* (Shepherd's beaked whale, Tasman beaked whale) | DD | C | 2 |
| *Ziphius cavirostris* (Cuvier's beaked whale, Ginkgo-toothed beaked whale) | LC | C | 2 |

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**Footnotes:**

**Significant bird population**: a – most genetically distinct race in the species (Driskell *et al.*, 2002); b – meets 1% of EAAF population threshold; c – meets staging threshold (0.25% of flyway); d – meets 1% of global population threshold (Bamford & Moro 2011); e – 2.4 % of known trans-equatorial migratory population supported seasonally; f – 5.5 % of known trans-equatorial migratory population supported seasonally; g – 6.6 % of known trans-equatorial migratory population supported seasonally; h – 8.3 % of known population; i – staging criterion of 0.25% a species population; j – significant resident site (1.1 % of known population) of northern race (*ophthalmicus*) of the species (Chevron 2005, appendix C3).

**State conservation codes:** CR – Critically Endangered; E – Endangered; V – Vulnerable; IA – Migratory birds protected under an international agreement; CD – Conservation dependent fauna; OS – Other specially protected fauna (*Wildlife Conservation Act 1950*); P2 – Priority species 2; Poorly known species; P4 – Priority species 4; Rare, near threatened and other species in need of monitoring; Prf – Protected fish (*Fish Resources Management Act 1994*).

**Nationally threatened codes: CR** – Critically Endangered; **EN** – Endangered; **VU** – Vulnerable (*Environment Protection and Biodiversity Conservation Act 1999*).

**IUCN:** CR – Critically Endangered; EN – Endangered; VU – Vulnerable; NT – Near Threatened; DD – Data Deficient; LC – Least Concern (IUCN 2018).

**Table 2**

Invertebrate taxa on Barrow Island of conservation significance.

| ORDER | FAMILY | GENUS SPECIES | Endemic to Montebello/ Lowendal/ Barrow islands sand bars | Island endemic or short-range endemic | State listed species | Nationally listed species |
|---|---|---|---|---|---|---|
| **MARINE INVERTEBRATES** | | | | | | |
| (Class Gastropoda) Hypsogastropoda | Volutidae | *Amoria macandrewi* [@] | X | | | |
| **TERRESTRIAL INVERTEBRATES** | | | | | | |
| Araneae (spiders) | Ammoxenidae | *Barrowammo waldockae* [@] | | X | | |
| Araneae | Barychelidae | *Synothele butleri* (brush-footed trapdoor spider)[@] | | X | | |
| Araneae | Miturgidae | *Miturga serrata* [@] | | X | | |
| Araneae | Oonopidae | *Orchestina* 'barrow'[@] | | X | | |
| Araneae | Pholcidae | *Trichocyclus* sp. 1 [@] | | X | | |
| Araneae | Prodidomidae | *Wydundra barrow* [@] | | X | | |
| Araneae | Selenopidae | *Karaops burbidgei* | | X | | |
| Araneae | Zodariidae | *Spinasteron* 'harveyi' [@] | | X | | |
| Collembola (springtail) | Entomobryidae | *Acanthocyrtus barrowensis* | | X | | |
| Collembola | Entomobryidae | *Drepanura liuae* | | X | | |
| Collembola | Entomobryidae | *Drepanura polychaeta* | | X | | |
| Collembola | Paronellidae | *Metacoelura majeri* | | X? | | |
| Diptera (flies) | Dolichopodidae | *Pseudoparentia niharae* | | X | | |
| Diptera | Dolichopodidae | *Thinophilus sp. (female)* | | X | | |
| Diptera | Dolichopodidae | *Teuchophorus sp.* | | X | | |
| Hemiptera (true bugs) | Cicadellidae: | *Gunawardenea linnaei* | | X? | | |
| Hemiptera (true bugs) | Cicadellidae | *Horouta darwini* | | X | | |
| Hymenoptera (ants) | Eulophidae | *Elasmus curticornis* | | X? | | |
| Neuroptera (lace wings) | Ascalaphidae | *Suhpalacsa barrowensis* | | X? | | |
| Polydesmida (millipede) | Paradoxosomatidae | *Boreohesperus dubitalis* | | X | | |
| Polydesmida | Haplodesmidae | *Genus and species indet.* | | X | | |
| Pseudoscorpiones (pseudoscorpions) | Garypidae | *Anagarypus heatwolei* [@] | | X | | |
| Pseudoscorpiones | Garypidae | *Synsphyronus* sp. nov. 'barrow' [@] | | X? | | |
| Pseudoscorpiones | Syarinidae | *Ideoblothrus nesotymbus* | | X | | |
| Pseudoscorpiones | Chthoniidae | *Tyrannochthonius garthhumphreysi* | | X | | |
| Stylommatophora (land snails) | Camaenidae | *Rhagada barrowensis* | | X | | |
| Stylommatophora | Camaenidae | *Rhagada plicata* | | X | | |
| Stylommatophora | Camaenidae | *Quistrachia montebelloensis* | | X | | |
| Scorpiones (scorpions) | Urodacidae | *Aops oncodactylus* | Endemic genus | X | | |
| Scorpiones | Urodacidae | *Urodacus* sp. nov. 'barrow' [@] | | X | | |
| Thysanoptera (thrips) | Aeolothripidae | *Desmothrips barrowi* | | X? | | |
| Thysanoptera | Phlaeothripidae | *Majerthrips barrowi* | | X? | | |
| Thysanoptera | Phlaeothripidae | *Senithrips psomus* | Endemic genus | X? | | |
| Thysanoptera | Phlaeothripidae | *Jacotia rhodorcha* | | X? | | |
| Thysanoptera | Phlaeothripidae | *Podothrips barrowi* | | X? | | |
| Thysanoptera | Thripidae | *Anaphothrips barrowi* | | X? | | |
| Thysanoptera | Thripidae | *Neohydatothrips barrowi* | | X? | | |

