Preliminary appraisal of biota from methane-seep and associated deposits, lower Holmwood Shale, Early Permian (Sakmarian), Irwin Basin, Western Australia

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Abstract

Fossil assemblages preserved in nodules of the methane-seep deposits, recognized by Haig *et al.* (2022) in the lower Permian (Cisuralian, Sakmarian stage) of the Irwin Basin, include representatives of three ecosystems: seep, pelagic, and coastal plain. The seep biota, new to the Australian Permian, consists of small thickets with a framework of tubeworms, less common algal-like *Tubiphytes*, and problematica (? algae or sponges). Other components include microbial mats, macrophyte alga *Litostroma* (first report from Gondwana); foraminifers; sponges with siliceous monaxon spicules; a new group of small, lightly ornamented rostroconchs; microgastropods and rare larger types; ostracods and minute scolecodonts from polychaete jaws. Elements of the pelagic ecosystem are ammonoids (abundant in enclosing shale) and marine microphytoplankton. Probable vertebrate bone (possibly amphibians) and diverse spores and pollen from land plants come from the adjoining coastal plain. The surrounding mudstone lacks benthic macrofauna but includes an unusual assemblage of siliceous agglutinated foraminifers. The seeps were oases of high organic productivity on an otherwise barren muddy seafloor. The Holmwood Shale's seep carbonates have close similarities to modern seep deposits in shallow-marine settings.

Key words: Litostroma, Tubiphytes; foraminifers; rostroconchs; tube worms; palynomorphs

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INTRODUCTION

Carbonate nodules generated in methane-seeps were recognized by Haig *et al.* (2022) in blue-grey massive mudstone low in the Holmwood Shale (Fig. 1). The stratigraphic position is significant, lying at a short vertical distance (ca. 75–85 m) above the glaciogenic Nangetty Formation of the Lower Permian (Sakmarian) in the Irwin Basin (Fig. 1). The nodules are characterized by (1) cementstone with complex multiphase fabric, including yellow cement; (2) δ^{13} C values mostly within the range, -25 – -45 ‰ VPDB (Vienna Pee Dee Belemnite standard); and (3) an unusual biota with some similarities

to that found living in modern seeps (Haig *et al.* 2022). These seep-deposits are the first to be recognized from the Australian Upper Paleozoic and some of very few reported from Permian strata elsewhere.

Fossil assemblages found in the seep nodules are unlike those well-known from Permian limestone units elsewhere in Australian basins (Skwarko 1993; Archbold 2000). This paper presents a preliminary appraisal of the biota in the carbonate nodules and in the surrounding shale. It outlines the reasons for identifications and discusses general implications of the biota for understanding local palaeoecology and broader biogeography of Early Permian environments in this region. Specialist taxonomic studies on most of the

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Figure 1. Stratigraphic and regional setting of studied methane-seep deposits. A, Carboniferous (green) and Permian (orange brown) chronostratigraphy following the International Chronostratigraphic Chart v2023/09 (www.stratigraphy. org accessed on 7 December 2023). B, Climate trends following Haig *et al.* (2018). C, Broad-scale sequence stratigraphy with depositional cycles Cseq-1 and Pseq-1 to Pseq-6 following Haig *et al.* (2018); rectangles with green triangles on blue background indicate retrogradational phases (deepening - green triangle with apex upward) and progradational phases (shallowing - green triangle with apex downward and with junction of triangles the maximum marine flooding level) of the major cycles. Numbers on the side of column C are among the most recent references on each cycle: **1**, Vachard *et al.* 2014; **2**, Backhouse & Mory 2020 (regional hiatus); **3**, Davydov *et al.* 2013, 2014; **4**, Haig *et al.* 2014, 2022, Taboada *et al.* 2015, Tremblin & Haig 2023; **5**, Haig *et al.* 2017, Haig 2018; **6**, Haig & Mory 2016; **7**, Nogami 1963, Haig *et al.* 2018; **8**, McCartain *et al.* 2006; Haig *et al.* 2018. D, Schematic stratigraphic log of the Holmwood Shale in the study area (from Haig *et al.* 2022). E, Basement terrane map of the Western Australian part of the East Gondwana Lowlands (compiled by FROGTECH, www.frogtech.com,au accessed 7 December 2023) with dark blue areas along the present-day western margin of the continent outlining late Paleozoic depocentres with axial basins of the East Gondwana Interior Rift labelled A1 to A6, and marginal rift basins labelled M1 to M7 (see Haig *et al.* 2018, 2022 for details). The site of the present study is the Irwin Basin (M7).

groups still must be made and this preliminary account aims to encourage future more detailed systematic studies of this remarkable biota.

LOCALITY DESCRIPTIONS

Locality A

The locality is at Macaroni Hill on the western side of Nangetty Station (Fig. 2A) at 28.9714°S, 115.0471°E. It is located on a shale breakaway at the edge of a large

mesa about 1.5 km northwest of Nangetty Homestead (Fig. 2A). Nodular limestone (cementstone) forms three units on the hill in an exposed stratigraphic thickness of about 4 m (Figs. 2D). The limestone units seem to have limited lateral extent. Locality/sample co-ordinates are given in Appendix 1, and a description of rock types is provided by Haig *et al.* (2022). The section with limestone forming the hill seems to be a mound that was, before modern erosion, encased in grey shale. The shale includes sparsely scattered small carbonate mudstone nodules some of which contain the large ammonoid *Juresanites jacksoni*.



Figure 2. A–C, Google-Earth images. A, Country west of Nangetty Station Homestead. Note position of Macaroni Hill (Locality A) on "breakaway" (escarpment) with Holmwood Shale outcrop. The probable contact between the underlying glaciogenic Nangetty Formation and the Holmwood Shale is marked by yellow crosses. B, Positions of Localities B and C. The names of Mesas follow Clarke *et al.* (1951). A yellow X marks the contact between the glaciogenic Nangetty Formation (west) and the Holmwood Shale (east). Note: Locality B lies on a *Juresanites* ammonoid horizon marked on the Clarke *et al.* (1951) map. Locality C lies on a fossiliferous horizon marked by Clarke *et al.* (1951). To the immediate west of Locality C, the strata are structurally disturbed. Clarke *et al.* (1951) showed major faults in this area. Localities B and C are stratigraphically close and the strata around Locality C have been repeated by faulting. C, Position of sampling sites in Woolaga Creek area (Locality D, see Appendix 1 for details). D and E, schematic stratigraphic logs of sections containing methane-seep nodules at Locality A (D) and Locality B (E).

Locality B

Locality B lies at 28.9597° S, 115.4664° E on a mudstone scarp between prominent mesas in the northeastern sector of Nangetty Station (Fig. 2B). The stratigraphic log (Fig. 2E) was taken from the succession exposed in the major gully on the southern side of the scarp. Samples are listed in Appendix 1, and rock types are described in Haig *et al.* (2022). The nodular limestone level at Locality B is at the same altitude as Locality A. Given the negligible dip, it likely represents the same stratigraphic position.

Locality C

Locality C covers a flat area among cultivated paddocks strewn with dislocated nodules, around 28.9771°S and 115.5120°E (Fig. 2B). The nodules follow a trend along the structural strike of the Holmwood Shale here, near the boundary fence between Nangetty and Holmwood stations. This is in a faulted part of the succession. Similarities in the biota and cement fabrics (see Haig *et al.* 2022) suggest that the nodular carbonates here lie at the same level as those at localities A and B. Samples localities are listed in Appendix 1.

Locality D

Locality D covers a cultivated area (Fig. 2C) around 29.30°S, 115.655°E where scattered carbonate nodules have been moved to gutters besides the ploughed paddocks and along the southern gully leading northward into Woolaga Creek. Samples studied from this site are listed in Appendix 1 and include two from Playford's (1959) study. Rock types are described by Haig *et al.* (2022). As a result of his detailed mapping of the area, Playford (1959) estimated that the nodular limestone outcrops (which he called the Woolaga Limestone Member of the Holmwood Shale) were at least 76 m above the base of the Holmwood Shale.

METHODS

Multiple samples of nodular limestone were collected from each locality. These were slabbed with a diamond saw and acetate peels taken from the slabbed surfaces (several per sample). The surfaces were etched in 2% HCl acid for 4 minutes and then gently washed in a still water bath and air dried without touching the etched surface. Once dry, the surface was flooded with acetone and a sheet of acetate film (clear, 0.003 inch thick; commercially obtained) was carefully placed on the surface before the acetone evaporated. After several minutes, the film was removed producing a peel of the surface. Each peel was placed between glass plates and examined and photographed under a compound biological microscope. The advantages of acetate peels over thin sections for a preliminary investigation such as this is the much greater area available for study in a peel compared to a standard thin section. The peel also offers enhanced clarity of the cement fabrics and carbonate skeletal microstructures as evidenced in the photographic images illustrated in Haig et al. (2022) and in this paper.

