Late Triassic dinoflagellate cysts from the Northern Carnarvon Basin, Western Australia

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ABSTRACT

The Northern Carnarvon Basin was situated on the southern margin of the Tethys Ocean during the Late Triassic. This major depocentre accumulated extensive deltaic and shallow marine strata at this time and these successions have allowed the investigation of the initial radiation of cyst-forming dinoflagellates in the Southern Hemisphere. Numerous petroleum exploration wells in the basin have penetrated the fluvially dominated Mungaroo Formation and shallow marine Brigadier Formation of Carnian–Norian and Rhaetian age respectively. Consequently, huge numbers of cuttings and sidewall core samples from these northwest prograding deltaic systems are available for study. Many of the dinoflagellate cysts from the Mungaroo and Brigadier formations have not been taxonomically formalised, including many forms that are used in open nomenclature within the oil and gas industry. This study formally documents these occasionally abundant and diverse dinoflagellate cyst assemblages with the aim of providing a consistent taxonomic framework for future work on the Triassic successions of the Northern Carnarvon Basin. This will aid the recognition of individual flooding events via their characteristic palynomorph signatures and help to build on significant recent advances in regional sequence stratigraphy. One new genus, 14 new dinoflagellate cyst species and one new subspecies are described from the most diverse Late Triassic dinoflagellate assemblage yet published. A further nine genera and 17 dinoflagellate species are also recorded from the Carnian–Rhaetian *R. nagelii*, *R. wigginsii*, *W. listeri*, *H. balmei*, *R. rhaetica* and *D. priscum* dinoflagellate zones. The associations documented are significant biostratigraphically. It is postulated that high diversity Triassic dinoflagellate cyst associations were palaeoclimatically controlled, and were confined to the temperate and cool temperate palaeolatitudes.

Keywords: biostratigraphy; dinoflagellate cysts; Late Triassic; Northern Carnarvon Basin, Western Australia; taxonomy.

1. Introduction

The Northern Carnarvon Basin, offshore Western Australia is a major Permian to Holocene depocentre containing ~15 km of sedimentary basin fill including extensive Triassic through Lower Cretaceous siliciclastic deltaic and marine successions (Fig. 1). These Mesozoic sequences host the majority of the commercial oil and gas reserves in the Northern Carnarvon Basin and are typically capped by the major Lower Cretaceous regional seal, the Muderong Shale, or by intraformational claystones. The first hydrocarbon exploration well targeting these hydrocarbon reservoirs was Rough Range-1, drilled by the West Australian Petroleum Pty Ltd (WAPET) in 1953. This well proved relatively small volumes of oil, thereby establishing the oil and gas industry in Australia (Johnstone, 1979). Over the subsequent 66 years, approximately a further 1000 exploration boreholes have been drilled in the Northern Carnarvon Basin according to the Western Australian Petroleum and Geothermal Information Management System (WAPIMS) database (https://wapims.dmp.wa.gov.au/wapims). These include many wells which targeted the deltaic and shallow marine successions of the Mungaroo and Brigadier formations of Carnian–Norian and Rhaetian age respectively (Fig. 2; Adamson et al., 2013; Heldreich et al., 2017). Successful drilling of these Upper Triassic successions has relied heavily on palynology to provide biostratigraphical control and to help establish a robust sequence stratigraphical framework (Helby et al., 1987a; Backhouse and Balme, 2002; Marshall and Lang, 2013). These studies revealed moderately diverse dinoflagellate cyst associations throughout the Upper Triassic. The current study seeks to build on this earlier research by utilising the huge volume of publically-available ditch cuttings and sidewall core samples to formally document the full diversity of Late Triassic dinoflagellate cysts in the Northern Carnarvon Basin. Although dinoflagellate cysts occur consistently through the Brigadier Formation, they have a much more sporadic distribution in the underlying Mungaroo Formation (Fig. 2). In the latter unit, dinoflagellate cysts are significantly more abundant in the offshore facies, or are associated with the periodic shallow marine flooding events within the otherwise fluvially-dominated Mungaroo Delta.

In recent years, there have been major breakthroughs in the detailing and understanding of the depositional environments, sedimentology and sequence stratigraphy of the Mungaroo and Brigadier formation deltas (Adamson et al., 2013; Marshall and Lang, 2013; Payenberg et al., 2013; Gartrell et al., 2016). These advances all made extensive use of biostratigraphical data (e.g. Backhouse and Balme, 2002; Backhouse et al., 2002), nonetheless, it is hoped that the formal description of additional dinoflagellate cyst taxa from this basin will further aid regional stratigraphical studies. Consistent taxonomy, based on well-described taxa, is crucial for the development of reliable, high resolution biozonations. By contrast, informal taxa names have considerable potential to introduce stratigraphical confusion and errors, particularly if the species concepts are applied too broadly or where multiple informal names exist for a single taxon. In summary, this contribution intends to consolidate the Late Triassic dinoflagellate cyst taxonomy of the Northern Carnarvon Basin and thus allow for a more consistent recognition of the individual marine flooding events based on their dinoflagellate cyst associations.

The Late Triassic is a critical interval for studying dinoflagellate evolution, because these unicellular, flagellate eukaryotes commonly formed fossilisable resting cysts for the first time during this interval (Mangerud et al. 2019). Although biogeochemical evidence suggests that the dinoflagellates have a much longer history, extending back to the earliest Cambrian or more likely the Proterozoic, the Ladinian to Carnian interval represents the first major experimentation with the formation of highly resistant, organic-walled cysts (Moldowan and Talyzina, 1998; Fensome et al., 1999). Both this initial experimentation phase and the subsequent radiation of these cyst-forming dinoflagellates in the Norian and Rhaetian are well-expressed in the Northern Carnarvon Basin. As such, this study provides an excellent opportunity to compare these well-preserved and diverse Australian assemblages with similar associations in the Northern Hemisphere, particularly those from the high palaeolatitudes such as Alaska, Arctic Canada and the Barents Sea region.

Samples from 33 wells in the Northern Carnarvon Basin (Fig. 1, Table 1) with known Carnian to Rhaetian dinoflagellate cyst associations were examined to: 1) fully document the dinoflagellate cyst diversity; 2) to find well-preserved specimens for the formal taxonomic descriptions; and 3) to establish the ranges and abundances of the various taxa. Two wells from the Roebuck Basin and one well from the Browse Basin were also included as they contained important Carnian dinoflagellate cysts and well-preserved Rhaetian assemblages respectively (Table 1).

2. Geological background

The Northern Carnarvon Basin is situated in the southwestern part of the North West Shelf of Australia and encompasses several major hydrocarbon-bearing Palaeozoic–Cenozoic depocentres (Fig. 1; Purcell and Purcell, 1988; Longley et al., 2002). The North West Shelf is a passive margin comprising an extremely large prograding wedge of carbonate sediments that have accumulated on the slowly subsiding margin of northwestern Australia since the Late Cretaceous (Cockbain 1989). This passive margin is underlain by the Bonaparte, Browse, Northern Carnarvon and Roebuck basins. These sedimentary centres, together with the Papuan Basin and the Timor-Banda Orogen, form the Westralian Superbasin (Yeates et al., 1987).

The geological history of the North West Shelf was discussed in detail by Purcell and Purcell (1988; 1994; 1998) and Longley et al. (2002). Marshall and Lang (2013) subsequently constructed a comprehensive sequence stratigraphical framework for this region that clearly demonstrated the relative uniformity of the stratal packages across the entire North West Shelf. These sediment packages were largely controlled by the breakup of Gondwana along the northwest margin of Australia. In summary, the North West Shelf overlies a marginal rift system that stretches ~2400 km from the Exmouth Plateau in the west to Melville Island in the east. It contains thick and extensive Jurassic–Cenozoic synrift and postrift strata which overlie variably thick Permian–Triassic intracratonic successions (Purcell and Purcell, 1988). The Mesozoic rift successions relate to the regional fragmentation of Gondwana when the Lhasa and West Burma blocks and Greater India rifted away from the northern and western margins of the Australian Plate. As a more passive margin developed during the Late Cretaceous and Cenozoic, thick carbonate successions developed in the warm shelfal seas along these margins.

The Northern Carnarvon Basin is the largest extensional basin in the North West Shelf and extends for >1000 km off northwestern Western Australia. It is bounded to the southwest by the Southern Carnarvon Basin, to the south by the Pilbara Craton, to the east by the Offshore Canning and Roebuck basins, and to the north and west by the Argo, Gascoyne and Cuvier abyssal plains (Fig. 1). It comprises the Lambert and Peedamullah shelves adjacent to the coast, the major depocentres of the Exmouth, Barrow, Dampier and Beagle subbasins orientated southwest to northeast through the centre of the basin and the vast outboard Exmouth Plateau. The Investigator Sub-basin and the Wombat Plateau are within the broader Exmouth Plateau, whilst the uplifted southern margin of this platform, the Rankin Platform, borders the Barrow and Dampier sub-basins. The regional geology of the Northern Carnarvon Basin was discussed by, for example, Hocking et al. (1987; 1994), Stagg and Colwell (1994), Jablonski (1997), Hocking (1988; 1990), Longley et al. (2002), and Chongzhi et al. (2013), and is not considered further herein. However, a brief summary of the major Late Triassic events affecting the basin, the depositional environments present through this interval and their associated palynofloras is summarised below.

The onset of Gondwanan rifting during the Late Triassic (Carnian and Norian) resulted in significant regional faulting and uplift along the northwestern margin of Australia (Longley et al., 2002). This tectonic event was termed the ‘Fitzroy Movement’ by Forman and Wales (1981). The resulting uplift in the Canning Basin and surrounding hinterland was associated with major erosive events that provided huge volumes of sediment to the developing depocentres in the Barrow, Beagle, Dampier, and Exmouth subbasins, and as far north as the outer Exmouth Plateau. The basin fill may also have included substantial volumes of sediment transported from further afield, for example Argoland, Central Australia, Greater India and/or West Myanmar (Jablonski and Saitta, 2004; Southgate et al., 2011). Together with the reworked Proterozoic basement terranes and Lower Palaeozoic strata, these erosive events also introduced moderate volumes of reworked Permian palynomorphs into the Upper Triassic successions of the Northern Carnarvon Basin. These include striate bisaccate pollen grains (e.g. *Protohaploxypinus* and *Striatopodocarpites*), ornate Late Permian marker taxa (e.g. *Dulhuntyispora*), and various distinctive cheilocardioid spores (e.g. *Didecitriletes* and *Microbaculispora*) (authors personal observations).