| | | | | | |
|---|---|---|---|---|---|
| **TROGLOBITIC FAUNA** | | | | | |
| Blattodea (cockroaches) | Nocticolidae | *Nocticola* sp. nov. 1 ^ | | X | |
| Spirobolida (millipede) | Trigoniulidae | *Speleostrophus nesiotes* (Barrow Island Millipede) ^@ | | X | VU |
| Schizomida (palpigrades) | Hubbardiidae | *Draculoides bramstokeri* (Barrow Island Schizomid) ^ | | | VU |
| Zgygentoma (silver fish) | Nicoletiidae | *Trinemura* sp. nov. 1 ^ | | X | |
| Zygentoma | Nicoletiidae | *Trinemura* sp. nov. 2 ^ | | X | |
| **STYGOFAUNA** | | | | | |
| Amphipoda (sand hoppers) | Hadziidae | *Liagoceradocus subthalassicus* (Barrow Island liagoceradocus amphipod) ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia chevronia* (Chevron's freshwater amphipod (Barrow Island) | | X | P2 |
| Amphipoda | Melitidae | *Nedsia fragilis* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia halletti* | | X | |
| Amphipoda | Melitidae | *Nedsia humphreysi* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia hurlberti* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia macrosculptilis* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia sculptilis* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia stefania* | | X | |
| Amphipoda | Melitidae | *Nedsia straskraba* ^ | | X | VU |
| Amphipoda | Melitidae | *Nedsia urifimbriata* ^ | | X | VU |
| Amphipoda | Bogidiellidae | *Bogidomma australis* (Barrow Island Bogidomma amphipod) ^ | | X | VU |
| Copepoda | Ameiridae | *Inermipes humphreysi* | | X? | |
| Copepoda | Tetragonicipitidae | *Dussartcyclops (Barrowcyclops) consensus* | | X? | |
| Copepoda | Tetragonicipitidae | *Phyllopodopsyllus wellsi* | also in Cape Range | X? | |
| Decapoda | Atyidae | *Stygiocaris stylifera* (Speak-beaked cave shrimp) ^ | | | P4 |
| Isopoda (woodlice, slaters) | Armadillidae | *Barrowdillo pseudopyrgoniscus* & | | X | |
| Isopoda | Armadillidae | *Buddelundia hirsuta* & | | X | |
| Isopoda | Armadillidae | *Buddelundia* sp. 2 & | | X? | |
| Isopoda | Armadillidae | *Buddelundia* sp. 4 & | | X? | |
| Isopoda | Armadillidae | Armadillidae genus 1 sp. 1 & | | X? | |
| Isopoda | Armadillidae | Armadillidae genus 2 sp. 1 & | | X? | |
| Isopoda | Armadillidae | Armadillidae genus 3 sp. 1 & | | X | |
| Isopoda | Armadillidae | Armadillidae genus 3 sp. 2 & | | X? | |
| Isopoda | Armadillidae | Armadillidae genus 4 sp. 2 & | | X? | |
| Isopoda | Cirolanidae | *Haptolana pholeta* ^ | | X | |
| Thermosbaenacea | Halosbaenidae | *Halosbaena tulki* ^ | | X | |

**Data sources:**
Chevron Australia (2005 p. 245 and appendix C4)@ ;
amphipods: Bradbury & Williams (1996a, 1996b), Bradbury (2002);
millipedes: Bickel (2013) and Car *et al.* (2013);
*Tyrannochthonius*: Edward & Harvey (2008);
Hemiptera: Fletcher & Moir (2008), Fletcher (2009);
Collembola: Greenslade (2013), Ma *et al.* (2015, 2016);
*Elasmus curticornis*: Gunawardene & Taylor (2012);
*Ideoblothrus nesotymbus*: Harvey & Edward (2007);
Camaenid land snails: Humphreys *et al.* (2013)^; Johnson *et al.* (2013);
*Suhpalacsa barrowensis*: Judd & Perina (2013)&; New (1984);

*Aops oncodactylus*: Volschenk & Prendini (2008);
*Thysanoptera* from Mound & Minaei (2007), Mound & Matsumoto (2009), Pereyra & Mound (2010); and
*Copepoda* from Karanovic (2003), Karanovic *et al.* (2001)

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**Table 3**

Vascular plant species on Barrow Island of conservation significance (from Chevron Australia 2005, appendix C1; Maslin & van Leeuwen 2008; Telford *et al.* 2011; and NatureMap 2018).

| **Family**<br>**Scientific name** | **Island or short-range endemic species/ form/ variant** | **State priority flora** | **Habitat reduced by human disturbance** |
|---|---|---|---|
| **Amaranthaceae** | | | |
| *Amaranthus* sp. Barrow Island D200 (R.Buckley 6884) [%] | X | | |
| **Asteraceae** | | | |
| *Helichrysum oligochaetum* | | P1 | |
| **Chenopodiaceae** | | | |
| *Dysphania kalpari* * | | | X |
| **Cucurbitaceae** | | | |
| *Cucumis* sp. Barrow Island (D.W. Goodall 1264) | | P2 | |
| *Cucumis variabilis* | X | | |
| **Euphorbiaceae** | | | |
| *Euphorbia* sp. A | | | X |
| **Fabaceae** | | | |
| *Acacia trudgeniana* (dwarf form) * | X | | |
| **Malvaceae** | | | |
| *Abutilon otocarpum* [#] | | | X |
| *Corchorus congener* * | | P3 | |
| *Gossypium australe* [#] | | | X |
| *Hibiscus sturtii* var. *platychlamys* | | | X |

* Listed in Chevron (2005) as *Acacia inaequilatera* (dwarf form) and *Corchorus interstans* Halford ms

[#] Listed in Chevron (2005) but not in Florabase (25/8/18) as present on Barrow Island

[%] From NatureMap query 22/8/18

**Table 4**

Corals of Barrow Island and Montebello Islands of international conservation significance (from Richards & Rosser 2012; status checked 1/10/18).

| FAMILY | GENUS SPECIES | IUCN listing |
|---|---|---|
| Acroporidae | *Acropora aculeus* | VU |
| | *Acropora acuminata* | VU |
| | *Acropora anthocercis* | VU |
| | *Acropora donei* | VU |
| | *Acropora horrida* | VU |
| | *Acropora listeri* | VU |
| | *Acropora lovelli* | VU |
| | *Acropora microclados* | VU |
| | *Acropora palmerae* | VU |
| | *Acropora polystoma* | VU |
| | *Acropora solitaryensis* | VU |
| | *Acropora spicifera* | VU |
| | *Acropora verweyi* | VU |
| | *Acropora willisae* | VU |
| | *Isopora brueggemanni* | VU |
| | *Montipora crassituberculata* | VU |
| | *Montipora turtlensis* | VU |
| Agariciidae | *Pachyseris rugosa* | VU |
| | *Pavona decussata* | VU |
| | *Pavona venosa* | VU |
| Dendrophylliidae | *Turbinaria bifrons* | VU |
| | *Turbinaria mesenterina* | VU |
| | *Turbinaria patula* | VU |
| | *Turbinaria peltata* | VU |
| | *Turbinaria reniformis* | VU |
| Euphyllidae | *Euphyllia (Fimbriaphyllia) ancora* | VU |
| | *Galaxea astreata* | VU |
| | *Physogyra lichtensteini* | VU |
| Lobophylliidae | *Acanthastrea hemprichii* | VU |
| | *Lobophyllia diminuta* | VU |
| | *Lobophyllia flabelliformis* | VU |
| | *Moseleya latistellata* | VU |
| Merulinidae | *Caulastraea curvata* | VU |
| | *Echinopora ashmorensis* | VU |
| | *Para montastraeasalebrosa* / syn. *Montastrea salebrosa* | VU |
| | *Pectinia lactuca* | VU |
| | *Platygyrayaeyamaensis* | VU |
| Poritidae | *Goniopora burgosi* | VU |
| | *Porites nigrescens* | VU |