Friable mudstone (shale) was disaggregated in water and the clean sand residue retained after successive decants of muddy water from the disaggregated slurry. Microfossils were picked from the dried sand fractions using a very fine 000 sable-hair brush and placed on gridded carboard micropaleontological slides.

Procedures used for processing samples for palynomorphs follow Playford (2021). All rock samples, acetate peels, washed sand residues and picked foraminiferal slides are housed in the collections of the Earth Science Museum at the University of Western Australia. The illustrated palynomorphs are curated in collections of the Geological Survey of Western Australia.

Results of the analysis of the biota are listed in Appendices 2 and 3. Curatorial details for the palynomorphs are listed in Appendix 4.

BIOTA

Bacterial indicators

Bacteria have been shown elsewhere to play an important role in carbonate cementation of nodules within organicrich shale facies (Case *et al.* 2015; Zhu & Dittrich 2016). However, direct observations in ancient nodules of microbial activities are limited. Among the chaotic



Figure 3. Laminations probably produced by successive microbial (bacterial) mats; from sample 175034. Bar scale = 0.5 mm.

cement fabrics of the studied nodules (Haig *et al.* 2022), laminations are present in some patches. These consist of alternating light and dark layers, < 0.1 mm thick, of microgranular carbonate (Fig. 3) with banded to streaky laminar architecture (as defined by Grey & Awramik 2020). This is consistent with the presence of microbial mats (Wilmeth *et al.* 2018). No evidence of cyanobacterial borings (or other endoliths, as defined by Günther 1990) in carbonate skeletons has been observed in the nodules.

Since publication of Haig *et al.* (2022), samples from each locality have been analysed for AOM (anaerobic oxidation of methane) biomarkers by Joern Peckmann and his research team at the University of Hamburg (J. Peckmann pers. comm. to D.W. Haig, 9 October 2023). They found good preservation of the biomarkers and different compound inventories of AOM biomarkers at different localities. These exciting results are being prepared for publication.

ALGAE

Unicellular algae

Algal microfossils form a minor component of the palynomorph preparations from Locality-D nodules,

with eight species recorded (Playford 2021). Playford illustrated these aquatic species and noted with reference to Brenner & Foster (1994), Grenfell (1995), and Mays *et al.* (2021): (i) the probable non-marine (freshwater or brackish) habitat of *Maculatasporites* spp., *Quadrisporites horridus*, *Spongocystia eraduica*, and *Tetraporina* sp.; and (ii) the variable marine or non-marine habitat of *Leiosphaeridia* sp. and *Cymatiosphaera gondwanensis* (see Playford 2021, for taxonomic identifications).

Litostroma

Litostroma oklahomense Mamay 1959 is present in nodules from each locality (Fig. 4A–F). It is most abundant at Locality C where concentrations of thalli are preserved in some nodules (Fig. 4A). At other sites, *L. oklahomense* occurs as isolated skeletal plates. Some of the thalli are >10 cm long. The identification is based on the monostromatic skeleton that is flexible, unattached, and apparently composed of dark organic material. The thalli are small and plate-like but their original shapes and the cell arrangements in horizontal view cannot be ascertained in the acetate peels. In oblique view (e.g., Fig. 4D), cells appear polygonal in cross-section. In vertical view (Fig. 4B, C), cells are of similar dimensions and shapes to those in the type specimens figured by Mamay (1959). The cells are normally just over 100 µm



Figure 4. "Algae" in nodular limestone. Bar scales = 1 mm (A, G–I) and 0.5 mm (B–F). A–F, *Litostroma oklahomense* Mamay; all specimens from Locality C, sample 175019. G–I, *Tubiphytes* sp., all specimens from Locality A, sample 175005.

wide and slightly exceed 160 μ m in height. The outer walls of the "cells" tend to be slightly convex giving a slightly lobate outline with cell contacts incised at the surface. The terminal faces of the final cells in a thallus are convex. The thalli do not appear to subdivide. Regular passageways between cells cannot be observed. The cells are infilled by cement. The flexible nature of the thalli is illustrated in Fig. 4E where a thallus has been tightly folded, and in Fig. 4F where the thallus has been sharply kinked. Some of the thalli (e.g., Fig. 4E) provided a substrate for encrusting porcelaneous and agglutinated foraminifers (see below).

Litostroma Mamay 1959, typified by *L. oklahomense* differs from *Eolithoporella* Johnson 1966 (their pl. 176, figs. 9, 10), which has cells with rectangular shapes in vertical section and flat rather than convex surfaces. It differs from *Nostocites* in which cells have circular cross-sections (see Groves 1983; and *Litostroma* sp. of Jansa *et al.* 1978, with "subrounded" cell cross-sections).

The type material of *L. oklahomense* is from the Boggy Shale of Early Pennsylvanian age in Oklahoma (dated by Thompson 1935, on the basis of fusulinids). It was originally described from a carbonate nodule (8 cm in maximum dimension) present in a shallow-marine shale succession that overlies a coal seam. Coal balls with a diverse marine assemblage occur in the shale (Mamay & Yochelson 1962), but the relative positions of these and the nodule containing the type material of L. oklahomense are not known. Accompanying the type specimens in the nodule are rare bivalves, gastropods, inarticulate brachiopod debris, foraminifers, and fish debris. Mamay (1959) illustrated porcelaneous foraminifers encrusting some of the thalli of Litostroma; these were described by Henbest (1958; see below). Beyond the type locality, Litostroma oklahomense has been described from the lower part of the Lower Permian of the Carnic Alps, Austria (Homann 1972) in facies interpreted as shallow-marine.

Because of the rectangular shape of cells with flat surfaces in vertical cross-section, *L. europaea* Kochansky-Devidé (1970, p. 15, figs 3–5), from the Pennsylvanian of Croatia, should be transferred to *Eolithoporella*. *Litostroma* has not been recorded previously from Australian or other Gondwanan successions. In the Irwin Basin, rare examples are present in carbonate nodules higher in the Holmwood Shale at a level about 50–60 m below the top of the formation (Tremblin & Haig 2023) and at the stratigraphic level of the Fossil Cliff Member in the uppermost part of the Holmwood Shale.

Bomfleur *et al.* (2009) characterized *Litostroma* oklahomense as a "putative red alga". Homann (1972) included it among the "Rhodophycophyta incertae sedis".

Tubiphytes

The algal affinities of *Tubiphytes* are uncertain (Vachard *et al.* 2001; Senowbari-Daryan 2013). Specimens observed in the nodular limestone from Locality A (Fig. 4G–I), have the typical tongue-shaped "segments", large central cavities, thick dark skeleton with "focculent microfabric", and crude layering that characterize *Tubiphytes* (see Vachard *et al.* 2001; Senowbari-Daryan 2013). However, studied specimens are very large in comparison to those

normally illustrated for *Tubiphytes*, some reaching almost 1.5 cm in maximum cross-sectional diameter.

Elsewhere in the Permian of the East Gondwana Interior Rift, *Tubiphytes* has been recorded from the upper Gzhelian, upper Sakmarian–lower Artinskian, and upper Artinskian–lower Kungurian in Timor (Davydov *et al.* 2013; Haig *et al.* 2014, 2017); and in the upper Sakmarian (viz. lower Callytharra Formation in the Merlinleigh Basin and equivalents of the Nura Nura Member in the Canning Basin; Haig *et al.* 2014) and upper Artinskian– lower Kungurian in the Noonkanbah Formation of the Canning Basin (Haig *et al.* 2017).

Problematica

Three groups which may have affinity to algae or sponges, or may be inorganic, are included here, informally labelled A, B, and C. Problematicum A has been found at Localities B–D and, very rarely, in nodules within the Fossil Cliff Member equivalents in the upper part of the Holmwood Shale. Problematica B and C have only been identified in nodular limestone at Locality A.

Problematicum A is usually represented by curved fragments (Fig. 5B) of objects that probably had a circular or ovoid cross-section (Fig. 5A, C). These consist of very thin, dark-coloured elements, ca. 0.3 mm long, with many branching approximately half-way lengthwise. The branches face outward toward the convex side, and some terminate with a small bifurcation on the outer (convex) periphery. The elements are preserved in a very fine, clear, granular matrix. Two interpretations of Problematicum A seem possible. (i) The matrix represents recrystallized skeleton (e.g., originally aragonite) and the elements are fine tubules infilled with micrite and perhaps with finely disseminated pyrite. If this is the case, these objects may be dasycladacean algae (see, e.g., poorly preserved skeletons illustrated by Homann 1972, pl. 7, figs. 56-58, as Salopekiella). (ii) The dark elements may be solid skeletal structures and the granular matrix may be a cavity with cement-infill.

Problematicum B includes cement-filled cavities up to 3–4 mm in maximum dimension (Fig. 5D, G). Bordering the inner edge of these major cavities is a zone containing "elements" set in a clear granular matrix. These resemble those in Problematicum A but are brown in colour in acetate peels. Surrounding the major cavities is a dark brown network that includes cavities (0.15–0.25 mm maximum diameter) with a roughly stellate outline (Fig. 5F).