Overall, the Upper Triassic successions of the Northern Carnarvon Basin represent a second order transgressive cycle (Adamson et al., 2013). This led to the deposition of the fluvially-dominated Mungaroo Delta (the Mungaroo Formation of Anisian–Norian age) overlain by the predominantly nearshore and shallow marine deltaic facies of the Brigadier Formation (Rhaetian). The significant lowermost Rhaetian flooding event that marks the abrupt shift from dominantly fluvial to shallow marine deltaic deposits was probably related to the rifting of the Lhasa Block that initiated during the Norian and progressed through the latest Triassic (Metcalfe, 1999; Longley et al., 2002).

The fluvially-dominated deltaic strata of the Mungaroo Formation were deposited in low accommodation space, broad sag depocentres. These gently structured downwarps filled at rates approaching one metre every 5000 years, and this unit is dominated by upper delta plain to alluvial plain channel sandstones with occasional brackish to marginal marine flooding events (Adamson et al., 2013). The delta plain and channelised deposits contain moderately diverse terrestrial palynofloras belonging to the Onslow Microflora of Dolby and Balme (1976). This latitudinally-restricted floral province extends from Timor, through northwestern Australia, India, easternmost Antarctica, northern Madagascar, and east Africa to northwestern Argentina (Césari and Colombi, 2013). It is interpreted to represent temperate to warm, humid conditions with monsoonal influences and periodic wet and dry phases (Dickens, 1985; Bradshaw et al., 1994; Ratcliffe et al., 2010). This palaeoclimate is entirely compatible with the location of the Northern Carnarvon Basin during the Late Triassic, along the southern margin of the Tethys Ocean and close to the Tropic of Capricorn.

The Onslow Microflora differs from the more southerly Ipswich Microflora by its greater diversity of gymnosperms and in containing various distinctive Eurasian taxa, such as *Aulisporites astigmosus*, *Camerosporites secatus*, *Enzonalasporites* spp., *Ephedripites macistriatus*, *Minutosaccus crenulatus*, *Ovalipollis* spp., *Rimaesporites aquilonalis* and *Samaropollenites speciosus* (see Dolby and Balme, 1976; Césari and Colombi, 2013). The Onslow Microflora in the Northern Carnarvon Basin also includes abundant to super-abundant *Falcisporites* (pteridosperm pollen largely from the seed fern *Dicroidium*) and very common *Dictyophyllidites* fern spores. The proportions of these dominant taxa, together with the fluctuations in abundance of pollen and spores from conifers, cycads, gingkos, sphenosids and other ferns, have been used to correlate the palynofacies and palynofloras to alternating channel, floodplain, swampy, lacustrine and marginal marine depositional environments (Bint and Helby, 1988; Backhouse and Balme, 2002; Backhouse et al., 2002; Dixon et al., 2012). It is the marine intervals, containing dinoflagellate cyst assemblages, which were studied herein. These are typically relatively thin, marginal to shallow marine successions, including interdistributary bays and pro-delta deposits (Adamson et al., 2013). There is no persuasive evidence linking these flooding events to significant Late Triassic tectonic activity (Marshall and Lang, 2013). However, because this region is interpreted to have had very low relief (mostly low-lying coastal plains), even modest sea-level rises resulted in widespread marine flooding events. Thus, even some very marginal to brackish facies (including coastal soil horizons) contain sparse dinoflagellate cyst assemblages of typically thin-walled, proximate taxa such as *Dapodinium* and *Hebecysta*. These lower diversity associations may, in part, have been deposited by major tidal events, or were related to the localised development of brackish water conditions.

The Carnian–Norian was also a critical interval during the evolution of dinoflagellates because they first began to commonly form fossilisable cysts at this time. The abundant and varied coastal and shallow marine environments along the southern margin of the Tethys Ocean in the Late Triassic provided abundant suitable areas for phytoplankton to exploit, particularly as many marine organisms were still slowly recovering and diversifying after the end-Permian mass extinction (Chen and Benton, 2012). Furthermore, the Late Triassic dinoflagellate cyst suites of the North West Shelf are among the most diverse and abundant globally. They are equally or more species-rich than most coeval associations from Alaska, Arctic Canada and northern Europe, and therefore are critical to understanding the Late Triassic dinoflagellate evolutionary radiation (Mangerud et al., 2019).

The Carnian and Norian dinoflagellate cyst assemblages of the Northern Carnarvon Basin are typically associated with marine flooding surfaces that can also be recognised using ichnology and sedimentology on core material. However, these horizons are often difficult to recognise from their geophysical log profiles alone. Thus, in intervals lacking core, the palynomorph assemblages are often the best indicator of marine influence. Although the marine palynomorph associations are best represented in the outboard sections of the northwest prograding Mungaroo Delta, the larger flooding events such as the Hb4 main marine flooding event (TR26.5_MFS) are well-documented regionally, including in the more inboard predominantly delta plain settings. The Carnian assemblages, composed predominantly of early rhaetogonyaulacaceans, are typically relatively sparse and exhibit low diversities. However, the earliest Norian transgression (TR21.1_TS) was characterised by a substantial increase in dinoflagellate cyst diversity in the Northern Carnarvon Basin. This included distinctive new morphologies such as the proximochorate species, *Wanneria listeri*. Although fewer exploration wells have been drilled in the more outboard sectors of the basin, in 1988 the Ocean Drilling Program (ODP) drilled several wells on the Wombat Plateau that provided excellent sample material for the more strongly marine-influenced and distal successions, and their associated richer dinoflagellate cyst assemblages. Consequently, these samples were utilised extensively in this study.

The base of the Brigadier Formation is marked by the most significant regional marine transgression (TR30.1_TS) of the Upper Triassic, and covers the entire Northern Carnarvon Basin (Marshall and Lang, 2013). This transgression is expressed palynologically by a change from the dominantly terrestrial pollen-spore assemblages of the latest *M. crenulatus* Pollen-Spore Zone to the strongly marine-influenced assemblages of the overlying *A. reducta* Pollen-Spore Zone (Fig. 2; ref.). The latter zone is typified by increased proportions of acanthomorph (spine-bearing) acritarchs and dinoflagellate cysts, including frequent *Dapcodinium* and *Rhaetogonyaulax rhaetica* that are both cosmopolitan in the Rhaetian. The inboard successions are dominated by pro-delta, delta-front and lower delta plain siliciclastic facies, with increased volumes of pro-delta and shelfal siltstones and claystones to the north and west, in front of the prograding delta (Adamson et al., 2013; Marshall and Lang, 2013). The outboard successions are dominated by fine-grained carbonates, including reefal facies (Grain et al., 2013), with higher proportions of dinoflagellate cysts, particularly *Rhaetogonyaulax rhaetica*, than coeval inshore successions. A similar switch from *Dapcodinium priscum*-dominated to *Rhaetogonyaulax rhaetica*-dominated assemblages with increasingly open marine conditions was also noted by Courtinat and Piriou (2002) from the Rhaetian of southern France and by Lindström and Erlström (2006) when reviewing the distribution of these species in the Danish Basin. The former authors noted that *Dapcodinium priscum* occurs in both high and low energy environments, whilst both studies noted that this species was also tolerant of brackish and marginal marine environments. In the present study, this was observed not only for *Dapcodinium priscum* in the Rhaetian, but also for most of the dapcodinioid forms in the Norian of the Northern Carnarvon Basin. Although they occur in fully marine successions, these forms are also commonly the most abundant dinoflagellate cyst in the more marginal marine settings.

3. An overview of Triassic dinoflagellate cysts

The dinoflagellates are, together with the coccolithophores, among the most important groups of Mesozoic and Cenozoic marine phytoplankton. They are within the red lineage, which use chlorophyll *c* as their primary accessory pigment (Falkowski et al., 2004; Katz et al., 2007). Fossil dinoflagellates are predominantly the remains of hypnozygotes or resting cysts, and represent a somewhat selective fossil record from the Middle Triassic onwards (Evitt, 1985; MacRae et al., 1996; Riding and Lucas-Clark, 2016; Wiggan et al., 2018). These organic-walled resting cysts, typically 15–100 μm in maximum diameter, are formed of highly resistant biopolymers such as dinosporin and are readily preserved, often in very large numbers, in fine-grained sedimentary rocks. The cysts can be carefully isolated and concentrated using acid digestion of the major rock components, together with heavy liquid separation and oxidation to remove any extraneous materials (Riding and Kyffin-Hughes 2004). The relative abundance of dinoflagellate cysts in Late Triassic to Holocene fine-grained marine sediments and sedimentary rocks and their rapidly evolving morphologies, makes them an ideal group for use in biostratigraphy (Stover et al., 1996). The initial radiation of dinoflagellates in the Middle and Late Triassic is unlikely to represent their true inception, rather it was the start of their recognisable fossil record.

Biogeochemical evidence, including the isolation of dinosteranes and 4α-methyl-24-ethylcholestane (steroidal alkanes abundant in extant dinoflagellates), along with molecular clock data both suggest dinoflagellates originated in the earliest Cambrian or more likely the Neoproterozoic (Moldowan et al., 1996; Moldowan and Talyzina, 1998; Fensome et al., 1999; Medlin and Fensome, 2013). Furthermore, the strong correlation between the greater abundance of these dinosteranes and the higher acritarch diversities between the Proterozoic and Devonian, suggests that many acritarchs may have been cryptic dinoflagellates. The abundance of dinosteranes in the sedimentary record is considerably reduced in the Carboniferous to Early Triassic interval, prior to becoming common again from the Late Triassic onwards, thus mirroring the consistent and common presence of body fossils of dinoflagellate cysts since the Late Triassic (Moldowan et al., 1996). This strongly supports the contention that the major Late Triassic radiation of cyst-forming dinoflagellates reflects a real radiative event, rather than simply a change in preservational bias (Fensome et al., 1996). This major evolutionary event is well represented on the North West Shelf of Australia because cyst-forming dinoflagellates evolved to fill the available marine ecological niches following the break-up of Pangaea and the end Permian mass extinction.

The earliest records of unequivocal dinoflagellate cysts are the Middle Triassic (Ladinian–earliest Carnian) occurrences of *Sahulidinium ottii* in northern Australia (Stover and Helby, 1987). This is a monospecific and stratigraphically isolated association recorded between 3009 m and 3006 m in the Sahul Shoals-1 well drilled in the Ashmore Block in the Timor Sea between Timor and northern Australia (Jones and Nicoll, 1984). The evidence for the age of the *S. ottii* Range Zone of Helby et al. (1987a) is based on conodonts, molluscs and pollen-spores (Riding et al., 2010). *Sahulidinium ottii* has not been recorded extensively since its initial description with only a small number of unpublished industry occurrences (Jeff Goodall, personal communication). There was previously a substantial hiatus between the records of *Sahulidinium ottii* and the next youngest dinoflagellate cysts, an influx of dinoflagellate cysts in the late Carnian and Norian of Australia. However, the observations presented herein of rare to frequent, small rhaetogonyaulacacean forms in the early–middle Carnian of the Northern Carnarvon Basin partially fills this break in the Southern Hemisphere dinoflagellate cyst fossil record.