**Table 5**
Short-range endemism, affinities and vulnerability for taxa of Barrow Island.

| **Taxon group** | **Habitat preference** | **Vulnerability to sea level changes** | **Geographic affinities (+ve and -ve)** | **Level of endemism** |
|---|---|---|---|---|
| Flora | Terrestrial – coastal and inland arid zone | High vulnerability | Pilbara IBRA region, plus Cape Range and Kimberley | Low. Two plant forms or variants of 406 species |
| Ants (Hymenoptera) | Terrestrial | High vulnerability | | Low. Potentially 5 of 117 species endemic |
| Terrestrial mammals | Terrestrial | High vulnerability | | Four subspecies and one island form endemic |
| Reptiles | Terrestrial | High vulnerability | | None known |
| Reptiles | Troglobites | Low vulnerability | | Endemic skink and blind snake |
| Fish | Stygobites | Low vulnerability | Cape Range and west Pilbara | Endemic gudgeon and short range endemic blind cave eel |
| Birds | Littoral or terrestrial or arboreal or migratory | High vulnerability for resident birds, low for migratory birds | | Endemic subspecies. Depauperate land birds but non-migratory species assumed to be genetically distinct |
| Marine vertebrates | Marine to intertidal or littoral | Low vulnerability | | None known |
| Invertebrates – Odonata, Embiidina, Isoptera, Termites | Terrestrial | High in situ, low vulnerability for vagile life stages | | Low. Often are vagile species and widespread |
| Terrestrial invertebrates | Terrestrial moist areas or rock crevices | High vulnerability | | 22 endemic to island: 8 Arachnids, 2 millipedes, 3 Camaenid land snails, 1 mollusc, 1 pseudoscorpion, 5 silverfish, 3 thrips, 1 booklice, 6 Isopods |
| Collembola | Terrestrial or marine littoral | | | 7 of 71 species endemic (low endemism most spp in northern Aust). |
| Collembola | Subterranean | Low vulnerability | | 1+ subterranean species endemic and 3 others potential endemics |
| *Elasmus* (parasitoid wasps) | Terrestrial | High vulnerability | | Low. 1 of 11 species is potential endemic |
| Dolichopodidae (Diptera) | Terrestrial - moist areas or rock crevices | High vulnerability | Pilbara, tropical and monsoonal Australasia | Low. 1 island endemic and one short range endemic of 41 species in the Pilbara |
| Marine invertebrates | Marine water | Low vulnerability | | One endemic to island complex |
| Stygofauna invertebrates | Freshwater | Low vulnerability | | 7 endemic *Nedsia* species, 1 endemic genus *Bogidomma* |
| Stygofauna invertebrates | Marine or brackish water | Low vulnerability | | 1 anchialinetroglobite (*Liagoceradocus*) |
| Invertebrates - Schizomid | Troglobytes | Low vulnerability | Cape Range | One species endemic to BI and Cape Range |
| Invertebrates - millipede | Troglobytes | Low vulnerability | | Two short range endemic species |
| Invertebrates - millipede | Terrestrial (epigeal) | | | One endemic species |
| Invertebrates - scorpion | Troglobitic | | | One endemic which may be the most basal member of the family |

**Table 6**

Approximate sea level depths over the last 150 000 years in the Barrow Island region and effect on its isolation from other Western Australian islands and the mainland (based on data in Grant *et al*. 2012, suppl. material).

| Age (ky) | Depth * (m) | Trend | Effect on Barrow Island |
|---|---|---|---|
| Current | 0 | Rising | Isolated from other islands and landmasses |
| 5 | -10 | Rising | Isolated from mainland but connected to Montebello Islands and Lowendal Islands |
| 10 | -28 | Rising | On edge of coastal plain. Connected to coast swampy to east and north with rugged topography to NW Cape |
| 15 | -78 | Rising | Midway across coastal plain. Midway across coastal plain. Connected to coast sandy desert to east and north-east. Rugged topography to NW Cape |
| 20 | -97 | Rising | “ |
| 22. | -110 | Peak low | “ |
| 25 | -104 | Falling | “ |
| 29 | -105 | Minor fluctuations | “ |
| 30 | -101 | Falling | “ |
| 35 | -84 | Falling | “ |
| 40 | -83 | Fluctuations | “ |
| 60 | -70 | Fluctuations | “ |
| 65 | -100 | Peak low | “ |
| 75 | -70 | Falling with fluctuations | “ |
| 85 | -36 | Peak high | Midway across coastal plain. Connected to coast wetlands to east and north with some water barriers. Rugged topography to NW Cape |
| 87.5 | -73 | Peak low | “ |
| 106.5 | -30 | Peak high | “ |
| 110 | -50 | Peak low | ” |
| 119 | -20 | Falling | On edge of coastal plain |
| 122.5 | -10 | Falling | Isolated from mainland but connected to Montebello Islands and Lowendal Islands |
| 128 | +7 | Peak high | Partial Inundation of island. Isolated from other islands and landmasses |
| 130 | -10 | Rising | Isolated from mainland but connected to Montebello Islands and Lowendal Islands |
| 132 | -20 | Rising | On edge of coastal plain |
| 133 | -60 | Rising | Midway across coastal plain. Connected to coast sandy desert to east, wetlands to north east, with rugged topography to NW Cape |
| 140 | -90 | Rising | “ |
| 150 | -90 | Minor fluctuations (<5 | “ |

* Modelled relative sea level (RSL ProbMax) with 2 standard errors approximately +/- 3.5 m

**Appendix 2.** Taxa referred to in main text and Appendix 1.

**Class or above** **Order** **Family** *genus & species*

**PLANTS — ANGIOSPERMS**
**Amaranthaceae**
*Amaranthus* sp. Barrow Island (R. Buckley 6884) in Chevron Australia (2005)
**Asteraceae**
*Helichrysum oligochaetum* F. Muell.
**Chenopodiaceae**
*Dysphania kalpari* Paul G. Wilson
**Cucurbitaceae**
*Cucumis* sp. Barrow Island (D.W. Goodall 1264)
*Cucumis variabilis* P. Sebastian & I. Telford
**Euphorbiaceae**
*Euphorbia* sp. A in Chevron Australia (2005)
**Fabaceae**
*Acacia trudgeniana* Maslin (dwarf form) in Chevron Australia (2005)
**Malvaceae**
*Abutilon otocarpum* F. Muell.
*Corchorus congener* Halford
*Gossypium australe* F. Muell.
*Hibiscus sturtii* var. *platychlamys* Benth.
**Myrtaceae**
*Eucalyptus xerothermica* L.A.S. Johnson & K.D. Hill