Problematicum C forms part of the framework of the small bioherms represented in the nodular limestone at Locality A. It encrusts on skeletal plates (e.g. Fig. 5I) and forms irregularly erect columns (several centimetres in diameter) with circular cross-sections that branch (Fig 5H).

We have not recognized Problematicum B or C elsewhere in the Western Australian Permian. Very rare Problematicum A is also present at a level much higher than the studied horizon in nodular limestone of the Fossil Cliff Member near the top of the Holmwood Shale.

Foraminifera

Two different foraminiferal associations with little in



Figure 5. Problematica from nodular limestone. Bar scales = 0.5 mm (A–G) and 1 mm (H, I). A–C, Problematicum A from Locality D, sample 175029. D–G, Problematicum B from Locality A, unit 3, sample 175482. H, I, Problematicum C from Locality A, unit 1, H from sample 175470, I from sample 181377.

common are present in the studied interval within the Holmwood Shale: (i) an organic-cemented siliceous agglutinated fauna with mainly single-chambered morphotypes extracted from friable-shale samples (Fig. 6); and (ii) sparse assemblages of multichambered coiled agglutinated species as well as calcareous, porcelaneous, free and attached forms in the carbonate nodules (Fig. 7). These are outlined separately below.

Shale-facies foraminifers

Foraminifers were recovered from friable shale samples collected from Localities A, B, and D, and from similar rocks in a transect across the lower Holmwood Shale in Beckett's Gully (Appendix 3). In the latter, the ammonoid *Juresanites jacksoni* (see below) is preserved in a nodule within shale at about 61 m above the exposed top of the Nangetty Formation. This ammonoid was also found in the shale at Localities A and B and has been reported from Locality D (Skwarko 1993; and recorded as *Metalegoceras campbelli* by Playford 1959, see Glenister *et al.* 1993 for synonymy).

The foraminiferal assemblage is composed entirely of organic-cemented siliceous agglutinated tests belonging to 14 species. The tests now have secondary silica cement agglutinating the quartz grains of the wall (probably as silica overgrowths on these grains, precipitated during silica diagenesis during burial). They show the typical preservation of organic-cemented types that have undergone burial deformation in shale.

All but one of the species are single-chambered morphotypes (Fig. 6) belonging to Thuramminoides sphaeroidalis, Thurammina texana, Sansabaina elegantissima, Sansabaina? acicula, Kechenotsike hadzeli, Hyperammina coleyi, Sacculinella australae, Placentammina ampulla, Placentammina? sp., Pseudohyperammina? sp., Lagenammina sp., Glomospirella nyei, and Ammodiscus nitidus. A minute trochamminid with irregular coiling is only found in two samples in the Beckett Gully section just above the Juresanites level. Skwarko (1993, p. 89, 90) listed a similar assemblage of agglutinated species from the Holmwood Shale, as distinct from the more diverse microfauna, including calcareous species, recorded from the Fossil Cliff Member in the upper part of the formation. No foraminifers were recorded by Skwarko (1993) in the Woolaga Limestone Member of the Holmwood Shale. Precise localities were not documented



Figure 6. Foraminifera from mud facies of the lower Holmwood Shale. All species are organic-cemented, siliceous, agglutinated types consisting of single chambers. Bar scale = 0.1 mm. A–C, *Thuramminoides sphaeroidalis* Plummer; A, B, from 181397; C from 181384. D, E, *Thurammina texana* Cushman & Waters; D from 181385; E from 181384. F, *Sansabaina elegantissima* (Plummer); from 181397. G, H, *Sansabaina? acicula* (Parr); G from 181386; H from 181384. I, J, *Kechenotiske hadzeli* (Crespin); I from 181397; J from 181385. K–M, *Hyperammina coleyi* Parr; K, L from 181386; M from 181381. N–P, *Sacculinella australae* Crespin; N, P from 181384; O from 181397. Q–S, *Placentammina ampulla* Crespin; Q from 181390; R, S, from 181384. T, U, *Placentammina*? sp.; T from 181385; U from 181397. V, W, *Pseudohyperammina*? sp.; V from 181390; W from 181397. X–Za, *Lagenammina* sp.; from 181394. Zb–Ze, *Glomospirella nyei* Crespin; from 181394. Zf, *Ammodiscus nitidus* Parr; from 181394.



Figure 7. Foraminifera from nodular limestone at studied localities A–D. Images A–E and G–T are from acetate peels. Note that walls (e.g. whether dark or light) have different appearances than in thin sections because in the peels light does not pass through a mineralized wall. Well-preserved porcelaneous walls are usually pale. Bar scales = 0.1 mm. A–D, Multichambered forms with thick agglutinated tests probably *Verispira holmesorum* Tremblin & Haig (2023, fig. 7), A from 175472, B–D from 175481. E, Equatorial section of either a planispiral test or a very low trochospiral agglutinated morphotype, from 175474. F, An organic lining from a foraminiferal wall, observed in palynomorph preparation from 175035. G, *Tolypammina* encrusted onto *Litostroma* alga from 175019. H–J, *Calcitornella* sp.; I and J are attached to *Litostroma*; the attachment surface for H is recrystallized; H from 175034; I and J from 175019. K–M, *Hedraites* sp.; K and L are attached to crinoid columnals; the attachment surface for M is not preserved; K and L from 175034; M from 175035. N?, possible transitional morphotype between *Calcitornella* Cushman & Waters and *Glomomidiella* Vachard, Rettori, Angiolini & Checconi; the early whorls are attached to a small fragment of Problematicum A, the final stage of growth may have been unattached; from 175034. O–S, ?T, *Glomomidiella* sp.; apparently free-living morphotypes; O from 175027; P, S and T from 175035; Q and R from 175029.

by Skwarko (1993) nor by Palmieri (1993) in the same bulletin. Assemblages from the Fossil Cliff Member in the uppermost Holmwood Shale were described and illustrated by Crespin (1958), Foster *et al.* (1985), and Ferdinando (2001).

Elsewhere in Australian Permian basins, similar agglutinated assemblages with a range of singlechambered siliceous-agglutinated morphotypes seem to be best represented in basal marine transgressive muds of the Early Permian in Queensland's Bowen Basin (Crespin 1958; Palmieri 1994, 1998), the Sydney–Hunter basins of New South Wales (Crespin 1958; Scheibnerová 1982) and in Tasmania (Conkin & Conkin 1993). In North American interior basins of the Pennsylvanian, similar microfaunas from shallow-marine shale successions have been recorded and reviewed by Plummer (1945). However, most of these assemblages also contain multichambered agglutinated types.

Carbonate-nodule foraminifers

Carbonate nodules at all studied localities contain a sparse foraminiferal assemblage (Fig. 7; Appendix 2) of very different aspect to that in the surrounding shale. Two distinct groups are represented. Coiled chambered agglutinated morphotypes have walls with scattered grains (? quartz) in a dense microgranular matrix. Coiling in the agglutinated group seems to be of two types: (i) Irregular to streptospiral coiling observed in random sections (Fig. 7A–D) with rapid increase in chamber size; and (ii) planispiral or very low trochospiral coiling (Fig. 7E, F) with gradual increase in chamber size. Morphotype (i) may belong to the organic-cemented agglutinated Verispira holmesorum Tremblin & Haig (2023, p. 277, fig. 7, nos. 1a-6c) which has Ataxophragmium-like coiling. This species was described from carbonate mudstone nodules higher in the Holmwood Shale at about 50-60 m below the top of the formation. No similar morphotypes have been found elsewhere in the Western Australian Permian, but Verispira was first described as a globivalvulinid from Artinskian shale in the Permian of the Bowen Basin in Queensland by Palmieri (1988). The planispiral or very low trochospiral tests (Fig. 7E, F) may be either a Haplophragmoides or a low spired Trochammina. Very rare tubular, coiled, agglutinated Tolypammina sp. lived as epiphytes on the alga Litostroma (Fig. 7G). All the agglutinated types are organic-cemented types.

The calcareous porcelaneous species are tubular calcivertellines (Miliolata). These were either free living in the benthic environment (e.g., *Glomomidiella* sp.; Fig. 7O–S, ?N, ?T) or attached. The latter include *Calcitornella* sp. with smooth outer wall, attached to the alga *Litostroma* (Fig. 7H–J); and *Hedraites* sp. with spinose granules on outer wall, attached for example to the sides of crinoid columnals (Fig. 7K–M). Some porcelaneous foraminifers recorded here are present in the Fossil Cliff Member in the uppermost Holmwood Shale (Crespin 1958; Foster *et al.* 1985; Ferdinando 2001). However, *Hemigordius*, which is common in the Fossil Cliff Member, is absent from the assemblages in the carbonate nodules studied here.