Intriguingly, the first records of fossilisable dinoflagellate cysts occur almost simultaneously with the rapid expansion of scleractinian corals during the Middle and Late Triassic. Photosymbiosis between zooxanthellae (endocellular dinoflagellates) and scleractinian corals is well known from modern reefal corals. This mutualistic relationship allows the zooxanthellae to photosynthesise in a sheltered position within shallow, clear, sunlit waters and to utilise the ammonium and other waste products of the coral host (Stanley, 2003; 3006). In return, the photosynthetic by-products such as glucoses and oxygen help the corals to increase their calcification rates and thus to be more effective reef builders (Frankowiak et al., 2016; Tornabene et al., 2017). This symbiotic relationship is considered crucial to the evolutionary successes and diversification of the scleractinian corals during the Mesozoic and Cenozoic. However, as the endocellular dinoflagellates are not preserved within the fossilised corals, the initial evolution of this symbiotic relationship has proven difficult to prove and to study. Previously, the large number of thecal plate series of *Symbiodinium*, the predominant modern zooxanthellate genus, was considered possible evidence that it has a shared ancestry with the multiserial, Late Triassic suessioid dinoflagellates (Bucefalo Palliani and Riding, 2003a). However, Saldarriaga et al. (2004) and Zhang et al. (2007) demonstrated that *Symbiodinium* is a highly derived genus, and is not closely related to *Suessia*. Subsequently, the recognition that the coralline microstructures, particularly macro- and microscopic growth bands, provide a diagnostic signature of symbiosis in scleractinian corals, together with greatly improved abilities to measure the proportions of $^{15}N/^{14}N$ preserved within the intracrystalline organic matter, and the distinctive $^{13}C/^{12}C$ and $^{18}O/^{16}O$ ratios, all strongly indicate that the Late Triassic scleractinian corals were indeed photosymbiotic (Frankowiak et al., 2016; Tornabene et al., 2017). This provides strong support to the hypothesis that the inception of cyst-forming dinoflagellates and Mesozoic scleractinian corals in the Ladinian and the subsequent diversification of both groups in the Carnian–Rhaetian are, at least, partly linked. Furthermore the two groups were severely affected by the end Triassic mass extinction, and both had prolonged recoveries during the Early Jurassic.

Following the isolated Ladinian–earliest Carnian record of *Sahulidinium ottii* in northern Australia, there are several records of rare, very low diversity Carnian dinoflagellate cyst assemblages from Alaska, the Canadian and Norwegian Arctic and Australia (Wiggins, 1973; Felix and Burbridge, 1978; Helby et al, 1987a; Helby et al, 1987b; Vigran et al., 2014). These assemblages substantially increased in abundance and diversity throughout the Norian and Rhaetian, and these increases appear to be broadly eustatically controlled and hence correlatable with global transgressive events (Lindström and Erlström, 2006; Mangerud et al., 2019). For example, the Triassic dinoflagellate cyst record in the UK is confined to the upper part of the Blue Anchor Formation and the Penarth Group, both of Rhaetian age (Warrington, 1981; Warrington and Whittaker, 1984; Warrington et al., 1994; 1995; Powell, 1992; Riding and Thomas, 1992). The uppermost Blue Anchor Formation, the Williton Member, represents a regional marine transgression (Warrington et al., 1980; Mayall, 1981). Similarly, the lowermost Rhaetian transgression in the Northern Carnarvon Basin resulted in the widespread distribution of lower delta plain, marginal and shallow marine environments, and this gave rise to increased abundances of dinoflagellate cysts, including a near-continuous Rhaetian record in the outboard regions of the basin.

Late Triassic dinoflagellate cysts also exhibited moderate levels of provincialism. Although the diverse Carnian and Norian suites from Alaska and Arctic Canada, typified by the cavate genus *Sverdrupiella*, together with *Hebecysta, Heibergella* and *Noricysta* (see Bujak and Fisher, 1976) share some similarities with those described from the Norian of the Barents Sea region by Vigran et al. (2014), the overall diversity and distribution of *Sverdrupiella* species is notably reduced in the latter area. These differences were even more pronounced in the Barents Sea assemblages of Norian age studied by Paterson and Mangerud (2015). The latter associations contained only rare and very low diversity assemblages of *Sverdrupiella*, thereby indicating that there may have been some provincialism in the Boreal Realm at this time, or differences in parameters such as salinity between the basins. The extreme rarity of *Sverdrupiella* records in Sub-Boreal Europe (Morbey and Dunay, 1978; Riding and Thomas, 1992) appears to be mostly facies related, as there was limited development of marine successions during the Norian. More recently, Bucefalo Palliani and Buratti (2006) documented 22 dinoflagellate cyst taxa from the Rhaetian of St Audrie's Bay in west Somerset, southwest England. These include all the genera in the *Sverdrupiella* Flora of Bujak and Fisher (1976) except *Hebecysta*. Bucefalo Palliani and Buratti (2006) proposed a migration event of *Sverdrupiella* and its relatives from Alaska and the Sverdrup Basin into northwest Europe at the Norian–Rhaetian transition. They considered that this floral shift resulted from the opening of extensive seaways during the breakup of Pangaea and the associated changes in oceanic circulation and the creation of suitable marine niches for colonisation. However, this is not fully supported by the earlier presence of *Sverdrupiella* and its relatives in the Tethys, such as the records from Iran (Aghanabati et al., 2002; 2004; Ghasemi-Nejad et al., 2004; 2008; Sabbaghiyan et al., 2015) and Australasia (e.g. Helby et al., 1987b; Helby and Wilson, 1988).

Although there are relatively few published records of *Sverdrupiella* from the Southern Hemisphere (Helby et al., 1987a; Helby and Wilson, 1988; Backhouse and Balme, 2002), they are apparently common in Indonesia, New Zealand and the North West Shelf of Australia (Helby et al., 1987b). Certainly, their Australian diversity is greater than the published record, particularly in the more open marine environments that existed in the northern Bonaparte Basin during the Late Triassic (Robin Helby, personal communication). *Sverdrupiella* was also infrequently recorded in the Northern Carnarvon Basin during this study, invariably in the more open marine successions or associated with the more substantial marine flooding events. Helby et al. (1987b) postulated that *Sverdrupiella* may have had a circum-Pacific (Panthalassan) distribution, and was essentially a warm water species, but again the recent records from the Barents Sea region and Iran do not support this. Further evidence of some Late Triassic provincialism are the relatively common occurrences of *Hebecysta balmei* and *Wanneria listeri* in Australia (Helby et al., 1987a; Helby et al., 1987b; Backhouse and Balme, 2002) and Indonesia (Below, 1987), and their absence or extreme rarity in the Northern Hemisphere. The only record of *Wanneria listeri* in Europe is from the upper Rhaetian Kössen Beds of the Northern Calcareous Alps of Austria (Feist-Burkhardt et al., 2002; Holstein, 2004) and there is a single questionable record of *Hebecysta* sp. cf. *H. balmei* from the Norian of northeastern Iran (Ghasemi-Nejad et al., 2008).

Perhaps more striking than the modest provincialism exhibited by Late Triassic dinoflagellate cysts are the broadly similar evolutionary trajectories in both hemispheres, incorporating the northern Boreal seas, and the Tethys and Panthalassic oceans. This phenomenon is described below:

1. Rhaetogonyaulacaceans are the earliest dinoflagellates cysts in both hemispheres. *Sahulidinium ottii* in the Ladinian–earliest Carnian in northern Australia (Stover and Helby, 1987), *Rhaetogonyaulax* spp. from the Carnian of Arctic Canada (Wiggins, 1973) and *Noricysta*, *Rhaetogonyaulax* and *Sverdrupiella* in the Barents Sea region (Vigran et al., 2014).
2. Similar medium to small, biconical to ovoidal *Rhaetogonyaulax* species (*Rhaetogonyaulax arctica*, *R. nagelii* and *R. wigginsii*) first appear in the Carnian in northern Australia (Helby et al., 1987a and herein), in the Canadian Arctic (Wiggins, 1973) and in the Alborz Mountains of Iran (Ghasemi-Nejad et al., 2004). These first appearances are followed by closely comparable acmes of these small rhaetogonyaulacaceans in the earliest Norian of the Barents Sea region (Vigran et al., 2014; Paterson and Mangerud, 2015) and the late Carnian–earliest Norian of the North West Shelf of Australia (Helby et al., 1987a and herein).
3. Suessioid genera with more than six latitudinal plate series first appeared in the late Carnian–Norian in both hemispheres (Helby et al., 1987a; Below, 1987; Suneby and Hills, 1988; Courtinat et al., 1998; Holstein, 2004).
4. *Sverdrupiella* are notably most prominent in the middle Norian in both hemispheres (Bujak and Fisher, 1976; Wiggins, 1978; Helby et al., 1987a; Helby et al., 1987b; Helby and Wilson, 1988; Backhouse and Balme, 2002) and are considerably rarer in the Rhaetian.
5. *Rhaetogonyaulax rhaetica* is also most abundant and widespread in the Rhaetian in both hemispheres. Similarly, *Suessia swabiana* is much more frequent in the Rhaetian of Australia and Europe, than in older successions.
6. *Beaumontella* first occurs in the Norian of Australia (herein) and Indonesia (Martini et al., 2004), before becoming more widespread in the Rhaetian in both Australia (Backhouse and Balme, 2002; herein) and Europe (Morbey, 1975; Morbey and Dunay, 1978; Riding and Thomas, 1992).

7. *Dapcodinium priscum* is widespread in the Rhaetian in Australia (Helby et al., 1987a; Helby et al., 1987b; Brenner, 1992; Burger, 1996; Backhouse and Balme, 2002), Europe (Morbey, 1975; Warrington, 1974, 1997; Riding and Thomas, 1992), Iran (Sabbaghiyan et al., 2015) and Libya (Brugmann and Visscher, 1988). It is one of the very few dinoflagellate cyst species to survive the end Triassic mass extinction and is also commonly recorded in the Early Jurassic in both hemispheres.

There are also a number of common morphologies shared by many Triassic dinoflagellate cyst genera; particularly striking is the greater number of plates and plate series than are exhibited by most Jurassic to Quaternary forms. The rhaetogonyaulacaceans all have at least one or more series of plates between the apical and precingular series, and between the antapical and postcingular series, with the suessioid subgroup commonly containing seven or more latitudinal plate series (Morbey, 1975; Below 1987). Although most Jurassic and Cretaceous dinoflagellate cyst genera bear fewer latitudinal plate series than many of their Triassic counterparts (Dörhöfer and Davies, 1980; Eaton, 1980), it is not accepted that the dinoflagellates evolved along a ‘plate reduction model’. Although this model is broadly sustained by the fossil record, it is not supported by the neontological evidence and cannot accommodate for the anterior insertion of the flagellae as a primitive feature (Bujak and Williams, 1981). Indeed, the plate reduction, plate increase and plate fragmentation models of Bujak and Williams (1981) are all considered overly simplistic by Fensome et al. (1999) and Medlin and Fensome (2013), who both noted that molecular evidence strongly suggests a substantially more complex evolutionary scenario. However, the overall stabilisation of dinoflagellate cyst tabulation by the Middle Jurassic is broadly accepted, as is the considerable experimentation in tabulation during the Late Triassic. This strongly supports the theory that the diversification of dinoflagellate cysts in the Carnian–Norian was a genuine evolutionary event, and not simply the result of preservational bias due to the evolution of resistant (i.e. geologically-preservable) resting cysts (Fensome et al., 1999).