**VERTEBRATE ANIMALS (Phylum Chordata, Subphylum Vertebrata)**
**TERRESTRIAL MAMMALS (Class Mammalia)**
**Subclass Marsupalia**
**Order Dasyuromorphia**
**Dasyuridae**
*Planigale* sp. 1 in Westermans *et al.* (2016)
**Order Diprotondontia**
**Macropodidae**
*Lagorchestes conspicillatus* Gould, 1842
*Lagorchestes conspicillatus conspicillatus* Gould, 1842
*Osphranter robustus isabellinus* (Gould, 1842) [syn. *Macropus robustus isabellinus* in Chevron Australia (2005)]
*Petrogale lateralis lateralis* Gould, 1842
**Phalangeridae**
*Trichosurus vulpecula arnhemensis* Collett, 1897
**Potoroidae**
*Bettongia lesueur* (Quoy & Gaimard, 1824)
**Order Peramelemorphia**
**Peramelidae**
*Isoodon auratus* (Ramsay, 1887)
*Isoodon auratus barrowensis* (Thomas, 1901)
**Subclass Eutheria**
**Order Rodentia**
**Muridae**
*Hydromys chrysogaster* Geoffroy, 1804
*Mus musculus* Linnaeus, 1758 (exotic species)
*Pseudomys nanus* (Gould, 1858)
*Rattus rattus* (Linnaeus, 1758) (exotic species)

**MARINE MAMMALS**
**Order Cetacea**
**Balaenidae**
*Eubalaena australis* (Desmoulins, 1822)

**Appendix 2.** (cont.)

**Balaenopteridae**
- *Balaenoptera acutorostrata* Lacépède, 1804
- *Balaenoptera borealis* Lesson, 1828
- *Balaenoptera edeni* Anderson, 1878
- *Balaenoptera musculus* (Linnaeus, 1758)
- *Balaenoptera physalus* (Linnaeus, 1758)
- *Megaptera novaeangliae* (Borowski, 1781)

**Delphinidae**
- *Delphinus delphis* Linnaeus, 1758
- *Feresa attenuata* J.E. Gray, 1874
- *Globicephala macrorhynchus* J.E. Gray, 1846
- *Globicephala melas* (Traill, 1809)
- *Grampus griseus* (Cuvier, 1812)
- *Lagenodelphis hosei* Fraser, 1956
- *Lagenorhynchus obscurus* (J.E. Gray, 1828)
- *Lissodelphis peronii* (Lacépède, 1804)
- *Orcaella heinsohni* Beasley, Robertson & Arnold, 2005 [syn. *O. brevirostris* in Chevron Australia (2005)]
- *Orcinus orca* (Linnaeus, 1758)
- *Peponocephala electra* (J.E. Gray, 1846)
- *Pseudorca crassidens* (Owen, 1846)
- *Sousa sahulensis* Jefferson & Rosenbaum, 2014 [syn. *S. chinensis* in Chevron Australia (2005)]
- *Stenella attenuata* (J.E. Gray, 1846)
- *Stenella coeruleoalba* (Meyen, 1833)
- *Stenella longirostris* (J.E. Gray, 1828)
- *Steno bredanensis* (Lesson, 1828)
- *Tursiops aduncus* (Ehrenberg, 1832)
- *Tursiops truncatus* (Montagu, 1821)

**Dugongidae**
- *Dugong dugon* (P.L.S. Müller, 1776)

**Kogiidae**
- *Kogia breviceps* Duvernoy, 1851
- *Kogia sima* (Owen, 1866) [syn. *Kogia simus* in Chevron Australia (2005), SPRAT database 2018]

**Physeteridae**
- *Physeter macrocephalus* Linnaeus, 1758

**Ziphiidae**
- *Berardius arnuxii* Duvernoy, 1851
- *Hyperoodon planifrons* Flower, 1882
- *Indopacetus pacificus* (Longman, 1926) [syn. *Mesoplodon pacificus* in Chevron Australia (2005)]
- *Mesoplodon bowdoini* Andrews, 1908
- *Mesoplodon densirostris* (Blainville, 1817)
- *Mesoplodon grayi* Von Haast, 1876
- *Mesoplodon hectori* (J.E. Gray, 1871)
- *Mesoplodon layardii* (J.E. Gray, 1865)
- *Mesoplodon mirus* True, 1913
- *Tasmacetus shepherdi* Oliver, 1937
- *Ziphius cavirostris* Cuvier, 1823

**BIRDS (Class Aves)**

**Order Apodiformes**

**Apodidae**
- *Apus (Apus) pacificus* (Latham, 1801)
- *Hirundapus caudacutus* (Latham, 1801)

**Order Charadriiformes**

**Burhinidae**
- *Esacus magnirostris* Vieillot, 1818 [syn. *Esacus neglectus* in Chevron Australia (2005)]

**Charadriidae**
- *Charadrius (Charadrius) leschenaultii* Lesson, 1826
- *Charadrius (Charadrius) mongolus* Pallas, 1776
- *Charadrius (Charadrius) ruficapillus* Temminck, 1821
- *Charadrius (Eupoda) veredus* Gould, 1848