Elsewhere in the Permian of the East Gondwana Interior Rift, elements of a coeval porcelaneous assemblage are known from the Merlinleigh (Southern Carnarvon) and Canning basins (Crespin 1958; Dixon & Haig 2004, Haig *et al.* 2014); and in Timor (Haig *et al.* 2014). In eastern Australian basins, similar porcelaneous morphotypes to those present in the studied nodules have not been illustrated from coeval strata (e.g., by Crespin 1958, and Palmieri 1994). The porcelaneous assemblage recorded here resembles microfaunas, associated with siliceous agglutinated foraminifers, recorded from the Pennsylvanian interior basins of southern North America (Cushman & Waters 1928a, b). From the lower Pennsylvanian of Oklahoma, Henbest (1958) and Mamay (1959) described and illustrated an association, like that recorded here, of *Calcitornella* sp. epiphytic on the alga *Litostroma*.

Sponges

Monaxon siliceous sponge spicules are rare in some nodules at all studied localities (Appendix 2). The Problematica A–C described above may be of sponge affinity.

Brachiopods

Very rare thin-shelled brachiopod debris occurs in some nodules at Localities B–D, and possibly in one nodule from Unit 2 at Locality A (Appendix 2). The brachiopods have pseudopunctate shell microstructure. Their rarity here contrasts with their usual notable abundance in other Permian carbonate units in Western Australia.

Rostroconchs

The main bivalved group in the nodules are probably rostroconchs, an enigmatic molluscan group extinct at the end of the Paleozoic (Pojeta & Runnegar 1976). Small bivalved morphotypes (Fig. 8A-G) that have nonfunctional hinges and are identified as rostroconchs have been observed in all units at Locality A and in one nodule from Locality D. At all localities, many nodules contain rare disarticulated and fragmented shells with similar microstructure to those identified as rostroconchs. Clarke et al. (1951) noted that a "species of Conocardium", a genus now referred to the Class Rostroconchia (Pojeta & Runnegar 1976), is present in the Macaroni Hill "serpulid reef". We could not find clear macrofossil examples of the genus in the nodular limestone at Locality A, nor in samples from the study of Clarke et al. (1951) in the collections of the Earth Science Museum at the University of Western Australia. Skwarko (1993, p. 90) recorded as Bivalvia, a single incomplete specimen identified as Conocardium sp. A from the Fossil Cliff Member in the upper Holmwood Shale. This specimen had been figured by Dickins (1963, pl. 16, fig. 1) and shows strong ribbing characteristic of the genus but not present on the material present in the methane-seep deposits. 'Conocardium sp.' was also listed by Skwarko (1993, p. 91; perhaps the internal cast identified as Conocardium sp. B in Skwarko, 1993, their appendix) from an unknown level in Holmwood Shale. The genus has not been recognized elsewhere in the Western Australian Permian.

The species recorded from the carbonate nodules (Fig. 8A–G) lacks the coarse ribbing characteristic of *Conocardium* (see Pojeta & Runnegar 1976, p. 69, pl. 37–40; and Ambler 2016), and is considerably smaller than most species attributed to this genus. The shells had dorsal-ventral heights ranging from 7.4 to 6.5 mm, but this is



Figure 8. Molluscs occurring commonly in the nodular limestone. Bar scales = 1 mm (A–D), and 0.5 mm (E–J). A–G, Probable rostroconchs: A–D are dorsal–ventral cross-sections through the valves with the hinge dorsally placed. These probably belong to one species; differences being attributed to sections at different anterior to posterior positions. Note: (1) hinge structures that appear non-functional, with F an enlarged view of the hinge in A; (2) "shelves", perhaps in the anterio-ventral part of the valves, in A and C and in G an enlarged view of the shelves in A; A and B from 175477; C from 175470; D from 175481. E, dorsal section cut approximately tangential along the hinge; from 175477. In E, the gap between valves, the large depression on one valve and the "fractures" in the hinge area match with similar structures observed in the dorsal–ventral cross-section shown in A and suggest that the right-hand side of E may be the anterior side (as A contains anterior-ventral shelves). H–J, Gastropod A.; note very thin wall, globose chambers, and large umbilical cavity; H and I from 175482; J from 175474.

probably dependent on where the sections fall along the anterior-posterior axis. The valves are asymmetric. One valve seems slightly larger than the other and the hinge structures are asymmetric. The outer surface of the wall is made up of a very thin clear external layer that forms fine corrugations due to thickening of the layer (e.g. Fig. 8A, B and E). The hinge as viewed in dorsal-ventral section is clearly non-functional with, in Fig. 8A at least, shell material extending along the inner side across the junction between valves. In tangential view along the dorsal side, closely interlocking "teeth" are present. On the ventral side of two sections (Fig. 8A and C), distinct shelves (e.g. Fig. 8G) are composed of skeletal material of different (microgranular) microstructure than featured by the laminated valves (shown best in Fig. 8C). These may correspond to the anterior longitudinal shelves described by Pojeta & Runnegar (1976). Their anterior position is supported by the deduction made in the caption to Fig. 8 about the relationship of Figs. 8A and E. In addition to the arguments advanced there, the abrupt termination of the left-hand side of the section in Fig. 8E probably indicates that this is the posterior side where a rostrum is developed (see Rogalla et al. 2003, fig. 1). Sections shown in Fig. 8B and D may be on the posterior side of the shell.

The species observed in the studied carbonate nodules probably belongs to a new conocardioid genus. Taxonomic study, beyond the scope of the present study, would best be done by using serial acetate peels and then reconstructing a three-dimensional model of the shell.

Bivalves

Some of the unidentified bivalved shell fragments observed in the acetate peels (Appendix 2) may belong to the Bivalvia. Shell fragments with prismatic calcitic microstructure are attributed to the Bivalvia; others with different microstructure may also belong here. Un-named nuculid bivalves were reported by Clarke *et al.* (1951) from the Macaroni Hill "serpulid"-rich limestone. We could not recognize them in the field. These are probably among the indeterminant shell material observed in the acetate peels. Skwarko (1993) recorded 'Sanguinolites' sp. from the Woolaga Limestone Member of the Holmwood Shale (Locality D of this paper) but did not include it in the systematic descriptions in his accompanying compilation of the Permian bivalves of Western Australia.

Gastropods

Clarke et al. (1951, p. 52) noted that the gastropod fauna in the Macaroni Hill "serpulid" limestone (Locality A of this study) was "peculiar" but did not identify the types present. We observed rare moderately high-trochospiral morphotypes with thick shells at this site, some having transverse and longitudinal ribs. However, because these were visible only as sections in hard rock, they proved unidentifiable. The most common gastropods, observed only in the acetate peels, are minute shells (Fig. 8H-J; Appendix 2, designated as Gastropod A) with some resemblance to skeneimorphs described from Cretaceous seep deposits in Japan (Kaim et al. 2009, fig. 14). They are characterized by an inflated low trochospiral shell with a very thin smooth wall and a deep "cylindrical" umbilical cavity beneath the spire. No gastropods of this type have been previously recorded from the Western Australian Permian (see Dickins 1963; Skwarko 1993)

Ammonoids

Two ammonoids are well known from the studied localities. The large metalegoceratid Juresanites jacksoni (Etheridge) was reviewed and illustrated by Glenister & Furnish (1961, p. 705, 706, pl. 81, figs 1, 2), Glenister et al. (1973, p. 1033–1035, pl. 2, figs. 2, 3), and Glenister et al. (1993, pl.52, figs 1–5). It is scattered within the calcareous mudstone nodules in shale deposits surrounding the Macaroni Hill nodular limestone (Locality A). We have collected in situ specimens in nodules in a gully immediately west and at the same stratigraphic level as Unit 1 of the Macaroni Hill limestone succession. *Juresanites jacksoni* is abundant in shale deposits associated with calcareous mudstone nodules at Locality B. It was recorded by Glenister et al. (1973) together with its synonym J. campbelli (see Glenister et al., 1993) from Woolaga Creek Locality D. Glenister & Furnish (1961, p. 706) noted that "several parallel exposures" of beds containing J. jacksoni, e.g., as mapped by Clarke et al. (1951), are probably fault repeats of the same bed. Where we have found J. jacksoni in the shale succession (in nodules), it is the only macrofossil present. Glenister & Furnish (1961, p. 705) noted that in a thin bed designated the "Beckett Member", the species forms an almost monospecific "ammonoid coquina" associated with very rare indeterminant nautiloids, gastropods and bivalves.

The other ammonoid, *Uraloceras irwinense* Teichert & Glenister (1952; following the nomenclature of Leonova 2011), is a small evolute species. We have found very rare specimens in Unit 1 at Locality A, and at Locality C. Glenister & Furnish (1961) noted that it is abundant together with *Juresanites* at one site in Locality D.

Echinoderms

Rare crinoid columnal plates are preserved in the nodular limestone at localities B and D (Appendix 2). The plates are present in small stem segments or as isolated columnals with circular cross sections. Very rare indeterminate skeletal material of possible echinoderm origin is present in units 2 and 3 at Locality A. Most of the nodular limestone shows no evidence of crinoidal or other echinodermal debris. Elsewhere in the Lower Permian limestones of Western Australia, crinoid debris forms one of the main biogenic components.