This experimental phase is demonstrated by the large number of new morphological features and tabulation patterns throughout the Late Triassic. It is possible that the cingulum and sulcus first evolved during this radiation (Fensome et al., 1999), as both are somewhat vaguely discernible in many suessioids and in *Sahulidinium ottii*. By contrast, a prominent (high), well-defined cingulum is one of the characteristic features of both *Dapcodinium* and *Rhaetogonyaulax*, and is already clearly evident in the latter in the Carnian (Wiggins, 1973; Below, 1987; Helby et al., 1987a; Vigran et al. 2014). Indeed, the cingulum is broader in these taxa than in most younger dinoflagellate cyst genera.

A further notable feature of some Triassic dinoflagellate cysts is the relatively small precingular plates; this is particularly characteristic of *Dapcodinium* and *Rhaetogonyaulax* but is also displayed by some species of *Hebecysta* and *Heibergella*. Precingular plates in the Jurassic were significantly longer; the number of plates, particularly the number and size of anterior intercalary plates, and plate series were reduced in most genera. Further Late Triassic morphological experimentation was evident by the appearance in the fossil record at this time of chorate (e.g. *Beaumontella*), proximate (e.g. *Rhaetogonyaulax* and *Sahulidinium ottii*), and proximochorate (e.g. *Wanneria listeri*) forms. Although the majority of Late Triassic dinoflagellate cysts are proximate, and the chorate forms possessed only very simple processes, it is considered significant that all these three major morphological branches appeared during this early developmental phase.

There were also a broad array of archaeopyle types that evolved during the Late Triassic. The Ladinian–earliest Carnian species *Sahulidinium ottii* possessed a simple, apical archaeopyle, [tA], with an angular margin indicating the presence of gabled anterior intercalary plates. Later in the Carnian, *Rhaetogonyaulax* species appeared that shed these anterior intercalary plates as part of a compound archaeopyle. It is uncertain if the further loss of apical, preapical and postapical plates as a single opercular piece was an integral part of the archaeopyle of *Rhaetogonyaulax*, or if this was due to mechanical breakage. Further 'disintegration type' archaeopyles also appeared in the Late Triassic, such as those exhibited by *Suessia*, which initially involves the anterior intercalary and postapical plates, prior the further disintegrative loss of up to all of the climactal plates. Other suessioids had simple anterior archaeopyles involving all the climactal plates (e.g. *Wanneria*) or compound archaeopyles involving only the apical plates (e.g. *Beaumontella*). Compound apical-intercalary (AI) archaeopyles (e.g. *Dapcodinium* and *Noricysta*) also first appeared in the latest Carnian–Norian together with anterior intercalary (I–3I) archaeopyles (e.g. *Hebecysta* and *Heibergella*). Overall, 'disintegration type' archaeopyles dominated in the Late Triassic, but this did not endure into the Jurassic. With the emergence of gonyaulacaceans as the dominant dinoflagellate cyst types in the Jurassic, there was considerably less experimentation (Wiggan et al., 2017). The tabulation models and position of the archaeopyle stabilised, and the Triassic phase of major morphological innovation had ended.

There was a major turnover of pollen and spore assemblages at the Triassic–Jurassic boundary, together with the loss of most dinoflagellate cyst genera (van de Schootbrugge et al., 2007). This mass extinction event affected most marine and terrestrial organisms. It is widely linked to the emplacement of the Central Atlantic Magmatic Province (CAMP), and the associated release of huge volumes of carbon dioxide, sulphur dioxide and thermogenic methane (Palfy, 2003; Nomade et al., 2006; van de Schootbrugge and Wignall, 2015). Although the timing of the CAMP eruptions is debated, many authors now accept that this major volcanic episode was initiated prior to the Triassic–Jurassic transition, thus supporting the critical role of the CAMP eruptions to the end Triassic biotic crisis (Cirilli, 2010). In the Northern Carnarvon Basin, the only dinoflagellate cyst species to survive these adverse conditions and range into the Early Jurassic was *Dapcodinium priscum*. This was a probable generalist taxon, and also spanned the Triassic–Jurassic transition in the Northern Hemisphere (Woollam and Riding, 1983). The post extinction recovery of the dinoflagellate cysts was particularly prolonged and, in the Northern Carnarvon Basin, newly evolved taxa only began to appear in the latest Pliensbachian and early Toarcian (Riding et al., 2010).

4. Late Triassic palynozonations applicable to the Northern Carnarvon Basin

The Late Triassic pollen and spore floras of northern and northwestern Australia have a relatively long history of study, and there are several well-established zonal schemes (Balme, 1969; Helby, 1974; Dolby and Balme, 1976; Helby et al., 1987a; Backhouse and Balme, 2002; Dixon et al., 2012). These studies have provided the principal basis for the biostratigraphy of the predominantly terrestrial Late Triassic palynofloras of the North West Shelf. However, the sparser dinoflagellate cyst assemblages have played an increasingly important role in the stratigraphical subdivision of the Mungaroo and Brigadier formations, as the intermittent flooding surfaces provide excellent correlative bioevents. Although there have been fewer published taxonomic and zonal studies on Late Triassic marine palynomorphs from the North West Shelf, the original dinoflagellate cyst zonation of Helby et al. (1987a) provided an excellent template for all subsequent research. Further pivotal studies were undertaken by Backhouse and Balme (2002) and Backhouse et al. (2002), who synthesised the work of various industrial palynologists and formalised a Late Triassic zonal scheme that was specific to the Northern Carnarvon Basin. Both the pollen-spore and dinoflagellate cyst zones as outlined in Helby et al. (1987) and Backhouse and Balme (2002) are largely followed in the taxonomic section below (see ‘local stratigraphical range’ for each taxon in section 5). However, there are some notable differences at the subzonal level. The subzones used herein (Fig. 2) were developed by MGPalaeo with support from industry, particularly Chevron Australia Pty Ltd, Shell Development Australia and Woodside Energy Ltd. These subzones have been partially published by Dixon et al. (2012).

The ages of the Late Triassic dinoflagellate cyst zones were reviewed by Riding et al. (2010) and are largely followed herein (Fig. 2). However, the age of the upper boundaries of the *S. speciosus* Oppel Zone and the *R. wigginsii* Interval Zone have proved somewhat controversial. These units are pollen-spore and dinoflagellate cyst zones respectively (Dolby and Balme, 1976; Helby et al., 1987a). The tops of these zones were placed within the middle Norian by Riding et al. (2010) based on conodont evidence from the type section of the *R. wigginsii* Zone in the Shaul Shoals-1 well (Nicoll and Foster, 1994). However this considerable change from the original chronostratigraphical ties of Helby et al. (1987a), who placed these zonal tops at the Carnian–Norian boundary, have not been widely endorsed within the Australian petroleum industry. Furthermore, the last appearance datum of consistent *Camerosporites secatus* occurs at, or close to, the top of the *S. speciosus* Zone in many wells in the Northern Carnarvon Basin. This is a widely used marker for the latest Carnian globally (Cirilli, 2010). Thus, the age of the tops of the *S. speciosus* and *R. wigginsii* zones remains somewhat uncertain. These horizons may be either at the Carnian–Norian boundary (Helby et al., 1987a), or may be within the middle Norian (Nicoll and Foster, 1994; Riding et al., 2010).

5. Systematic palaeontology

In this, the principal, section of this contribution, one new dinoflagellate cyst genus, 14 new dinoflagellate cyst species and one new dinoflagellate cyst subspecies are formally described. Twenty further dinoflagellate cyst taxa are treated systematically. The type specimens of the new taxa are all housed in the collections of GSWA/UWA (TBC). Type specimens and selected representatives of the material studied herein are figured in Plates 1–X, and several line drawings are included (Figs 3–X). The taxonomic classification follows Fensome et al. (1993), except where subsequent emendations have been made.

?refer to appendix here?

Division DINOFLAGELLATA (Bütschli 1885) Fensome et al. 1993

Subdivision DINOKARYOTA Fensome et al. 1993

Class DINOPHYCEAE Pascher 1914

Subclass GYMNODINIPHYCIDAE Fensome et al. 1993

Order SUESSIALES Fensome et al. 1993

Family SUESSIACEAE Fensome et al. 1993

Genus *Beaumontella* Below 1987

1987 *Beaumontella* Below, p. 69–70.

Type: *Beaumontella langii* (Wall 1965) Below 1987

Remarks: *Beaumontella* is one of the oldest proximochorate to chorate dinoflagellate cyst genera, and one of the few taxa to survive the end-Triassic extinction event (van de Schootbrugge et al., 2007). It is therefore a critically important link between the multiserial (7–10 latitudinal plate series) Late Triassic dinoflagellate cysts and the dominant gonyaulacacean-peridinacean forms that followed in the Jurassic and Cretaceous (Evitt 1985). *Beaumontella* has a somewhat reduced number of latitudinal plate series (7), compared to earlier suessioid genera (7–10) and a compound apical archaeopyle. The compound nature of the archaeopyle is similar to *Suessia* but differs from all earlier suessioid dinoflagellate cysts in only losing the apical plates during excystment (there is no detachment of the anterior intercalary plates). Apical archaeopyles, together with single plate precingular archaeopyles, became the dominant archaeopyle type throughout the rest of the Mesozoic and Cenozoic. Below (1987) considered the tabulation formula 4–5n^2, 7–9n^1, 7–9c, 9–10n$_1$, 8–11n$_2$, 5–8n$_3$, 2–6n$_4$, ns to include two anterior latitudinal series, a cingular series and four posterior latitudinal series. This differs markedly from the more symmetrical arrangement of series immediately either side of the cingulum for *Suessia* and *Wanneria*. Both these genera commonly have four main plate series above and below the cingulum. Other than the archaeopyle margin, the plate boundaries are not expressed in *Beaumontella*. The plate-centred processes (i.e. one process per plate) are thus used to distinguish the number of plates and the plate series. It is hence extremely difficult to identify the cingular series, a phenomenon that Below (1987) noted when describing the offset nature of the ls and rs sulcal plates (or sulcal spines on *Beaumontella*) as the critical feature for determining the cingular plate series, particularly as he placed this series anterior of the more usual equatorial position. Therefore, there is a degree of uncertainty as to the order of the latitudinal plate series and the overall tabulation formula of *Beaumontella*.