*Pluvialis fulva* (Gmelin, 1789)
*Pluvialis squatarola* (Linnaeus, 1758)
**Glareolidae**
*Glareola (Glareola) maldivarum* J.R. Forster, 1795
*Stiltia isabella* (Vieillot, 1816)
**Haematopodidae**
*Haematopus fuliginosus* Gould, 1845
*Haematopus fuliginosus opthalmicus* Castelnau & Ramsay, 1877
**Laridae**
*Anous tenuirostris* (Temminck, 1823)
*Chlidonias (Chlidonias) leucopterus* (Temminck, 1815) [syn. *Chlidonias leucoptera* in Chevron Australia (2005)]
*Chroicocephalus novaehollandiae* (Stephens, 1826) [syn. *Larus novaehollandiae* in Chevron Australia (2005), NatureMap 2018]
*Gelochelidon nilotica* (Gmelin, 1789)
*Hydroprogne caspia* (Pallas, 1770) [syn. *Sterna caspia* in Chevron Australia (2005)]
*Onychoprion anaethetus* (Scopoli, 1786) [syn. *Sterna anaethetus* in Chevron Australia (2005)]
*Sterna (Sterna) dougallii* Montagu, 1813
*Sterna (Sterna) hirundo* Linnaeus, 1758
*Sternula albifrons* (Pallas, 1764) [syn. *Sterna albifrons* in Chevron Australia (2005)]
*Sterna nereis* Gould, 1843
*Sternula nereis* (Gould, 1843) [syn. *Sterna nereis* in Chevron Australia (2005)]
*Thalasseus bengalensis* (Lesson, 1831) [syn. *Sterna bengalensis* in Chevron Australia (2005)]
*Thalasseus bergii* (Lichtenstein, 1823) [syn. *Sterna bergii* in Chevron Australia (2005)]
**Scolopacidae**
*Actitis hypoleucos* (Linnaeus, 1758) [syn. *Tringa hypoleucos* in Chevron Australia (2005)]
*Arenaria interpres* (Linnaeus, 1758)
*Calidris (Erolia) acuminata* (Horsfield, 1821)
*Calidris (Crocethia) alba* (Pallas, 1764)
*Calidris (Calidris) canutus* (Linnaeus, 1758)
*Calidris (Erolia) ferruginea* (Pontoppidan, 1763)
*Calidris (Ereunetes) ruficollis* (Pallas, 1776)
*Calidris (Calidris) tenuirostris* (Horsfield, 1821)
*Limosa lapponica* (Linnaeus, 1758)
*Limosa lapponica menzbieri* Partenko, 1936
*Limosa limosa* (Linnaeus, 1758)
*Numenius (Numenius) madagascariensis* (Linnaeus, 1766)
*Numenius (Mesoscolopax) minutus* Gould, 1841 [syn. *Numenius minutes* in Chevron Australia (2005)]
*Numenius (Phaeopus) phaeopus* (Linnaeus, 1758)
*Tringa (Heteroscelus) brevipes* (Vieillot, 1816)
*Tringa (Rhyacophilus) glareola* Linnaeus, 1758
*Tringa (Glottis) nebularia* (Gunnerus, 1767)
*Tringa (Rhyacophilus) stagnatilis* (Bechstein, 1803)
*Xenus cinereus* (Güldenstädt, 1775) [syn. *Tringa terek* in Chevron Australia (2005)]
**Order Ciconiiformes**
**Ardeidae**
*Ardea (Casmerodius) modesta* J.E. Gray, 1831 [syn. *Ardea alba* in Chevron Australia (2005)]
*Egretta garzetta* (Linnaeus, 1766)
*Egretta sacra* (Gmelin, 1789) [syn. *Ardea sacra* in Chevron Australia (2005)]
**Order Columbiformes**
**Columbidae**
*Geopelia humeralis* (Temminck, 1821)
**Order Coraciiformes**
**Halcyonidae**
*Todiramphus (Todiramphus) sanctus* (Vigors & Horsfield, 1827)
**Meropidae**
*Merops (Merops) ornatus* Latham, 1801
**Order Cuculiformes**
**Cuculidae**
*Cacomantis (Vidgenia) pallidus* (Latham, 1801) [syn. *Cuculus pallidus* in Chevron Australia (2005)]
*Cuculus (Cuculus) optatus* Gould, 1845 [syn. *C. saturatus* in Chevron Australia (2005)]

**Appendix 2.** (cont.)

**Order Falconiformes**
- **Accipitridae**
  - *Haliaeetus (Pontoaetus) leucogaster* (Gmelin, 1788)
  - *Haliastur indus* (Boddaert, 1783)
  - *Pandion cristatus* (Vieillot, 1816) [syn. *Pandion haliaetus* in Chevron Australia (2005)]
- **Falconidae**
  - *Falco (Tinnunculus) cenchroides* Vigors & Horsfield, 1827

**Order Gruiformes**
- **Otididae**
  - *Ardeotis australis* (J.E. Gray, 1829)

**Order Passeriformes**
- **Campephagidae**
  - *Coracina (Coracina) novaehollandiae* (Gmelin, 1789)
- **Hirundinidae**
  - *Hirundo (Hirundo) neoxena neoxena* Gould, 1843
  - *Hirundo (Hirundo) rustica* Linnaeus, 1758
  - *Petrochelidon (Hylochelidon) nigricans* (Vieillot, 1817) [syn. *Hirundo nigricans* in Chevron Australia (2005)]
- **Maluridae**
  - *Malurus (Musciparus) leucopterus edouardi* A.J. Campbell, 1901
- **Megaluridae**
  - *Eremiornis carteri* North, 1900
- **Meliphagidae**
  - *Gavicalis virescens* (Vieillot, 1817)
- **Motacillidae**
  - *Anthus (Anthus) novaeseelandiae* (Gmelin, 1789) [syn. *A. australis* in NatureMap 2018)

**Order Pelecaniformes**
- **Fregatidae**
  - *Fregata ariel* (G.R. Gray, 1845)
- **Sulidae**
  - *Sula dactylatra bedouti* Mathews, 1913
  - *Sula leucogaster* (Boddaert, 1783)

**Order Procellariiformes**
- **Diomedeidae**
  - *Thalassarche chlororhynchos* (Gmelin) [syn. *Diomedea chlororhynchos* in Chevron Australia (2005)]
- **Oceanitidae**
  - *Oceanites oceanicus* (Kuhl, 1820)
- **Procellariidae**
  - *Ardenna pacifica* (Gmelin, 1789) [syn. *Puffinus pacificus* in Chevron Australia (2005)]
  - *Puffinus (Puffinus) huttoni* Mathews, 1912

**FISH**

MARINE FISH

**Order Lamniformes**
- **Lamnidae**
  - *Carcharodon carcharias* (Linnaeus, 1758)
- **Odontaspididae**
  - *Carcharias taurus* Rafinesque, 1810

**Order Orectolobiformes**
- **Rhincodontidae**
  - *Rhincodon typus* Smith, 1828

**Order Perciformes**
- **Serranidae**
  - *Epinephelus tukula* Morgans, 1959

**Order Syngnathiformes**
- **Solenostomidae**
  - *Solenostomus cyanopterus* Bleeker, 1854
- **Syngnathidae**
  - *Bulbonaricus brauni* (Dawson & Allen, 1978)
  - *Campichthys tricarinatus* Dawson, 1977
  - *Choeroichthys brachysoma* (Bleeker, 1855)

*Choeroichthys latispinosus* Dawson, 1978
*Choeroichthys suillus* Whitley, 1951
*Doryrhamphus janssi* (Herald & Randall, 1972)
*Festucalex scalaris* (Günther, 1870)
*Filicampus tigris* (Castelnau, 1879)
*Halicampus brocki* (Herald, 1953)
*Halicampus grayi* Kaup, 1856
*Halicampus nitidus* (Günther, 1873)
*Halicampus spinirostris* (Dawson & Allen, 1981)
*Haliichthys taeniophora* Gray, 1859
*Hippichthys penicillus* (Cantor, 1849)
*Hippocampus angustus* Günther, 1870
*Hippocampus histrix* Kaup, 1856
*Hippocampus kuda* Bleeker, 1852
*Micrognathus micronotopterus* (Fowler, 1938)
*Phoxocampus belcheri* (Kaup, 1856)
*Phycodurus eques* (Günther, 1865)
*Phyllopteryx taeniolatus* (Lacépède, 1804)
*Syngnathoides biaculeatus* (Bloch, 1785)
*Trachyrhamphus bicoarctatus* (Bleeker, 1857)
*Trachyrhamphus longirostris* Kaup, 1856