Ostracods

Ostracods are found in the nodular limestone at all studied localities (Appendix 2). Specimens having thin, smooth, articulated valves are most common (Fig. 9). Without three-dimensional images, the ostracods are impossible to identify. By comparison to diverse assemblages described from the Fossil Cliff Member of the uppermost Holmwood Shale (Foster *et al.* 1985; Ferdinando 2001), it is clear that the ostracod assemblages at the studied localities lack the thick-walled ornamented species so conspicuous in the Fossil Cliff fauna.

Polychaetes

Tube worms

Tube-worm calcareous skeletons (Fig. 10) form a major part of the framework, together with Problematica B and C and minor *Tubiphytes*, of the small thickets in all units at Locality A and are also scattered in the nodular limestone



Figure 9. Representative ostracods from the nodular limestone. Bar scales = 0.1 mm. Note the smooth very thin walls without lamination, the inner lamella and selvage in each valve, and slight differences in valve size in each specimen. A and C from 175470, B from 175471, D from 175472.

at Locality D. They are rare in the carbonate nodules at localities B and C (Appendix 2).

There is no evidence to suggest that the calcareous skeletons in many of the tubes from the Locality A thickets are either extensively recrystallized or a product of replacement. The skeleton is finely laminated, probably with an original fine fibrous microstructure (Fig. 10A, B). In some specimens, the outer laminae have partially defoliated from the inner wall layers with cement infilling the gaps created. The tubes are cylindrical; the wall is very thin compared to the tube diameter (Fig. 10C). In many of the tubes, as observed in both acetate peels and thin sections, the wall has a brown colour, perhaps reflecting an organic (chitinous) component (e.g. Fig. 10B-D, H). Most tubes are approximately circular in cross-section with diameters < 2 mm, but a few have more irregular outlines (e.g. Fig. 10E, F). Irregularly positioned low longitudinal keels, involving a thickening of the wall, are present in many tubes (e.g. Fig. 10D-H). The inner and outer wall surfaces are sharply defined in the acetate peels. The tubes are not cemented to neighbouring tubes, but close contact can modify the cross-sectional shape (Fig. 10F). On their wall surfaces, they do not carry epibionts with mineralized skeletons, nor are they bored.

Georgieva *et al.* (2019, p. 288) noted that, among modern tube worms, "calcareous tubes are almost exclusively confined to the Family Serpulidae". Other tubeworms may have organic or agglutinated skeletons. Modern organic-walled sigoglinids (notably vestimentiferans) are widely distributed and abundant around methane seeps as well as hydrothermal vents (Bright & Lallier 2010; Hass *et al.* 2009; Hilário *et al.* 2011; Georgieva *et al.* 2019). Vestimentiferans lack a digestive system and most rely on sulphide oxidizing, intercellular bacterial symbionts (Bright & Lallier 2010; Reveillaud *et al.* 2018). Around seeps, even in shallow water, vestimentiferans form small thickets/bioherms (e.g. Hashimoto *et al.* 1993; Miura *et al.* 1997; Karaseva *et* al. 2020) and their "root-balls" (= posterior part of tubes that grow downward into the sediment) are closely associated with carbonate nodules forming within the sediment at the seeps (Hass et al. 2009). Among modern vestimentiferans are examples (e.g. at deep-water seeps in the Congo fan) where the posterior tubes of a living species are variably replaced by diagenetic aragonite when still in growth position (Peckmann et al. 2005; Hass et al. 2009; Hilário et al. 2011). In the Congo-fan examples most of the outer wall layers remain in place whereas the inner layers are delaminated, and needle-like clumps of aragonite seem optically continuous through the layers. Accordingly, some late Paleozoic tube worms have been referred to the vestimentiferans (e.g. Peckmann et al. 2005; Himmler et al. 2008; Georgieva et al. 2019) although the molecular phylogeny of the modern species suggests a Cretaceous evolutionary divergence established the group (Little & Vrijenhoek 2003; Campbell 2006).

The tube-worm skeletons studied here show some similarities to those described by Himmler et al. (2008) from methane-seep carbonates in the Gzhelian (uppermost Pennsylvanian) of the glaciomarine Dwyka Group in southern Namibia. The African types are slender tubes with partly delaminated walls that characterize the Western Australian examples. The wall laminae have a similar brown colour (see thin section illustrated in Hilário et al. 2011, fig. 5F). However, keels and variability in cross-sectional shapes were not described and the tubes seem poorly preserved. Himmler et al. (2008) noted that the Dwyka Group tube worms were "vestimentiferan-like". The tube worms described by Peckmann et al. (2005) from the Middle Devonian of Morocco and suggested as possible vestimentiferans also show a delaminated wall but seem much more poorly preserved than the Dwyka Group and Western Australian examples.

The tube worms at the studied Irwin Basin localities either form small thickets (i.e., colonies of apparently



Figure 10. Polychaetes from the nodular limestone. Bar scales = 0.5 mm (A–H) and 0.1 mm (I, J). A–H, Tube worms; note laminated crystalline carbonate wall (not diagenetically replaced); longitudinal keels positioned irregularly on some tubes (observed mainly in cross-section). A, Enlarged view of wall shown in B revealing very fine laminae in inner part of wall, from 181377; C, longitudinal section, from 175470; D, slightly oblique cross section, from 175479; E, cross section, from 175481; F, G, cross sections, from 175482; H, oblique section, from 175476. I, J, Scolecodonts; I from palynomorph preparation 175035; J from palynomorph preparation 175029.

unconnected individuals, e.g., in units 1–3 at Locality A) or are isolated individuals, as observed in nodules from Locality D. In the thickets it is not possible at this stage to confirm that these are "root balls" formed from the posterior parts of tubes. Although more detailed petrography is required, the carbonate in most of the skeletons from Locality A seems to be primary rather than a replacement. Notably, laminations appear much finer in the inner wall (Fig. 10A) than in the modern vestimentiferans. The tubes of the Irwin Basin examples have well defined inner and outer surfaces and delamination has taken place between outer lamellae rather than from the inner layers as reported in modern

mineralized vestimentiferan tubes. The presence of keels and variability in cross-sectional shape of tubes has not been described previously for the Paleozoic tube worms considered of vestmentiferan affinities. These features are like those recorded in modern serpulids (Ten-Hove & Kupriyanova 2009).

The tube worms found at the studied localities probably belong to a group separate from the vestimentiferans (and perhaps the parent sigoglinids) as well as the serpulids. They may have possessed characters that include (i) a primary calcareous skeleton with incorporated layers perhaps rich in chitinous crystallites (Neville *et al.*, 1976); (ii) outer layers tending to delaminate during diagenesis; and (iii) variable development among colonial individuals of crosssectional shape of the tube and the presence of low keels formed by wall thickening (not through delamination).

Scolecodonts

The presence of other polychaete groups at the studied sites is indicated by very rare scolecodonts, from the jaw apparatuses, in palynomorph preparations from nodule samples at Locality D (Fig. 10I, J; and Playford 2021, their fig. 9J, K). From a very small sample, several morphotypes are present.

Possible vertebrate bone fragments

Fragmental skeletal elements that reach > 1 cm long (Fig. 11) from an unknown animal are present at localities B and D. The fragments are irregularly shaped with a smooth outline. Although the fragments are dense, laminated and fibrous fabrics are locally observed. Large cavities of variable shape are present together with small elongate cavities arranged in layers around the larger cavities. These may constitute large medullary and smaller vascular cavities in bone.

The fragments could be from fish, amphibians (see bone cross-sections from Triassic examples illustrated



Figure 11. Skeletal fragments of possible vertebrates (? amphibians). Bar scales = 1 mm. Note irregular large cavities within dense skeleton that are infilled by sediment, and rows of smaller elongate cavities infilled by cement around the larger cavities. Also note ball and socket joint in C, suggestive of a tetrapod. A and B from 39251; C from 175034, D from 175035, E–G from 175028.

by Konietzko-Meier & Sander 2013 and Canoville & Chinsamy 2015) or primitive reptiles. The articulation between two separate parts of a skeleton illustrated in Fig. 11C may represent the articulation of limb bones (e.g. ulna and humerus). This suggests that these fragments are from tetrapods, most likely amphibians.

Much more work needs to be done on these interesting structures, including acid digestion of the nodules and micro-CT scanning of the rock, before their taxonomic affinities can be ascertained.

Palynomorphs from land plants

As reported by Playford (2021), nodules from Locality D preserve an abundance and diversity of palynomorphs: predominantly spores and pollen grains (Figs. 12, 13), together with some algal microfossils, rare scolecodonts, and foraminiferal cell linings. The quality of both palynopreservation and -yield is of high standard, unusually so, given that the samples are from weathered outcrop and from a commonly sparsely palyniferous lithology.