***Beaumontella*? *caminuspina* (Wall 1965) Below 1987**

Plate 1, figs 11–20

1965 *Hystrichosphaeridium caminuspinum* Wall, p. 165, pl. 9, fig. 4.

1972 *Polysphaeridium*? *caminuspinum* (Wall 1965) Riley & Sarjeant, p. 3.

1975 *Cleistosphaeridium mojsisovicsii* Morbey, p. 40, pl. 15, figs 5a–b, 6–9.

1981 *Dapsilidinium*? *caminuspinum* (Wall 1965) Lentin & Williams, p. 69.

1987 *Beaumontella*? *caminuspina* (Wall 1965) Below, p. 70.

Dimensions (based on 12 measured specimens): overall length (including operculum and spines) 20 µm (26 µm) 30 µm; maximum width (excluding spines) 16 µm (18 µm) 23 µm; length of spines, 3–18 µm.

Local stratigraphical range: *Beaumontella*? *caminuspina* is frequent to very rare in the Rhaetian Brigadier Formation (Lower *R. rhaetica* Subzone to Lower *D. priscum* Subzone) in the Northern Carnarvon Basin.

Previous records: *Beaumontella*? *caminuspina* was first described from the Shales With Beef Member of the Charworth Mudstone Formation (lower Sinemurian *Caenisites turneri* ammonite zone) east of Lyme Regis, Dorset, southern England (Wall, 1965). Further European Rhaetian–Pliensbachian records include: Morbey (1975), Morbey and Dunay (1978; as *Cleistosphaeridium mojsisovicsii*), Courtinat et al. (1989), Riding and Thomas (1992), Heunisch (1996), Prauss (1996), Poulsen (1996), Warrington (1997), Cole and Harding (1998), Courtinat et al. (1998), Lindström (2002), van de Schootbrugge et al. (2007), Kürschner et al. (2007) and Bonis et al. (2009). There is also a single record from the Rhaetian of north-east Libya (Brugman and Visscher, 1988). Further to the various Australian occurrences noted herein, the only other Southern Hemisphere record of *Beaumontella*? *caminuspina* is from the Norian of Seram, Indonesia (Martini et al., 2004).

Remarks: there are no published images of *Beaumontella*? *caminuspina* that unequivocally confirm this species as a dinoflagellate cyst. It is very similar to some broadly coeval acritarchs (e.g. *Baltisphaeridium delicatum* Wall 1965). Although some images of *Beaumontella*? *caminuspina* appear to show the loss of the apical part of the cyst (e.g. Morbey 1975, pl. 15, fig. 7), there are none that demonstrate definite plate boundaries. Thus, Below (1987) only questionably transferred this species to *Beaumontella* when erecting this genus. However, Below (1987, pl. 5, figs 1–5, 11–16) illustrated a transitional form of *Beaumontella langii* with fewer projections, which lack cingular and secposterior appendages that may be acuminate or blunt-tipped, but not expanded, furcate or stellate as in *Beaumontella langii sensu stricto*. These transitional forms are hence very similar to *Beaumontella*? *caminuspina* (see Wall 1965, pl. 9, fig. 4; Morbey 1975, pl. 15, figs 5–9; and herein). However, because the transitional specimens of Below (1987) exhibit an apical archaeopyle and polygonal opercular pieces, they are clearly dinoflagellate cysts. Furthermore, if they are considered more closely comparable to *Beaumontella*? *caminuspina* than *Beaumontella langii*, they would confirm the dinoflagellate affinity of this species. None of the Australian specimens of *Beaumontella*?

caminuspina displayed definite plate margins although an apical aperture, whether an excystment structure or mechanical damage, is frequently noted (Plate 1, figs 13, 20).

Beaumontella langii (Wall 1965) Below 1987

Plate 1, figs 1–10

1965 *Hystrichosphaeridium langii* Wall, p. 165, pl. 6, figs 9–11, pl. 9, fig. 9.

1972 *Polysphaeridium*? *langii* (Wall 1965) Riley & Sarjeant, p. 3.

1975 *Hystrichodinium langii* Wall 1965 emend. Morbey, p. 41–42, pl. 15, figs 10–13.

1981 *Dapsilidinium*? *langii* (Wall 1965) Lentin & Williams, p. 69.

1987 *Beaumontella langii* (Wall 1965) Below, p. 70–71, pl. 4, figs 1–15, pl. 5, figs 1–5, 11–16.

Dimensions (based on 20 measured specimens): overall length (including operculum, excluding spines) 19 µm (25 µm) 27 µm; maximum width (excluding spines) 13 µm (17 µm) 22 µm; length of spines 3–11 µm.

Local stratigraphical range: *Beaumontella langii* is common to rare in the Rhaetian Brigadier Formation (Lower *R. rhaetica* Subzone to Lower *D. priscum* Subzone), and extremely rare in the upper Mungaroo Formation (the oldest occurrences are in the Hb4 marine event) in the Northern Carnarvon Basin. Although *Beaumontella langii* is not recorded in younger intervals herein, it has been noted, albeit very rarely, from the Hettangian–?Sinemurian of the North West Shelf (unpublished data) and a similar overall range is known from the Bonaparte Basin.

Previous records: *Beaumontella langii* was first described by Wall (1965) from the Blue Lias Formation (lowermost Hettangian *Psiloceras planorbis* ammonite zone) to the Black Ven Marl Member of the Charworth Mudstone Formation (uppermost Sinemurian

Echioceras raricostatum ammonite zone) of Lyme Regis, Dorset, southern England. Further Rhaetian–Pliensbachian European records include those of: Morbey (1975), Morbey and Dunay (1978), Below (1987), Riding and Thomas (1992), Heunisch (1996), Poulsen (1996), Warrington (1997), Cole and Harding (1998), Courtinat et al. (1998), Bucefalo Palliani and Riding (2002), Holstein (2004), Kürschner et al. (2007), van de Schootbrugge et al. (2007), and Bonis et al. (2009). This species has also been recorded from the Rhaetian of north-east Libya (Brugman and Visscher, 1988) and from Andhra Pradesh, India (Mehrotra et al., 2002).

Remarks: The Australian specimens of *Beaumontella langii* represent the first published records of this species from the Southern Hemisphere, and one of few occurrences outside Europe (see above). These specimens conform very closely with the original material of Wall (1965), and the later emended material of Below (1987). For example, the 40–54 plate-centred processes with furcate or stellate distal terminations, and the smooth to root-like connections to the main cyst body illustrated herein, are closely comparable in both number and form to those illustrated by Wall (1965) and Below (1987). The number of latitudinal plate series is not clearly observable on all the Australian specimens, but consistently appears to comprise seven plate series; this is also consistent with the tabulation formula of Below (1987).

Genus *Noricysta* Bujak & Fisher 1976 emend. Dörhöfer & Davies 1980

1976 *Noricysta* Bujak & Fisher, p. 58.

1980 *Noricysta* Bujak & Fisher 1976 emend. Dörhöfer & Davies, p. 23–24.

Type: *Noricysta fimbriata* Bujak & Fisher 1976 emend. Dörhöfer & Davies 1980

Noricysta spp.

Plate 11, figs 1–12

Dimensions (based on 20 measured specimens): overall length (including operculum) 31 µm (39 µm) 49 µm; maximum width 24 µm (35 µm) 53 µm; maximum separation of wall layers 1–4 µm.

Local stratigraphical range: rare components of the *R. wigginsii* Zone (late Carnian) to *H. balmei* Zone (middle–late Norian) in the Northern Carnarvon Basin. They are most prominent in the *W. listeri* Zone assemblages from ODP wells drilled on the Wombat Plateau. The Late Triassic successions in these outboard wells are considered to represent more marine palaeoenvironments than the mixed deltaic successions present in the majority of Northern Carnarvon Basin wells.

Remarks: There are probably several taxa grouped herein as *Noricysta* spp., of varying shape, size and surface ornament. They share several key generic features, principally a clear and substantial (1–4 µm) separation of the endophragm and periphragm, and combination AI archaeopyles. The majority of these specimens are very thin-walled (particularly the periphragm), commonly folded and with the tabulation poorly or unexpressed. The archaeopyle margin, opercular pieces and wide cingulum, are typically the only indication of tabulation. This is enough to indicate a likely suessioid plate arrangement including at least three epicystal plate series (n', 6+a, 8–10+''); the hypocystal tabulation is not evident on any of these Northern Carnarvon Basin specimens. The surface ornament varies from granulate to scabrate to rarely short baculae, with an alignment of the coarser sculptural elements (typically grana) bordering the cingulum.

Comparisons: the images of the type specimens of *Noricysta pannucea* Bujak & Fisher 1976 (pl. 9, figs 6–10) are not easy to interpret and may be similar to some of the Northern Carnarvon Basin specimens. However, the separation of wall layers is much reduced, and the minor antapical swellings that 'may reflect positions of two antapical horns' were not recorded on any of the specimens studied herein.

Genus *Suessia* Morbey 1975 emend. Below 1987

1975 *Suessia* Morbey, p. 38
1987 *Suessia* Morbey 1975 emend. Below, p. 87

Type: *Suessia swabiana* Morbey 1975 emend. Below 1987

Remarks: *Suessia* is distinguished from the closely related genus *Wanneria* in having fewer postapical plates (*sensu* Morbey, 1975) that do not form a complete ring series (see Fig. Xa, b). Below (1987) labelled these as intercalary plates but considered them to be the equivalent to the secanterior plates that he designated on *Wanneria*. Furthermore, *Suessia* has a compound disintegration type archaeopyle that may involve the loss of all the apical, postapical and anterior intercalary plates (*sensu* Morbey, 1975), though typically only a subset of the postapical and anterior intercalary plates are lost. By contrast, *Wanneria* loses a simple, single opercula piece involving all the climactal plates.

Archaeopyle formulae:

	Suessia	*Wanneria*
Morbey (1975)	t' + ta + tap	$(t' + ta + tap)_s$
Below (1987)	$tn^3 + tn^2 + tn^a$	$(tn^4 + tn^3 + tn^2)_s$

Although both genera develop spines and/or fine baculae along the sutures, *Suessia* is typically a proximate genus with only sparse or very short spines. This differs from the mostly proximochorate *Wanneria* which commonly exhibits numerous sutural spines that may be acuminate, bifurcate or blunt, with fused distal terminations and of varying length (0.5–6 µm). We agree with Below (1987) that the presence or absence of spines is not a key generic feature, however, the consistent development of conspicuous spines on *Wanneria* remains an important initial aid to the separation of *Suessia* and *Wanneria*.

However generic identification should be confirmed by the archaeopyle type and, where possible, the tabulation.

Suessia cristatus sp. nov.