STYGIAL FISH
**Order Perciformes**
**Eleotridae**
*Milyeringa justitia* Larson & Foster, 2013
**Order Synbranchiformes**
**Synbranchidae**
*Ophisternon candidum* (Mees, 1962)

**REPTILES (Class Reptilia)**
TERRESTRIAL LIZARDS
**Order Squamata**
**Scincidae**
*Ctenotus pantherinus acripes* Storr, 1975
STYGIAL SNAKES
**Order Squamata**
**Typhlopidae**
*Anilios longissimus* (Aplin, 1998) [syn. *Ramphotyphlops longissimus* in Aplin (1998)]
MARINE SNAKES
**Order Squamata**
**Elapidae**
*Aipysurus apraefrontalis* Smith, 1926
*Aipysurus duboisii* Bavay, 1869
*Aipysurus eydouxii* Gray, 1849
*Aipysurus foliosquama* (Smith, 1926)
*Aipysurus laevis* Lacépède, 1804
*Emydocephalus annulatus* Krefft, 1869
*Ephalophis greyi* Smith, 1931
*Hydrophis czeblukovi* (Kharin, 1984)
*Hydrophis elegans* (Gray, 1842)
*Hydrophis kingii* (Boulenger, 1896) [syn. *Disteira kingii* in Chevron Australia (2005), SPRAT database 2018]
*Hydrophis major* (Shaw, 1802) [syn. *Disteira major* in Chevron Australia (2005), SPRAT database 2018]
*Hydrophis peronii* (Duméril, 1853) [syn. *Acalyptophis peronii* in Chevron Australia (2005), SPRAT database 2018]
*Hydrophis platurus* (Linnaeus, 1766) [syn. *Pelamis platurus* in Chevron Australia (2005), SPRAT database 2018
*Hydrophis stokesii* (Gray, 1846) [syn. *Astrotia stokesii* in Chevron Australia (2005), SPRAT database 2018]
*Hydrophis* Sonnini & Latreille sp. [syn. *H. ornatus* in Chevron Australia (2005), SPRAT database 2018, NatureMap 2018)
TURTLES
**Order Testudines**
**Cheloniidae**
*Caretta caretta* (Linnaeus, 1758)
*Chelonia mydas* (Linnaeus, 1758)

**Appendix 2.** (cont.)

*Eretmochelys imbricata* (Linnaeus, 1766)
*Lepidochelys olivacea* (Eschscholtz, 1829)
*Natator depressus* (Garman, 1880)
**Dermochelyidae**
*Dermochelys coriacea* (Vandelli, 1761)

**INVERTEBRATES**
**MARINE INVERTEBRATES**
GASTROPODS (Phylum Mollusca, **Class Gastropoda**)
**Order Cerithimorpha**
**Cerithiidae**
*Rhinoclavis* sp. Swainson, 1840
**Order Hypsogastropoda**
**Conidae**
*Conus* sp. Linnaeus, 1758
**Volutidae**
*Amoria macandrewi* (Sowerby, 1887)
BIVALVES (Phyllum Mollusca, **Class Bivalvia**)
**Order Mytilida**
**Mytilidae**
*Modiolus* sp. Lamarck, 1799
CORALS (Phylum Cnidaria, **Class Anthozoa**)
**Order Scleractinia**
**Acroporidae**
*Acropora aculeus* (Dana, 1846)
*Acropora acuminata* (Verrill, 1864)
*Acropora anthocercis* (Brook, 1893)
*Acropora donei* Veron& Wallace, 1984
*Acropora horrida* (Dana, 1846)
*Acropora listeri* (Brook, 1893)
*Acropora lovelli* Veron & Wallace, 1984
*Acropora microclados* (Ehrenberg, 1834)
*Acropora palmerae* Wells, 1954
*Acropora polystoma* (Brook, 1891)
*Acropora solitaryensis* Veron & Wallace, 1984
*Acropora spicifera* (Dana, 1846)
*Acropora verweyi* Veron & Wallace, 1984
*Acropora willisae* Veron & Wallace, 1984
*Isopora brueggemanni* (Brook, 1893)
*Montipora crassituberculata* Bernard, 1897
*Montipora turtlensis* Veron & Wallace, 1984
**Agariciidae**
*Pachyseris rugosa* (Lamarck, 1801)
*Pavona decussata* (Dana, 1846)
*Pavona venosa* (Ehrenberg, 1834)
**Dendrophylliidae**
*Turbinaria bifrons* Brüggemann, 1877
*Turbinaria mesenterina* (Lamarck, 1816)
*Turbinaria patula* (Dana, 1846)
*Turbinaria peltata* (Esper, 1794)
*Turbinaria reniformis* Bernard, 1896
**Euphylliidae**
*Euphyllia (Fimbriaphyllia) ancora* Veron & Pichon, 1980
*Galaxea astreata* Lamarck, 1816
*Physogyra lichtensteini* (Milne Edwards & Haime, 1851)
**Lobophylliidae**
*Acanthastrea hemprichii* (Ehrenberg, 1834)
*Lobophyllia diminuta* Veron, 1985
*Lobophyllia flabelliformis* Veron, 2000
*Moseleya latistellata* Quelch, 1884

**Merulinidae**
*Caulastraea curvata* Wijsmann-Best, 1972
*Echinopora ashmorensis* Veron, 1990
*Paramontastraea salebrosa* (Nemenzo, 1959)
*Pectinia lactuca* (Pallas, 1766)
*Platygyra yaeyamaensis* (Eguchi & Shirai, 1977)
**Poritidae**
*Goniopora burgosi* Nemenzo, 1955
*Porites nigrescens* Dana, 1846

**TERRESTRIAL INVERTEBRATES**
**PHYLUM ARTHROPODA**
**Class Arachnida**
SPIDERS (**Order Araneae**)
**Ammoxenidae**
*Barrowammo waldockae* Platnick, 2002
**Barychelidae**
*Synothele butleri* Raven, 1994
**Miturgidae**
*Miturga serrata* in Chevron Australia (2005)
**Oonopidae**
*Orchestina* (Simon, 1882) 'barrow' in Chevron Australia (2005)
**Pholcidae**
*Trichocyclus* (Simon, 1908) sp. 1 in Chevron Australia (2005)
**Prodidomidae**
*Wydundra barrow* Platnick & Baehr, 2006
**Selenopidae**
*Karaops burbidgei* Crews & Harvey, 2011
**Zodariidae**
*Spinasteron* (Baehr, 2003) 'harveyi' in Chevron Australia (2005)
SCORPIONS (**Order Scorpiones**)
**Urodacidae**
*Aops oncodactylus* Volschenk & Prendini, 2008
*Urodacus* (Peters, 1861) sp. nov. 'barrow' in Chevron Australia (2005)
PSEUDOSCORPIONS (**Order Pseudoscorpiones**)
**Garypidae**
*Anagarypus heatwolei* Muchmore, 1982
*Synsphyronus* (Chamberlin, 1930) sp. nov. 'barrow' in Chevron Australia (2005)
**Syarinidae**
*Ideoblothrus nesotymbus* Harvey & Edward, 2007
**Chthoniidae**
*Tyrannochthonius garthhumphreysi* Edward & Harvey, 2008
**Class Collembola**
SPRINGTAILS (**Order Entomobryomorpha**)
**Entomobryidae**
*Acanthocyrtus barrowensis* Zhang, Deharveng, Greenslade & Chen, 2009
*Calx* (Christiansen, 1958) sp. in Greenslade (2013)
*Drepanura liuae* Ma, Chun & Greenslade, 2015
*Drepanura polychaeta* Ma, Chun & Greenslade, 2015
*Pseudosinella* (Schäffer, 1897) sp. in Greenslade, 2013
**Neanuridae**
cf. *Kenyura* Salmon, 1954 in Greenslade (2013)
**Neelidae**
*Megalothorax* (Willem, 1900) sp. in Greenslade, 2013
**Odontellidae**
*Caufrenyllodes* Greenslade & Deharveng, 1984
**Paronellidae**
*Cyphoda* (Delamare-Deboutteville, 1948) sp. in Greenslade, 2013
*Metacoelura majeri* Ma, Zhao & Greenslade, 2016