Figure 12. Representative spores from nodules at Locality D (B, F–J, L, M from 175029; A, C–E, K, N–P from 175035), *Punctatisporites gretensis* Balme & Hennelly. B, *Leiotriletes directus* Balme & Hennelly. C, *Apiculiretusispora* sp. D, *Microbaculispora tentula* Tiwari. E, F, *Converrucosisporites confluens* (Archangelsky & Gamerro). G, H, *Horriditriletes ramosus* (Balme & Hennelly). I, *Brevitriletes cornutus* (Balme & Hennelly). J, *Diatomozonotriletes townrowii* Segroves. K, *Diatomozonotriletes* sp. L, *Secarisporites lacunatus* (Tiwari). M, *Densoisporites solidus* Segroves. N, *Indotriradites niger* (Segroves). O, P, *Gondisporites ewingtonensis* Backhouse. Scale bars = 20 µm. For full taxonomic attribution and other spore species present in the samples, see Playford (2021). For curatorial details see Appendix 4.



Figure 13. Representative pollen grains from nodules at Locality D (A–E, G–I, K, P–S from 175029; F, J, L–O, T from 175035). A, *Cannanoropollis janakii* Potonié & Sah. B, cf. *Cannanoropollis* sp. C, *Barakarites* sp. D, *Plicatipollenites gondwanensis* (Balme & Hennelly). E, *Plicatipollenites densus* Srivastava. F, *Plicatipollenites malabarensis* (Potonié & Sah). G, *Plicatipollenites onvicus* Bhardwaj. I, *Caheniasaccites* sp. J, *Limitisporites rectus* Leschik. K, *Protohaploxypinus amplus* (Balme & Hennelly). L, *Protohaploxypinus limpidus* (Balme & Hennelly). M, *Striatoabieites multistriatus* (Balme & Hennelly). N, *Vittatina fasciolata* (Balme & Hennelly). O, *Vittatina scutata* (Balme & Hennelly). P, Q, *Cycadopites cymbatus* (Balme & Hennelly). R, S, *Marsupipollenites striatus* (Balme & Hennelly). T, *Marsupipollenites* sp. cf. *M. striatus*. Scale bars = 20 µm. For full taxonomic attribution and other spore species present in the samples, see Playford (2021). For curatorial details see Appendix 4.

Reiterating Playford (2021), it would seem very likely that rapid lithification of the hosting calcareous sediment effectively protected the palynomorphs from oxidation at the methane-seep site and also from weathering desiccation. Early cementation of the nodules prevented burial-induced flattening.

DISCUSSION

Ecosystems represented in biota

Haig *et al.* (2022) distinguished representatives of three ecosystems in fossil assemblages from the carbonate nodules: (i) local marine seep ecosytem; (ii) broader marine pelagic ecosystem; and (iii) terrestrial ecosystem (probably coastal plain). They discussed possible palaeoecological relationships among these ecosystems, and the surrounding very poorly fossiliferous marine shale ecosystem. The biotic composition known from each ecosystem is summarized below.

The seep ecosystem includes (i) AOM archaea and bacteria (producing carbonate cement), (ii) microbial communities forming sediment laminations, (iii) small thickets of tube worms (that may have relied on chemosymbionts) and less common *Tubiphytes* and problematica B and C; (iv) other sessile inhabitants such as the organic macrophyte *Lithostoma* and its epiphytic porcelaneous and agglutinated foraminifers), rostroconch molluscs, very rare brachiopods and crinoids, and sponges that produced minute siliceous spicules. Benthic vagile foraminifers, gastropods, including microgastropods, ostracods, and polychaetes were also present. As Haig *et al.* (2022) noted, normal marine salinity is indicated by the seep fossil assemblage.

The marine pelagic ecosystem includes ammonoids, marine phytoplankton, and rare fish debris. Indeterminant nautiloids were also listed by Skwarko (1993). In muddy limestone nodules in the shale surrounding the seep deposits, the large ammonoid *Juresanites* (to at least 30 cm in diameter and in places forming a coquina) are common. Ammonoids are very rare elsewhere in the Western Australian Permian and the *Juresanites* occurrence suggests that (i) it was an opportunistic species attracted by the high organic productivity in the region of the methane seeps, and (ii) a more open-marine normal habitat for the ammonoid existed to the west of the Irwin Basin (the genus is not known further north in the contiguous marginal rift basins shown on Fig. 1E).

The marine shale ecosystem has benthic organisms with mineralized skeletons that are entirely different from those in the seep nodules. They consist only of organic-cemented siliceous agglutinated foraminifers. Haig *et al.* (2022) discounted the possibility that the shale hosted a benthic macrofauna whose calcareous skeletons suffered post-burial dissolution. They interpreted the shale deposits as suggesting very low-oxygen levels in the mud substrate and possible toxic pore water.

The coastal plain ecosystem includes spores and pollen grains preserved in the seep nodules. These were produced by diverse land plants probably living on the adjacent coastal plain. Some microphytoplankton preserved in the nodules signify freshwater inflow, via sediment-laden surface-water plumes from rivers and streams, coming from the coastal plain into the shallow interior sea.

The possible vertebrate remains (e.g., questionably very small amphibians) may have come from transitional shoreline environments. The animals may have been opportunistic feeders in surface waters above the seeps, being trapped and killed in methane eruptions sending their remains to the seafloor.

Criteria for water depth

Water depth is interpreted based on two main lines of evidence: (i) Stratigraphic criteria independent of fossil evidence; and (ii) fossil evidence.

Stratigraphic criteria independent of fossil evidence

Non-palaeontological palaeobathymetric evidence is derived from: (i) the low dip of strata and uniform thickness across the basin (see Clarke et al. 1951), and (ii) evidence for the water depth of the change between shallower sand facies and deeper mud facies in the interior sea (positioned hundreds of kilometres from the open Mesotethyan Ocean; Haig et al. 2022). Apart from Mesozoic faulting related to the breakup of Gondwana and later re-activation of faults due to late Miocene orogenesis on the far north-western margin of the Australian continent (Haig et al. 2018; Nano et al. 2023), the Permian strata in the Irwin Basin are little deformed and were not covered by any substantial thickness of post-Permian strata. The seafloor topography was locally flat grading into an extensive low coastal plain to the south, upland areas to the east (across the Darling Fault, see Clarke et al. 1951) and west (the Gascoyne Platform, recognized as a topographic high by Iasky et al. 2003, p. 30) and contiguous shallow seas to the north.

The water depth of the facies change is derived from the contact between the High Cliff Sandstone and the uppermost Holmwood Shale at High Cliff in the North Branch of the Irwin River (at 28.947°S, 115.548°E; Fig. 14). A muddy sandstone bed (2 m thick) at the base of the High Cliff Sandstone overlies carbonaceous mudstone of the uppermost Holmwood Shale (Fig. 14). The sandstone unit contains clinoforms, marked by more muddy horizons that extend from an erosion surface at the top of the bed to the basal planar contact with the Holmwood Shale (Fig. 14A). The clinoforms dip 5-10° SW, in the same dip direction as a higher 2 m thick tabular crossbedded coarse sandstone (see Fig. 14 and Dillinger et al. 2021, fig. 7). There is no evidence for substantial sea-floor gradients in this area. Major bedding surfaces in the High Cliff Sandstone parallel the contact with the Holmwood Shale and with beds in the Fossil Cliff Member. The uppermost part of the Holmwood Shale is devoid of a shelly fauna except for a very low diversity assemblage of siliceous organic-cemented agglutinated foraminifers with simple tubular morphology. As indicated in Fig. 14B, beneath the uppermost shale is a unit equivalent to the highly fossiliferous Fossil Cliff Member with a shelly fauna indicating normal-marine salinities (Haig et al. 2014). The basal bed of the High Cliff Sandstone at this location is interpreted as a small deltaic deposit that prograded over a flat muddy seafloor (of the Holmwood Shale). The unfossiliferous uppermost part of the



Figure 14. The Holmwood Shale–High Cliff Sandstone contact, North Branch of Irwin River. This is a critical section for interpretation of the depositional water depth for the upper part of the Holmwood Shale.

Holmwood Shale probably reflects an advancing brackish water front associated with the prograding delta. The erosional top of the basal sandstone bed may be close to sea level in the interior sea which would have had a low energy, probably microtidal, shoreline. The sand/mud facies change was probably at a few metres water depth assuming that the erosional surface was at approximate sea level.

Fossil assemblage evidence

The presence of probable photosynthetic *Litostroma* (possible red macrophytic algae) in the seep nodules and at other levels higher in the Holmwood suggests very shallow water, not much less than 30 m as deduced by Haig *et al.* (2022). This is supported by the presence of large porcelaneous (Miliolata) foraminifers which are most abundant in the inner neritic zones of normalmarine seas and absent in brackish environments (Murray 1991). The other components (including possible calcareous algae) of the seep assemblage are compatible with the shallow-water environments. The presence of calcareous fauna at several levels in the Holmwood Shale (including the methane-seep level) perhaps indicates intervals of maximum marine flooding.