Plate 4, figs 9–14; Text-fig. X

Derivation of name: From the Latin *cristatus,* after the prominent sutural crests.

Previous Australian usage:

Shublikodinium sp. 251 Helby 1976, p. 11, pl. 6, figs 6–8, 11–16.

Suessia sp. A Helby et al. 1987a, fig. 9Q.

Suessia sp. A Backhouse and Balme 2002, p. 113, pl. 15, figs 15–16.

Holotype and type locality: Plate 4, figs 13a, b; Geryon-2 well at 2965.3 m, Northern Carnarvon Basin; slide B, EF X53/4.

Paratype: Plate 4, fig. 14; Geryon-2 well at 2965.3 m, Northern Carnarvon Basin; slide A, EF Add here.

Description: small to medium, proximate to proximochorate, biconical, ovoidal or subspherical, acavate dinoflagellate cysts. The hypocyst is slightly larger than the epicyst. Only a single, moderately thin granulate, microreticulate or scabrate wall layer (autophragm) is present. The suessioid tabulation is expressed by low sutural ridges that are commonly surmounted by thin membranous crests, 2–5 μm high. These strongly perforate crests may be partly or strongly distally spinate, generally increase in prominence on the hypocyst and are absent apically. The folded and thin nature of these crests obscures the full tabulation, but this appears to involve seven to nine latitudinal plate series.

Tabulation formula (*sensu* Below 1987): xn^3, xn^2, xn^a, $8–12n^1$, 10+c, xn_1, xn_2, xn_3, $2–3n_4$

Tabulation formula (*sensu* Morbey 1975): x’, xa, xap, 8–12’’, 10+c, x’’’, xp, xpa, 2–3’’’’

It is possible that the study of further well-preserved specimens may reveal forms with more than 12 precingular plates. The archaeopyle is commonly formed through the loss of 3–8 anterior intercalary and postapical plates, though rarely, it may also involve the loss of all the climactal plates. The compound operculum forms via the loss of individual plates or occasionally a small cluster of two or three plates.

Dimensions (based on 10 measured specimens): overall length (including apical plates) 44 µm (48 µm) 52 µm; maximum width 36 µm (41 µm) 48 µm.

Local stratigraphical range: *Suessia cristatus* sp. nov. is rare to frequent in the Brigadier Formation (Rhaetian) of the Northern Carnarvon Basin. It is most persistent in the Lower *D. priscum* Subzone but is also irregularly recorded in the Upper *R. rhaetica* Subzone. Extremely rare specimens have been noted from the base of the *W. listeri* Zone (early Norian). *Suessia cristatus* sp. nov. has also been recorded from the *R. rhaetica* and *D. priscum* zones (Rhaetian) of the Bonaparte Basin.

Remarks: *Suessia swabiana* was originally described by Morbey (1975) as being ‘pseudocavate’ with a periphragm that may be partially detached apically or equatorially. Below (1987) confirmed the presence of an outer pellicle with a peridiniacean tabulation pattern, thus differing substantially from the tabulation of the inner cyst wall. However, most specimens of *Suessia swabiana* do not exhibit this outer wall layer. A definite outer pellicle layer is not apparent on *Suessia cristatus* sp. nov., but it may be present on exceptionally preserved specimens.

Comparison: The high, membranous, perforate crests of *Suessia cristatus* sp. nov. readily distinguish it from *Suessia swabiana*, although these species are probably very closely related. There are no substantial differences in archaeopyle development, size or tabulation. The distally connected sutural spines of *Wanneria misolensis* may be broadly similar to the perforate crests of some specimens of *Suessia cristatus* sp. nov. However, the irregular distal edge, often surmounted by short spines, and membranous nature of the crests on *Suessia cristatus* sp. nov. differ substantially from the well-ordered and thicker bifurcating spines of *Wanneria misolensis*. The generic differences are also significant; *Suessia cristatus* sp. nov. commonly loses only 3–8 anterior intercalary and postapical plates to form the archaeopyle, whereas *Wanneria misolensis* loses all the apical, anterior intercalary and postapical plates as a single opercular piece.

Suessia disintegra sp. nov.

Plate 2, figs 6–14; Plate 3, figs 1–12; Plate 5, figs 12–14; Figure X

Derivation of name: after the characteristic disintegration type archaeopyle.

Previous Australian usage:

cf. M.P. 457 Helby 1976, p. 15, pl. 4, figs 8–10, 13, 14.

cf. *Chytroeisphaeridia* sp. A Helby 1976, p. 19, pl. 8, figs 13, 14.

cf. *Chytroeisphaeridia* sp. B Helby 1976, p. 19, 20, pl. 8, fig. 15.

Holotype and type locality: Plate 3, figs 12a, b; ODP well 760A at 241.0 m, Northern Carnarvon Basin; slide 1761652GCR, EF Need to get.

Paratype: Plate 3, fig. 8; ODP well 760B at 303.4 m, Northern Carnarvon Basin; slide 1761692GCR, EF V52/1.

Description: small to medium, proximate, broadly ellipsoidal or subspherical dinoflagellate cysts with approximately equant epicysts and hypocysts. A thin, smooth to scabrate, membranous periphragm separated by 1–4 μm from the thicker endophragm, is only rarely preserved. In most specimens the periphragm is either not preserved or is too closely appressed to the microgranulate, scabrate or smooth endophragm to be observable.

The endophragm varies from moderately rigid (on thicker walled specimens) to comprehensively folded (often with sub-concentric folds around the margin of the cyst). Other than the archaeopyle margins and the opercular plates, the suessioid tabulation is unexpressed or is indicated only by thin, very low sutural ridges. Thus, the full tabulation formula is unknown, but involves at least nine latitudinal series and appears in full agreement with typical Suessiacean formula.

Tabulation formula (*sensu* Below 1987): 1–?2n^{3}, ?4–6n^{2}, 6–8n^{a}, 12–14n^{1}, 12–15c, 12±n$_{1}$, 10+n$_{2}$, ?6–8n$_{3}$, ?2–3n$_{4}$

Tabulation formula (*sensu* Morbey 1975): 1–?2’, ?4–6a, 6–8ap, 12–14’’, 12–15c, 12+’’’, 10+p, ?6–8pa, ?2–3’’’’

Examination of further well-preserved material may reveal specimens with a greater number of plates for each latitudinal series than is noted herein. The disintegration archaeopyle is one of the most distinctive features of this species, and commonly forms by the loss of a small number of apical, anterior intercalary and postapical plates, though it may progress to the loss of all the climactal plates. The operculum is compound. Many specimens contain a sub-rounded red-brown accumulation body, 5–13 µm in diameter, close to the cingulum.

Dimensions (based on 25 measured specimens): overall length (including apical plates) 27 µm (40 µm) 56 µm; maximum width 24 µm (34 µm) 43 µm.

Local stratigraphical range: *Suessia disintegra* sp. nov. is rare in the *W. listeri*, *H. balmei* and *R. rhaetica* zones (Norian–Rhaetian) of the Northern Carnarvon Basin. A minor acme was noted at the base of the *W. listeri* Zone (Norian), further offshore in the ODP wells drilled on the Wombat Plateau. In the Bonaparte Basin, similar forms to *Suessia disintegra* sp. nov. are also present in the *W. listeri* Zone.

Remarks: The darker and thicker-walled specimens of *Suessia disintegra* sp. nov. are slightly larger than their thinner-walled, commonly folded counterparts (8 µm longer and 5 µm wider on average, although there is overlap). The former group is commoner in the *R. rhaetica* Zone and the latter in the *H. balmei* and *W. listeri* zones. However, because there is substantial overlap in the sizes, and there are no major morphological differences, these two forms are considered to be within the limits of intraspecific variation.

Comparison: *Suessia disintegra* sp. nov. is marginally smaller than *Suessia swabiana* and is readily distinguished in lacking the well-developed sutural ridges in the latter, often surmounted by grana or small spines. Both taxa have similar archaeopyle types (typically losing a subset of the anterior intercalary and postapical plates), however the apical plates are more regularly detached during excystment in *Suessia disintegra* sp. nov. than by *Suessia swabiana*. *Suessia disintegra* sp. nov. is larger than *Suessia*? *scabrata* sp. nov., with a more complete expression of the tabulation. It differs from all species of *Wanneria* by having a compound disintegration style archaeopyle that commonly involves only a small subset of the apical, anterior intercalary and postapical plates, rather than a simple opercular piece formed from the loss of all the climactal plates.

***Suessia*? *scabrata* sp. nov.**

Plate 2, figs 1–5

Derivation of name: from the Latin *scabrata*, after the rough or scabrate endophragm.

Holotype and type locality: Plate 2, fig. 4; Geryon-2 well at 3017.45 m, Northern Carnarvon Basin; slide 2, EF T40/2.

Paratype: Plate 2, fig. 3; Geryon-2 well at 3046.55 m; Northern Carnarvon Basin; slide 1, EF Need to get.

Description: small, acavate, proximate, subspherical dinoflagellate cysts with approximately equant epicysts and hypocysts. The autophragm is microgranulate to scabrate and commonly folded. The suessioid tabulation is only partially expressed around the archaeopyle margins and the number of latitudinal plate series is not known (though it appears to have at least six plate series and likely more). The archaeopyle is formed by the progressive loss of the apical and intercalary plates (probably involving the anterior intercalary and postapical plates). The operculum is compound. A small, subcircular, red-brown accumulation body (4–6 µm) is occasionally present close to the cingulum.

Dimensions (based on 10 measured specimens): overall length (excluding apical plates) 27 µm (29 µm) 30 µm; maximum width 26 µm (32 µm) 36 µm.

Local stratigraphical range: *Suessia*? *scabrata* sp. nov. is a very rare component of the *R. wigginsii* to *R. rhaetica* zones (Norian–Rhaetian) in the Northern Carnarvon Basin.

Remarks: Morbey (1975) and Below (1987) both recorded a thin outer wall layer on well preserved specimens of *Suessia swabiana*. Thus, the single wall layer observed herein for *Suessia*? *scabrata* sp. nov. may represent closely appressed periphragm and endophragm, or the former is not preserved in the material studied herein. The suessioid tabulation formula is only expressed faintly, therefore a questionable generic assignment is made. However, the lack of spinose elements, and the compound rather than simple operculum, is strongly suggestive of *Suessia* rather than *Wanneria*.

Comparison: *Suessia*? *scabrata* sp. nov. is, on average, substantially smaller than *Suessia disintegra* sp. nov., has more prominent surface ornament and typically lacks any sutural features other than the archaeopyle margin. It could possibly be considered an extreme end member of *Suessia disintegra* sp. nov., but as it is considerably different to the larger or more strongly tabulate forms of that taxon it is considered separate herein.

***Suessia swabiana* Morbey 1975 emend. Below 1987**

Plate 4, figs 1–8

1975 *Suessia swabiana* Morbey, p. 39–40, pl. 14, figs 5–11, pl. 17, figs 4–9, text-figs 12–15.