**Appendix 2.** (cont.)

**Class Diploda**
MILLIPEDES (**Order Polydesmida**)
**Paradoxosomatidae**
*Boreohesperus dubitalis* Car & Harvey, 2013
**Haplodesmidae**
Genus and species indet. in Car *et al.* (2013)
**Class Insecta**
FLIES (**Order Diptera**)
**Dolichopodidae**
*Pseudoparentia niharae* Bickel, 2013
*Teuchophorus* (Loew, 1857) sp. in Bickel (2013)
*Thinophilus* (Wahlberg, 1844) sp. in Bickel (2013)
TRUE BUGS (**Order Hemiptera**)
**Cicadellidae**
*Gunawardenea linnaei* Fletcher & Moir, 2008
*Horouta darwini* Fletcher, 2009
**Order Hymenoptera**
**Eulophidae**
*Elasmus* Westwood, 1833 spp.
*Elasmus curticornis* Gunawardene & Taylor, 2012
LACE WINGS (**Order Neuroptera**)
**Ascalaphidae**
*Suhpalacsa barrowensis* New, 1984
BOOKLICE (**Order Psocodea**)
**Amphientomidae**
*Lithoseopsis humphreysi* (New, 1994)
THRIPS (**Order Thysanoptera**)
**Aeolothripidae**
*Desmothrips barrowi* Pereyra & Mound, 2010
**Phlaeothripidae**
*Gynaikothrips* Zimmermann, 1900 sp.
*Jacotia rhodorcha* Mound & Minaei, 2006
*Majerthrips barrowi* Mound & Minaei, 2006
*Podothrips barrowi* Mound & Minaei, 2007
*Senithrips psomus* Mound & Minaei, 2006
**Thripidae**
*Anaphothrips barrowi* Mound & Matsumoto, 2009
*Neohydatothrips barrowi* Mound & Tree, 2009
SILVERFISH (**Order Zygentoma**)
**Lepismatidae**
*Hemitelsella transpectinata* Smith, 2015
*Heterolepisma parva* Smith, 2013
*Qantelsella maculosa* Smith, 2015
*Qantelsella aurantia* Smith, 2015
*Xenolepisma perexiguum* Smith, 2015
**PHYLUM MOLLUSCA**
**Class Gastropoda**
LAND SNAILS (**Order Stylommatophora**)
**Camaenidae**
*Quistrachia montebelloensis* Preston, 1914
*Rhagada barrowensis* Johnson, Stankowski, Whisson, Teale & Hamilton, 2013
*Rhagada plicata* Preston, 1914

**TROGLOBITIC AND STYGIAL INVERTEBRATES**
**PHYLUM ARTHROPODA**
**Class Arachnida**
PALPIGRADES (**Order Schizomida**)
**Hubbardiidae**
*Draculoides bramstokeri* Harvey & Humphreys, 1995

- **Class Diplopoda**
  - MILLIPEDE (**Order Spirobolida**)
    - **Trigoniulidae**
      - *Speleostrophus nesiotes* Hoffman, 1994
- **Class Insecta**
  - COCKROACHES (**Order Blattodea**)
    - **Nocticolidae**
      - *Nocticola* sp. nov. 1 in Humphreys *et al.* (2013)
  - **Order Zgygentoma**
    - **Nicoletiidae**
      - *Trinemura* sp. nov. 1 in Humphreys *et al.* (2013)
      - *Trinemura* sp. nov. 2 in Humphreys *et al.* (2013)
- **Class Malacostraca**
  - SAND HOPPERS (**Order Amphipoda**)
    - **Bogidiellidae**
      - *Bogidomma* Bradbury & Williams, 1996
      - *Bogidomma australis* Bradbury & Williams, 1996
    - **Hadziidae**
      - *Liagoceradocus* Barnard, 1965
      - *Liagoceradocus subthalassicus* Bradbury & Williams, 1996
    - **Melitidae**
      - *Nedsia* Barnard & Williams, 1995
      - *Nedsia chevronia* Bradbury, 2002
      - *Nedsia fragilis* Bradbury & Williams, 1996
      - *Nedsia halletti* Bradbury, 2002
      - *Nedsia humphreysi* Bradbury & Williams, 1996
      - *Nedsia hurlberti* Bradbury & Williams, 1996
      - *Nedsia macrosculptilis* Bradbury & Williams, 1996
      - *Nedsia sculptilis* Bradbury & Williams, 1996
      - *Nedsia stefania* Bradbury, 2002
      - *Nedsia straskraba* Bradbury & Williams, 1996
      - *Nedsia urifimbriata* Bradbury & Williams, 1996
  - **Order Decapoda**
    - **Atyidae**
      - *Stygiocaris stylifera* Holthuis, 1960
  - WOODLICE, SLATERS (**Order Isopoda**)
    - **Armadillidae**
      - *Barrowdillo pseudopyrgoniscus* Dalens, 1993
      - *Buddelundia hirsuta* Dalens, 1992
      - *Buddelundia* sp. 2 in Judd & Perina (2013)
      - *Buddelundia* sp. 4 in Judd & Perina (2013)
      - Genus 1 sp. 1 in Judd & Perina (2013)
      - Genus 2 sp. 1 in Judd & Perina (2013)
      - Genus 3 sp. 1 in Judd & Perina (2013)
      - Genus 3 sp. 2 in Judd & Perina (2013)
      - Genus 4 sp. 2 in Judd & Perina (2013)
    - **Cirolanidae**
      - *Haptolana pholeta* Bruce & Humphreys, 1993
  - **Order Thermosbaenacea**
    - **Halosbaenidae**
      - *Halosbaena tulki* Poore & Humphreys, 1992
- **Class Maxillopoda**
  - **Order Cyclopoida**
    - **Cyclopidae**
      - *Dussartcyclops (Barrowcyclops) consensus* (Karanovic, 2003) in Karanovic, Eberhard & Murdoch (2011)
  - **Order Harpactidoida**
    - **Ameiridae**
      - *Inermipes humphreysi* Lee & Huys, 2002
    - **Tetragonicipididae**
      - *Phyllopodopsyllus wellsi* Karanovic, Pesce & Humphreys, 2001