Age

The age of the methane-seep deposits is based on ammonoids Juresanites jacksoni and Uraloceras irwinense

that indicate a Sakmarian (Early Permian, Cisuralian) age based on stratigraphic ranges of the genera and evolutionary trends of species in classical sections of the Permian in Russia (see discussion in Haig *et al.* 2022). Playford (2021) and Haig *et al.* (2022) indicated that the well-preserved diverse spore-pollen assemblage belongs to either the *Convertucosisporites confluens* Zone or to the succeeding *Pseudoreticulatispora pseudoreticulata* Zone (as defined by Mory & Backhouse 1997). The boundary between these zones is poorly marked in the Irwin Basin.

CONCLUSIONS

From Haig *et al.* (2022) and the descriptions above, the methane seeps are interpreted as sanctuaries of high organic productivity on an otherwise barren, shallow, muddy seafloor. They supported a biota that included forms resembling modern seep inhabitants that rely on chemosynthesis (AOM microbial suites) and photosynthesis (red monostromatic alga like *Litostroma*), as well as metazoans that possibly hosted chemosymbionts (e.g., vestimentiferan-like tube worms).

The shale surrounding the seep deposits lacks a benthic macrofauna. However, it includes a peculiar assemblage of organic-cemented foraminifers, mainly single chambered, that suggest low dissolved oxygen conditions on the seafloor. Carbonate nodules in the shale contain the skeletons of ammonoids including common large *Juresanites* (to 30 cm diameter) considered to be opportunistic feeders on organic material generated at the seeps.

Episodic influxes of freshwater (perhaps glacial meltwater) are evidenced by some of the microphytoplankton and the spores-pollen. Watercolumn stratification resulted with mud-laden freshwater surface plumes coming into the shallow interior from rivers on the nearby vegetated coastal plain.

The seep-nodule fossil assemblage is unlike any previously described from the Australian Permian. It warrants detailed taxonomic study and search for additional occurrences in the Irwin Basin and in other Australian basins.

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UWA Field No. °S Number		•S	٥Ē	Area	Basin	Formation/Age	Description				
Limestor	ne Nodules										
Locality	A: Unit 1										
175470	1_5_19-1	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit at base of succession; muddy limestone				
175471	1_5_19-2	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 1 at base of succession; muddy limestone				
175472	1_5_19-3	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 1 at base of succession; muddy limestone				
175473	1_5_19-4	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 1 at base of succession; muddy limestone				
181377	181377 1_5_19-5 28.97		115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 1 at base of succession; muddy limestone				
Locality	A: Unit 2										
175474	2_5_19_1	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
175475	2_5_19_2	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
175476	2_5_19_3	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
175477	2_5_19_4	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
175478	2_5_19_5	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
181378	27_5_21_	2 28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 2; muddy limestone				
Locality	A: Unit 3										
175479	2_5_19_6	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 3 at top of succession; muddy limestone				
175480	2_5_19_7	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 3 at top of succession; muddy limestone				
175481	2_5_19_8	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 3 at top of succession; muddy limestone				
175482	2_5_19_9	28.97144	115.4071	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" bioherm, unit 3 at top of succession; muddy limestone				
Locality	A: scree san	nples									
175000	28/11/201	6 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 2 large slabs				
175001	28/11/16_	2 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 4 slabs				
175002	28/11/16-	3 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 2 slabs				
175003	28/11/16-	4 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 2 slabs				
175004	28/11/16-	5 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 4 slabs				
175005	28/11/16_	_1 28.9714	115.40705	WA	Irwin Basin	Holmwood Shale, Permian	Macaroni Hill, "Serpulid" Reef, Nangetty Station ; 3 slabs (large tubes with concentric infill)				
Locality	В										
175023	9/9/16-7	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	Breakaway between mesas; 2 slabs of nodule				
175024	9/9/16-7	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	Breakaway between mesas; 2 slabs of nodule				
175025	175025 9/9/16-7 28°57'34.9"		115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	Breakaway between mesas; 1 slab of nodule				
175026	75026 9/9/16-7 28°57'34.9"		115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	Breakaway between mesas; 1 slab of nodule				
175027 9/9/16-7 28°57'34.9"		28°57'34.9"	7'34.9" 115°27'59.0"		Irwin Basin	Holmwood Shale, Permian	Breakaway between mesas; 2 slabs of nodule				
175028 9/9/16-7 28°5		28°57'34.9"	115°27'59.0"	WA Irwin Basin		Holmwood Shale, Permian	Breakaway between mesas; 1 slab of nodule				

Appendix 1. Localities and lists c	of studied samples
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UWA Number	Field No	. °S	°E	Area	Basin	Formation/Age	Description
Locality	С						
175007	10/9/16/1	28°58'37.6"	115°30'45.5"	WA	Irwin Basin	Holmwood Shale,	2 slabs of nodule; collected approximately
175012	10/9/16-2	28°58'37.4"	115°30'44.4"	WA	Irwin Basin	Permian Holmwood Shale,	2 slabs of nodule; collected approximately
175016	10/9/16-3	28°58'37.5"	115°30'43.1"	WA	Irwin Basin	Permian Holmwood Shale, Permian	along strike line in flat paddock 2 slabs of nodule collected by Arthur Mory in paddock about 100-200 m north of 175016
175019	10/9/16-5	28°58'37.5"	115°30'43.1"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of nodule collected by Arthur Mory in paddock about 100-200 m north of 175016
175020	10/9/16-4	28°58'37.5"	115°30'43.1"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of nodule collected by Arthur Mory in paddock about 100-200 m north of 175016
175021	10/9/16-8	28°58'37.5"	115°30'43.1"	WA	Irwin Basin	Holmwood Shale, Permian	4 slabs of nodule collected by Arthur Mory in paddock about 100-200 m north of 175016
175022	10/9/16-9	28°58'37.5"	115°30'43.1"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of nodule collected by Arthur Mory in paddock about 100-200 m north of 175016
Locality	D						
175029	5/9/16-1	29°12'12.7"	115°39'17.7"	WA	Irwin Basin	Holmwood Shale, Permian	1 slab of blocks of indurated fossiliferous carlcareous mudstone; moved and concentrated at edge of paddock; Woolaga
175033	5/9/16-1	29°12'12.7"	115°39'17.7"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of blocks of indurated fossiliferous carlcareous mudstone; moved and concentrated at edge of paddock
175034	5/9/16-1	29°12'12.7"	115°39'17.7"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of blocks of indurated fossiliferous carlcareous mudstone; moved and concentrated at edge of paddock
175035	5/9/16-2	29°11'53.5"	115°39'13.7"	WA	Irwin Basin	Holmwood Shale, Permian	2 slabs of blocks of indurated fossiliferous carlcareous mudstone; moved and concentrated at edge of paddock
175036	5/9/16-2	29°11'53.5"	115°39'13.7"	WA	Irwin Basin	Holmwood Shale,	2 slabs of blocks of indurated fossiliferous carlcareous mudstone; moved and concentrated at edge of paddock
39251		29°12'10"	115°39'30"	WA	Irwin Basin	Holmwood Shale, Permian	nodular limestone
39256		29°12'40"	115°39'30"	WA	Irwin Basin	Holmwood Shale, Permian	nodular limestone
Shale sa	mples						
Beckett's	Gully (Sam	ples collecte	d along Becke	tt's Gul	ly and tributari	ies)	
181379	6_9_16-3	29°01'25.8"	115°31'05.1"	WA	Irwin Basin	Holmwood Shale,	Shale outcrop in Beckett Gully, estimated
181380	6_9_16-8	29°01'21.0"	115°31'16.6"	WA	Irwin Basin	Holmwood Shale,	40 In above top Mangetty outcrop
181381	8_9_16-6	29°01'23.3"	115°31'21.2"	WA	Irwin Basin	Holmwood Shale,	same level as ammonoid (<i>Jurensanites</i> ;
181382	8_9_16-7(2)	29°01'23.2"	115°31'21.9"	WA	Irwin Basin	Holmwood Shale,	8_9_16_5); about 60 m above top Nangetty
181383	8_9_16-7(4)	29°01'23.2"	115°31'21.9"	WA	Irwin Basin	Holmwood Shale,	
181384	8_9_16-10	29°01'25.5"	115°31'45.7"	WA	Irwin Basin	Holmwood Shale,	
181385	8_9_16-12	29°01'16.7"	115°31'54.6"	WA	Irwin Basin	Permian Holmwood Shale, Permian	
181386	8_9_16-15	28°57'43.0"	115°31'51.2"	WA	Irwin Basin	Holmwood Shale,	
181397	8_9_16-2	29°01'24.0"	115°31'17.8"	WA	Irwin Basin	Fermian Holmwood Shale, Permian	Stratigraphically below <i>Juresanites</i> level (181381)