1987 *Suessia swabiana* Morbey 1975 emend. Below, p. 94–96, pl. 6, figs 1–15, pl. 7, figs 1–19, pl. 8, figs 1–21, text-figs 49–59.

Dimensions (based on 10 measured specimens): overall length (including apical plates) 28 µm (39 µm) 50 µm; maximum width 29 µm (37 µm) 50 µm.

Local stratigraphical range: *Suessia swabiana* is a rare to frequent component of the Lower *D. priscum* Subzone and the Upper *R. rhaetica* Subzone. It is also very rarely recorded in the *R. wigginsii, W. listeri* and *H. balmei* zones, however, it is possible that some of these older records relate to non-spinose or short-spined, unexcysted specimens of *Wanneria*. With the operculum still attached, short-spined *Wanneria* specimens may be very similar to *Suessia swabiana*.

Previous records: *Suessia swabiana* was first described from the lower part of the Rhaetian Swabian Facies in the Kendelbachgraben of Austria (Morbey, 1975). It is widely recorded from Rhaetian of Europe (e.g. Schuurmann, 1977; Morbey and Dunay, 1978; Warrington, 1978; Visscher and Brugman, 1981; Courtinat et al., 1998; Holstein, 2004; Bucefalo Palliani and Buratti, 2006; Lindström and Erlström, 2006; and Bonis et al., 2009), along with very rare Carnian and Norian records (Courtinat et al., 1998, and Holstein, 2004, respectively). However, *Suessia swabiana* is largely absent from the Arctic other than a single Alaskan report (Witmer et al., 1981) and records of *Suessia* sp. cf. *S. swabiana* from the Norian and latest Rhaetian–Hettangian of the Sverdrup Basin (Suneby and Hills, 1988; and Ford, 1979, respectively). This implies that *Suessia swabiana* may have been thermophilic to some extent. This is somewhat corroborated by the rare records from the Norian–Rhaetian and Rhaetian of Israel (Eshet, 1990) and Libya (Brugman and Visscher, 1988), respectively. In addition to the records from Australia (Helby et al., 1987a; Burger, 1996; Backhouse and Balme, 2002; Backhouse et al., 2002), the only other published Southern Hemisphere records are from Below (1987), who illustrated *Suessia swabiana* from the Norian of Misool Island, Raja Ampat archipelago, Indonesia.

Remarks: none of the Australian specimens of *Suessia swabiana* exhibit the thin outer wall layer recorded on a few well-preserved specimens by Morbey (1975) and Below (1987). However, they are identical in most other respects. These comprise: the number of latitudinal plate series; the number of plates per series is closely comparable; the compound operculum involving apical, anterior intercalary and postapical plates; and the low, smooth to granulate or occasionally spinose sutural ridges.

Genus *Wanneria* Below 1987

1987 *Wanneria* Below, p. 72–73, 76–77.

Type: *Wanneria misolensis* Below 1987

Remarks: The strongly spinose autophragm of *Wanneria* separates it from most *Suessia*. However, the degree of spinose ornament on *Suessia* is more variable than commonly illustrated and understood. Hence an appreciation of the tabulation, and particularly the operculum (compound versus simple), is critical for the identification of some of the shorter-spined forms of both these genera. Indeed, some suessioid dinoflagellate cysts with rare to frequent short spines may not be readily separated without observing the entire epicystal tabulation or the opercular pieces. Further discussion of the differences between these two genera are given under *Suessia* herein.

Wanneria backhousei sp. nov.

Plate 5, figs 2–11; Figures X

Derivation of name: after the eminent Australian palynologist John Backhouse, of Perth, Western Australia, who first recognised this species.

Previous Australian usage:

Wanneria sp. A Backhouse & Balme 2002, p. 115, pl. 14, figs 6–20.

Holotype and type locality: Plate 5, figs 8a, b; Dockrell-2 well at 2996.59 m, Northern Carnarvon Basin; slide 2, EF M38/1.

Paratype: Plate 5, fig. 4; Dockrell-2 well at 2996.59 m, Northern Carnarvon Basin; slide 2, EF E44/0.

Description: small to medium, proximate to proximochorate, subspherical, ovoidal or ellipsoidal dinoflagellate cysts with approximately equant epicysts and hypocysts. The autophragm is scabrate, microgranulate or microreticulate with very low ridges delimiting most of the polygonal plates. These low, thin sutural ridges are sparsely surmounted by variably elongate spines (1–5 µm) that are sharply acuminate, with blunt rounded tips or have thin sinuous tips. The spinose ornament is both gonal and intergonal, and is consistently of low density, but this is somewhat variable. The spines may be sparsely distributed on the sutures, they may be exclusively gonal, or there may be significant areas which are entirely devoid of spines. These relatively smooth/sparse areas are largely restricted to the epicyst and the ventral surface, and at least a few postcingular and antapical spines are always present. The tabulation is suessioid with nine latitudinal series (Fig. 6B). The cingulum is moderately laevorotatory, and is offset at the sulcus by up to half the height of a cingular plate. The archaeopyle is formed by the loss a simple opercular piece comprising all the climactal plates [(t’ + ta + tap)$_s$] (Fig. 6A). The tabulation formulae are:

Sensu Morbey (1975): 1–2’, 4–6a, 8–9+ap, 11–15’’, 10–14+c, 10–12+’’’, 9+p, 5–6pa, 1+’’’’

Sensu Below (1987): 1–2n^4, 4–6n^3, 8–9+n^2, 11–15n^1, 10–14+c, 10–12+n_1, 9+n_2, 5–6n_3, 1+n_4

Dimensions (based on 20 measured specimens): overall length (excluding apical plates) 35 µm (45 µm) 52 µm; maximum width 36 µm (43 µm) 51 µm.

Local stratigraphical range: *Wanneria backhousei* sp. nov. is very rare to frequent in the *R. rhaetica* Zone (Rhaetian) of the Northern Carnarvon Basin. It is largely restricted to the upper half of the Upper *R. rhaetica* Subzone, but there are occasional reports ranging into the Lower *R. rhaetica* Subzone. Some of the latter may be due to caving in uncased open holed wells.

Remarks: Backhouse and Balme (2002) considered that their *Wanneria* sp. A (now *Wanneria backhousei* sp. nov.) warranted specific status. However, these authors also speculated that it may represent a facies-controlled morphotype of *Wanneria listeri*. Rare intermediate forms were also noted herein, but as most of the Norian and Rhaetian *Wanneria* species grade into each other to some degree, we contend that this taxon should be formalised. Further examination of well-preserved material may also reveal specimens with a larger number of plates for each latitudinal series than are noted herein.

Comparisons: *Wanneria backhousei* sp. nov. differs from *Wanneria listeri* in having a relatively low number of spines, by the weakly expressed tabulation and, in some associations, the more elongate ambitus.

Wanneria hispida sp. nov.

Plate 6, figs 1–4

Derivation of name: From the Latin *hispida,* after the hirsute appearance of this species.

Holotype and type locality: Plate 6, fig. 3; Geryon-2 well at 3000.85 m, Northern Carnarvon Basin; slide 3, EF E53/0.

Paratype: Plate 6, fig. 2; Geryon-2 well at 3134.3 m, Northern Carnarvon Basin; slide 1, EF G34/3.

Description: small, proximate to proximochorate, subspherical dinoflagellate cysts with approximately equant epicysts and hypocysts. The autophragm is scabrate to granulate, with low ridges delimiting an apparently standard suessioid tabulation. These sutural ridges are surmounted by a dense covering of short (0.5–3 µm) spines that may be strongly acuminate or have blunt or rounded tips. The densely granulate autophragm and the abundant spines obscure the full tabulation pattern. However, there are at least seven, and possibly up to nine, latitudinal series. The archaeopyle is formed by the loss of a single opercular piece comprising all the apical plates and the adjacent latitudinal series. The latter may include both anterior intercalary and postapical plates.

Dimensions (based on 10 measured specimens): overall length (excluding apical plates) 25 µm (29 µm) 33 µm; maximum width 33 µm (39 µm) 47 µm.

Local stratigraphical range: *Wanneria hispida* sp. nov. is rare throughout the latest Carian, Norian and Rhaetian (*R. wigginsii*, *W. listeri*, *H. balmei* and *R. rhaetica* zones) of the Northern Carnarvon Basin.

Comparison: *Wanneria hispida* sp. nov. is substantially smaller than most specimens of *Wanneria listeri*. Furthermore, the former has a denser covering of spines and a rougher, granulate autophragm than the latter. Even the smaller specimens of *Wanneria listeri* normally retain the regular rows of sutural spines and the well-defined suessioid tabulation, although there is some intergradation between the two species. The dense spines, strongly granulate autophragm and simple operculum also distinguish *Wanneria hispida* from *Suessia scabrata,* which is similar in size.

Wanneria listeri **(Stover & Helby 1987) Below 1987**

Plate 5, fig. 1; Plate 6, figs 5–9, 12–14

1987 *Suessia listeri* Stover & Helby, p. 121–122, 124; figs 21A–C; figs 22A–D, figs 23A–L.

1987 *Wanneria listeri* (Stover & Helby 1987) Below, p. 77, 80; pl. 1, figs 1–14; text-figs 2, 11–13, 36h–s, 39–48.

Dimensions (based on 10 measured specimens): overall length (excluding apical plates) 24 µm (42 µm) 64 µm; maximum width 33 µm (46 µm) 68 µm.

Local stratigraphical range: *Wanneria listeri* is rare to abundant in the *W. listeri*, *H. balmei* and *R. rhaetica* zones (Norian–Rhaetian) in the Northern Carnarvon Basin. This species is especially prominent in the Brigadier Formation, with isolated acmes in the Upper *R. rhaetica* Subzone and upper half of the Lower *R. rhaetica* Subzone. Very rare specimens recorded from the Lower *D. priscum* Zone may be reworked.

Previous records: *Wanneria listeri* was first described from the Norian–Rhaetian of the Northern Carnarvon Basin, Australia (Stover and Helby, 1987; as *Suessia listeri*). It is only widely documented in the Southern Hemisphere with further published records from Australia (Brenner, 1992; Burger, 1994, 1996; Backhouse and Balme, 2002; Backhouse et al., 2002) and the Norian of Buru, Maluku Islands and Misool, Raja Ampat archipelago, Indonesia (Below 1987). The only Northern Hemisphere records are from the upper Rhaetian Kössen Beds of the Northern Calcareous Alps of Austria (Feist-Burkhardt et al., 2002; and Holstein, 2004).