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# Professor Sylvia Joy Hallam

## MA, PhD (Cantab.), FAHA

## 17th August 1927 – 3rd June 2019

As the first archaeologist at the University of Western Australia, Sylvia Hallam, together with Ian Crawford and Charlie Dortch at the Western Australian Museum, pioneered the study of archaeology in Western Australia. From her arrival in Perth in 1961 with her husband Herbert Hallam, medieval historian at The University of Western Australia (UWA), Sylvia was an energetic and tireless advocate for archaeology as a discipline. She lectured regularly in various departments at UWA and was finally appointed to a part-time lectureship in prehistory in 1970 and to a full-time lectureship in 1973. An independent department of archaeology eventually was established in 1983 and Sylvia was promoted to Associate Professor in 1984.

Sylvia and Herbert Hallam had met as students at Cambridge University. As was common at the time, when Herbert Hallam was appointed to a lectureship in medieval history at the University of Western Australia, he was accompanied by his wife and family. Sylvia Hallam, however, was already working on a major archaeological research program on patterns of settlement around the Wash in East Anglia from the first to fourth centuries AD. Her pioneering analysis of rural settlement during Roman times was published as a Royal Geographical Society Memoir in 1970 and in 2004, Sylvia finally obtained her PhD on the basis of this published work.

On arriving in Western Australia, Sylvia switched her interests from the Roman fenland to Aboriginal archaeology. Nevertheless, her research continued to focus on landscape studies and regional field survey—an emphasis unfashionable in Australian archaeology at the time. Her fieldwork focused mainly on the Swan–Avon region and especially the Perth Metropolitan area. This work compiled an invaluable record of the archaeology of the Swan Coastal Plain, now largely lost to urban development, and provided a training ground for a generation of students. Sylvia's approach to archaeology stressed landscape context and understanding the archaeological record in relation to changing environments, as well as the integration of a range of different types of evidence from the natural sciences to the archives. This led her to a detailed exploration of historical sources in order to investigate past Aboriginal land use and the nature of the environment encountered by the first European settlers. Her seminal work 'Fire and Hearth' was published in 1975. In it, she showed how the Noongar people of the South West used fire to radically remake the landscape thereby readily enabling its penetration and settlement. Rhys Jones had already coined the phrase 'firestick farming' in 1969 to characterise the interaction between Aboriginal people and the Australian environment. However, 'Fire and Hearth' remains one of the most detailed and meticulous explorations of the construction of the environment by Aboriginal people. Her later research on yams and

Resting next to petroglyphs at Murujuga (Burrup Peninsula), ~1975 (photo Robin Chapple).

Sylvia's research interests were wide-ranging and she connected with colleagues working in many other parts of the state, across Australia and internationally. These ranged from Professor Richard Gould then at the American Museum of Natural History, New York, for collaboration on the Warburton region, to Lesley Maynard in the Pilbara, and colleagues in Poona, India. Her published archaeological work includes such diverse topics as the colonisation of new continents, microliths worldwide, Aboriginal demography, the role of women in pre-European economy and society in Western Australia, as well as Aboriginal use of fire as a tool of land management and the archaeology of Western Australia. Following a serious illness in 1983, she switched her research interests from archaeological fieldwork to the archives. This led to a fruitful research collaboration with Lois Tilbrook and to her significant contribution to the Aboriginal volumes of the *Bicentennial Dictionary of Western Australians*.

As well as her advocacy for teaching and research in archaeology at UWA, Sylvia promoted the public pursuit of and engagement with archaeological research at state, national and international level. She was an Associate of the WA Museum and a member of the Australian Institute of Aboriginal Studies [later AIATSIS]. Sylvia was a fellow of the Royal Society of WA and in 1985–1986 became its first female president. She was also involved in ANZAAS and the university Staff Association. In 1984 she was elected a Fellow of the Australian Academy of the Humanities.

Sylvia continued to publish and contribute to the public face of archaeology after her retirement in 1989. She campaigned vigorously and tirelessly for the recognition of the outstanding significance of Murujuga. In 2006, she worked with Caroline Bird to produce a report for the National Trust, which provided strong supportive evidence for protection of this stunning art-rich cultural landscape location. The impact of chemical emissions on the rock art was a particular concern for her and she was an outspoken critic of the inaction of both industry and government.

Professor Sylvia Hallam died peacefully in Perth on 3 June 2019.

**Caroline Bird**

**Research Associate,**
**Western Australian Museum**

**Moya Smith**

**Head of Anthropology & Archaeology,**
**Western Australian Museum**

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# Margaret Ann Triffitt

## RSWA Librarian

## 5th March 1944 – 4th November 2019

Margaret Ann Triffitt who had been the Royal Society of Western Australia's Librarian for 25 years, passed away on 4 November 2019, aged 75. She was born in England in 1944 and her family migrated to Australia in the 1950s as '10 pound poms', settling in Hobart. Her father was involved in the Intelligence Services, which may explain her ability in research and information gathering. From 1961 to 1965 she attended the University of Tasmania where she could combine her love of reading working in the University Library while she studied. She met her husband Gary, an electrical engineer, at the Judo Club and they travelled around Australia for his work, eventually settling in Perth. Margaret was appointed as Librarian for the Western Australian Museum, her dream job, in August 1987 after working in a similar position for the State Energy Commission.

The Royal Society Library has been housed in the Western Australian Museum since April 1960, so Margaret was also responsible for cataloguing and maintaining the collection in addition to administering the exchange of the Royal Society journal with institutions around the world. Many of these exchange titles are not held elsewhere in the state.

Margaret arrived at the Museum when libraries were just starting to adjust to the digital age. She steadily computerized services throughout the 1990s and, through her efforts, subject lists of the Royal Society holdings were published in 2001 in volume 84 of the journal. Margaret was a great believer in making these valuable collections more widely accessible so, with the help of some funding from the Royal Society, was able to publish the combined Library catalogues on the internet in 2003. Throughout her tenure, she worked tirelessly on the Royal Society Council and was dedicated to making improvements to Library services particularly as access to digital resources became increasingly available; however, she was never too busy to assist students.

Margaret retired in December 2012 after which her love of history and learning prompted her to act as a guide at Peninsula Farm (Tranby House), and organize speakers for the University of the Third Age. She will always be remembered for her wisdom, knowledge and dedication.

**Wendy Crawford**
**Western Australian Museum**

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