UWA Number	Field No	. °S	°E	Area	Basin	Formation/Age	Description
Locality	A (shale in i	nterval with	<i>Juresanites</i> in o	calcareo	ous mudstone r	odules)	
181387	10_9_16-10	28°58'34.5"	115°24'24.7"	WA	Irwin Basin	Holmwood Shale, Permian	
181388	10_9_16-11	28°58'34.6"	115°24'22.2"	WA	Irwin Basin	Holmwood Shale, Permian	
181389	10_9_16-13	28°58'28.7"	115°24'27.1"	WA	Irwin Basin	Holmwood Shale, Permian	
181390	10_9_16-14	28°58'29.6"	115°24'27.8"	WA	Irwin Basin	Holmwood Shale, Permian	
181391	29_5_17-1	28.9714°	115.40705°	WA	Irwin Basin	Holmwood Shale, Permian	about 1 m below base of Unit 1 of "Serpulid" nodular limestone
Locality	В						
175040	9_9_16-7	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	at base of measured section
181392	9_9_16-8	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	about 0.85 m above base
181393	9_9_16-9	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	about 1.7 m above base
181394	9_9_16-10	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	about 2 m above base
181395	9_9_16-11	28°57'34.9"	115°27'59.0"	WA	Irwin Basin	Holmwood Shale, Permian	about 3.5 m above base; just below level with <i>Juresanites</i> in nodules
Locality	D						
181396	28/5/21-1	29.19494°	115.65154°	WA	Irwin Basin	Holmwood Shale, Permian	shale exposed on small scarp, Woolaga Creek

							For	amir	nifera	a	-			N	Iollu	isca			-					
	Microrobial (bacterial) lamination	Litostroma oklahomensis	Tubiphytes sp.	Problematica A	Problematica B	Problematica C	Microgranular /agglutinated morphotypes	Tolypammina sp.	Calcitornella sp.	Glomomidiella sp.	Hedraites sp.	monaxon siliceous sponge spicules	Brachiopod debris - pseudopunctate shells	Rostroconchs	Bivalve debris with prismatic microstructure	Bivalved shells of uncertain affinity	Gastropod A	Gastropods - other morphotypes	? Uraloceras sp.	Crinoid debris	? Echinoderm	Ostracods	Tube worms	probable vertebrate bone fragments (?amphibians)
Loc. A Unit 1 175470 175471 175472 175473 181377		x x		?	?	x x x	X X X X X X		x	?	X ?	X X		X X X		X X X X X X	X X X X	x x	x			X X X X X X	X X X X X X	
Unit 2 175474 175475 175476 175477 175478 181378			X		? ?		X X X X X X X		X X				?	x x x x x		X X X X X X	X X X X X	x x x			Х	X X X X X X X	X X X X X X X	
Unit 3 175479 175480 175481 175482		x	?		X X	? ?	X X		x	?				X X X	x	X X	X X X X	X X			X X	X X X X	X X X X	
scree 175001 175002 175003 175004 175005			? X		X	x x x	X X		?					X	X X	X X	X X					x x	X X X X X X	
Loc. B 175023 175024 175025 175026 175027 175028		X X X X X X		X X X			X		?	X		X X	X		X			x		x		X X X	X	x

Appendix 2. List of biota in studied nodules.

								Fora	amin	ifera	ı		Mollusca											
	Microrobial (bacterial) lamination	Litostroma oklahomensis	Tubiphytes sp.	Problematica A	Problematica B	Problematica C	Microgranular /agglutinated morphotypes	Tolypammina sp.	Calcitornella sp.	Glomomidiella sp.	Hedraites sp.	monaxon siliceous sponge spicules	Brachiopod debris - pseudopunctate shells	Rostroconchs	Bivalve debris with prismatic microstructure	Bivalved shells of uncertain affinity	Gastropod A	Gastropods - other morphotypes	? Uraloceras sp.	Crinoid debris	? Echinoderm	Ostracods	Tube worms	probable vertebrate bone fragments (?amphibians)
Loc. C 175007 175012 175016 175019 175020 175021 175022	X	X X X X X X X X		X X X X X X				x	Х			? X X X X X	? X X		x x x	x x		x	x			х	x	
Loc. D 175029 175033 175034 175035 39251 39256	x	x x x		X X X	X		x x		X X X X	x x x	X X	X X X X X X X	X	X		X X X X X X	x x	x x		X X X X X X X		X X X X	X X X X X X X	X X X X

Appendix 3. List of biota fi	rom studied shale samples.
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Foraminifera. (R = > 5 specimens; C = 5-20; A = >20)	Thuramminoides sphaeroidalis	Thurammina texana	Sansabaina elegantissima	Sansabaina? acicular	Kechenotiske hadzeli	Hyperammina coleyi	Sacculinella australae	Placentammina ampulla	Placentammina? sp.	Pseudohyperammina? sp.	Lagenamnina sp.	Glomospirella nyei	Ammodiscus nitidus	?minute trochamminid	Fish teeth	Jureasnites	
Beckett's Gu	ıllv																-
181379	R	R	С				С	А	R	R							
181380			R				R			R		R	R				
181381	R	R	R			А				?		А			Х	Х	
181382	R		R				?				R	А		С			
181383	R			?				R			С	А	R	R	Х		
181384	R	R	R				А	А	R								
181385	R	R	R		R		С	С	R		R						
181386			А	R	R	R	?					С					
181397	С		А		R		С		R	R							
Locality A (i	n inte	rval w	ith <i>Jure</i>	esanites	s in no	dules)											
181387	R		Ŕ			,	С					R					
181388			R		R		R										
181389	С	R	R				R	R									
181390	С		R				R	R		R							
181391	R						R					А					
Locality B (in	mmed	iately	below	level	with J1	ıresanit	tes										
175040	С	5			,	А	R					А					
181392	С		R			R	R	R			R	А			Х		
181393					R						R	А					
181394	R				R				R		R	А	R				
181395			R		R						R	А			Х		
Locality D																	
181396			С	R				?				R					

Palynomorphs	Fig. no.	Sample no.	Slide no.	EF coords	Photo no.	GSWA no.
Punctatisporites gretensis	12A	175035	3	V27/1	WL706	F55166
Leiotriletes directus	12B	175029	5	D16	WL74	F55167
<i>Apiculiretusispora</i> sp.	12C	175035	12	F18	WL1162	F55168
Microbaculispora tentula	12D	175035	3	T25	WL699	F55169
Converrucosisporites confluens	12E	175035	2	Q40	WL504	F55170
Converrucosisporites confluens	12F	175029	16	Q25	WL1301	F55171
Horriditriletes ramosus	12G	175029	16	Τ8	WL1292	F55172
Horriditriletes ramosus	12H	175029	16	P31/1	WL1305	F55173
Brevitriletes cornutus	12I	175029	9	Q21	WL169	F55174
Diatomozonotriletes townrowii	12J	175029	14	N30/1	WL1247	F55175
Diatomozonotriletes sp.	12K	175035	2	P28/2	WL437	F55176
Secarisporites lacunatus	12L	175029	14	W39/4	WL1254	F55177
Densoisporites solidus	12M	175029	5	L45	WL100	F55178
Indotriradites niger	12N	175035	2	U17	WL337	F55179
Gondisporites ewingtonensis	120	175035	1	O25/3	WL41	F55180
Gondisporites ewingtonensis	12P	175035	2	H47	WL553	F55181
Cannanoropollis janakii	13A	175029	8	E45	WL164	F55182
cf. Cannanoropollis sp.	13B	175029	13	V9	WL1192	F55183
Barakarites sp.	13C	175029	17	N34/4	WL1332	F55184
Plicatipollenites gondwanensis	13D	175029	14	G42	WL1258	F55185
Plicatipollenites densus	13E	175029	17	T36/4	WL1333	F55186
Plicatipollenites malabarensis	13F	175035	10	J27/3	WL1066	F55187
<i>Plicatipollenites</i> cf. <i>malabarensis</i>	13G	175029	13	E14/3	WL1198	F55188
Potonieisporites novicus	13H	175029	16	K10/2	WL1294	F55189
<i>Caheniasaccites</i> sp.	13I	175029	8	S18/3	WL112	F55190
Limitisporites rectus	13J	175035	2	T48/1	WL561	F55191
Protohaploxpinus amplus	13K	175029	5	S44	WL98	F55192
Protohaploxpinus limpidus	13L	175035	2	V39/4	WL503	F55193
Striatoabieites multistriatus	13M	175035	2	R10/2	WL209	F55194
Vittatina fasciolatus	13N	175035	2	E13	WL266	F55195
Vittatina scutata	13O	175035	12	R14/1	WL1153	F55196
Cycadopites cymbatus	13P	175029	14	R27	WL1243	F55197
Cycadopites cymbatus	13Q	175029	13	V19/4	WL1205	F55198
Marsupipollenites striatus	13R	175029	17	U21/1	WL1329	F55199
Marsupipollenites striatus	13S	175029	15	J40	WL1289	F55200
Marsupipollenites cf. striatus	13T	175035	10	E32/2	WL1076	F55201
Foraminiferal test lining	7F	175035	11	W30/3	WL1129	F55202
Scolecodont	10I	175035	11	S34/3	WL1133	F55203
Scolecodont	10J	175029	13	F45/2	WL1227	F55204

Appendix 4. Curatorial details for figured palynomorphs (Figs. 12, 13)