Remarks: relatively few assemblages examined herein include specimens of *Wanneria listeri* as large, and with such long spines, as the type material of Stover and Helby (1987). Many specimens were noted that were up to 50% smaller, and with very short (0.5–2 µm) spines or sutural grana or verrucae (cf. *Wanneria* sp. B of Backhouse & Balme, 2002, p. 115, pl. 15, figs 10–12). Because there is a complete and gradual gradation between the latter forms to the larger and markedly spinose forms, and as the overall morphology (archaeopyle type, ornamentation and tabulation) is closely comparable, members of this complex are all retained in *Wanneria listeri*.

Comparison: rare specimens of *Wanneria listeri* with strongly recurved spines, forming incomplete arches, were also noted. These forms are superficially very similar to *Wanneria misolensis,* and examination at high magnification is required to definitively separate the species. Specifically, this is to confirm that the spines are not bifurcate with fused distal terminations linking adjacent spines.

Wanneria misolensis Below 1987

Plate 6, figs 10, 11

1987 *Wanneria misolensis* Below, p. 80, 86; pl. 1, figs 15–18; pl. 2, figs 1–10, 14–15; pl. 3, figs 2–10, 12–13, 15; text-figs 36a–g, 37a–h, 39–47.

Dimensions (based on 10 measured specimens): overall length (excluding apical plates) 30 µm (36 µm) 41 µm; maximum width 38 µm (44 µm) 48 µm.

Local stratigraphical range: *Wanneria misolensis* is rare in the Lower *R. rhaetica* Subzone (Rhaetian), with a minor abundance peak in the uppermost part of this subzone in the Northern Carnarvon Basin. Extremely rare specimens were also noted from the Upper

R. rhaetica Subzone (Rhaetian) and the from the Hb4 Event and younger part of the *H. balmei* Zone (Norian).

Previous records: *Wanneria misolensis* is only known from the Southern Hemisphere with very few published records. These are the type material from the Norian of the Misool Islands, Raja Ampat archipelago, Indonesia (Below, 1987), and records from the Rhaetian of Australia (Burger, 1996; Backhouse and Balme, 2002; Backhouse et al., 2002).

Remarks: Below (1987) noted that the spines on some specimens of *Wanneria misolensis* are reduced. This causes the distal terminations of adjacent spine bifurcations to be separate, thereby not forming the diagnostic 'perforate sutural fence' that is normally distinctive of *Wanneria misolensis*. The forms with non-fused adjacent spines are thus extremely similar to some specimens of *Wanneria listeri*, particularly those with bent or curved spines. Herein, we only positively identified specimens with fused spinose tips, i.e. those with a 'perforate sutural fence', as *Wanneria misolensis*.

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order GONYAULACALES Taylor 1980

Suborder RHAETOGONYAULACINEAE Norris 1978

Family RHAETOGONYAULACACEAE Norris 1978 ex Norris in Fensome et al. 1998 nom. cons. prop.

Genus *Dapcodinium* Evitt 1961 emend. Below 1987

1961 *Dapcodinium* Evitt, p. 996.

1980 *Dapcodinium* Evitt 1961 emend. Dörhöfer & Davies, p. 23.

1987 *Dapcodinium* Evitt 1961 emend. Below, p. 141.

Type: *Dapcodinium priscum* Evitt 1961 emend. Below 1987

Remarks: *Dapcodinium* is arguably better known from the Lower Jurassic than the Triassic, and was first described from upper Hettangian (*Schlotheimia angulata* ammonite zone) strata in Jutland, Denmark (Evitt, 1961). The type, *Dapcodinium priscum*, is abundant in a single core sample, thereby allowing a comprehensive evaluation of the tabulation. Evitt (1961, p. 999) also astutely considered that the 'relatively advanced morphology of *Dapcodinium* implies an important pre-Jurassic history' for dinoflagellate cysts. The detailed scanning electron microscope (SEM) study of *Dapcodinium* by Below (1987) allowed for minor reassessment of the tabulation as: pr, 5', 4–6a, 7'', 8c, 6–8''', 3'''', ns. Furthermore, Below (1987) determined that the archaeopyle is compound; it is an AI excystment aperture, commonly formed through the loss of some or all of the apical and anterior intercalary plates. The 3', 4', 2a and 3a plates are commonly lost, but the 1', 2', 1a, and 4a plates may also be involved. In the Australian *Dapcodinium* assemblages, approximately 10% of the specimens are cavate, with clear separation of endophragm and periphragm. The cavation style is somewhat varied, with bicavate, circumcavate and epicavate individuals present (Plates 7–9). This has been observed previously; the specimen of *Dapcodinium priscum* from the Rhaetian of southern England figured by Riding (1984a, pl. 1, fig. 3) appears to be epicavate. A cavate cyst organisation is allowed in the emended diagnosis of *Dapcodinium* by Below (1987), but this was not further discussed by this author. Evitt (1961) noted that the cyst walls are especially thin in the apical region. This phenomenon was not mentioned by Below (1987), but it is apparent in most of the Australian species, particularly ?*Dapcodinium ovale* and *Dapcodinium prolongata* sp. nov. The relatively thin endophragm and periphragm (or autophragm) imparts a somewhat translucent appearance to the epicyst. This is the case in unexcysted specimens, therefore this wall thinning is a primary feature and is not solely due to the loss of the mediodorsal opercular plates. *Dapcodinium* is known to be useful in palaeoecology; representatives are most abundant in nearshore and restricted marine settings (Coutinat and Piriou 2002). This ecological preference is consistent with their common occurrence in brackish and marginal marine depositional environments in the Mungaroo Delta of the Northern Carnarvon Basin.

***Dapcodinium brenneri* sp. nov.**

Plate 9, figs 1–16

Derivation of name: this species is named after the German palynologist Wolfram Brenner, who first illustrated this form as *Noricysta*? sp.

Previous Australian usage:

Noricysta? sp. Brenner 1992, p. 423, pl. 1, figs 1–4.

Noricysta? sp. A Backhouse and Balme 2002, p. 109, pl. 13, figs 17–20.

Holotype and type locality: Plate 9, fig. 10; ODP well 760A at 241.0 m, Northern Carnarvon Basin; slide 1761652GCR, EF N20/4.

Paratype: Plate 9, fig. 12; ODP well 760A at 241.0 m, Northern Carnarvon Basin; slide 1761652GCR, EF C17/0.

Description: small, proximate, acavate to weakly cavate, ovoidal to sub-rhomboidal dinoflagellate cysts with a constricted apex and a comprehensively folded periphragm. The endophragm and periphragm are typically closely appressed although minor wall separation of 1–3 µm is occasionally evident antapically, or around the margins of the archaeopyle. The periphragm is smooth to scabrate with abundant, irregular, fine folds. Both wall layers commonly thin towards the apex. The pervasive folds mask any indications of tabulation other than the low sutural ridges bordering the broad cingulum. The cingulum profile varies from concave to straight-sided to rarely convex. The full tabulation formula is unknown. The precise nature of the archaeopyle is also not known, but it is formed through the loss of both apical and anterior intercalary plates. A dark brown accumulation body is commonly present close to the cingulum.

Dimensions (based on 16 measured specimens): overall length 28 µm (34 µm) 42 µm; maximum width 25 µm (29 µm) 37 µm.

Local stratigraphical range: *Dapcodinium brenneri* sp. nov. is typically very rare in the *R. wigginsii* to *R. rhaetica* zones (late Carnian to Rhaetian). However, it may be more frequent in the uppermost *R. wigginsii* to lowermost *W. listeri* zones, particularly in distal parts of the basin such as the ODP wells drilled on the Wombat Plateau.

Remarks: *Dapcodinium brenneri* sp. nov. was previously questionably attributed to *Noricysta* by Brenner (1992) and Backhouse and Balme (2002) due to its partially cavate cyst organisation. However, this form exhibits several features typical of *Dapcodinium*. These include a combination archaeopyle involving the loss of both apical and anterior intercalary plates and a broad, albeit poorly defined, cingulum. The extensive folding or wrinkled appearance of the periphragm, together with both wall layers commonly thinning apically, are also common features of *Dapcodinium*.

Comparisons: *Dapcodinium brenneri* sp. nov. is most similar to *Dapcodinium tabulodiniopsis* sp. nov. Both species are broadly similar in size and shape, and may develop minor cavation. However, *Dapcodinium brenneri* sp. nov. is readily differentiated by the dense, thin, irregular folds on the periphragm, the lack of well-defined tabulation and the narrower apical region. Most other species of *Dapcodinium* have a much more well-defined ambitus, as opposed to the somewhat irregular and ‘shrivelled’ margin of *Dapcodinium brenneri* sp. nov., and they also lack pervasive periphragmal folds and a substantially constricted apex.

?*Dapcodinium ovale* Below 1987

Plate 7, figs 16–25; Figure X

1987 *Dapcodinium ovale* Below 1987, p. 141–144; pl. 24, figs 1–15; pl. 25, figs 1–7, 11, 12, 14; text-figs 72a–f, 73a–h.

Description: small, proximate, acavate or cavate, spheroidal to ovoidal dinoflagellate cysts with rounded poles and approximately equant epicysts and hypocysts. The surface ornament varies from scabrate to granulate, with the grana commonly coalescing to form minute, longitudinal rugulae which impart a finely wrinkled appearance. The alignment of the grana, or very low ridges, indicate an incomplete tabulation of ?4', 4+a, 7'', nc, 6+''', n'''', ns. The broad (3–6 µm) cingulum is largely undivided, with only rare hints of internal tabulation and typically is not indented. The compound archaeopyle commonly only includes dorsal plates 3', 4', 3a, and 4a.

Dimensions (based on 20 measured specimens): overall length (excluding the apical plates) 26 µm (31 µm) 35 µm; maximum width 24 µm (28 µm) 32 µm.

Local stratigraphical range: ?*Dapcodinium ovale* is rare in the *W. listeri*, *H. balmei* and *R. rhaetica* zones (Norian–Rhaetian) of the Northern Carnarvon Basin. It is most prominent in the *H. balmei* Zone in the more open marine Late Triassic successions encountered in the ODP wells drilled on the Wombat Plateau.

Previous records: The reports of *Dapcodinium ovale sensu stricto* are all from the Lower and Middle Jurassic of the Northern Hemisphere. Below (1987) described the species from the Pliensbachian to Bajocian of Germany, Poland and Spitsbergen. Further reports include those of questionable specimens by Prauss (1989) from the Toarcian to Aalenian of northwest Germany, and Smelror (1993) from the Toarcian to Bajocian of the Barents Sea region.

Remarks: The incomplete tabulation of ?4’, 4+a, 7’’, nc, 6+’’’, n’’’’, ns observed herein for ?*Dapcodinium ovale* appears to be broadly consistent with that described by Below (1987), which was PR, 5’, 6a, 7’’, 8c, 7’’’, 3’’’’, as, y, z, ps. The combination, apical and anterior intercalary, archaeopyle is formed by the compound loss of plates. Normally this includes only the dorsal plates, i.e. 3’, 4’, 3a, and 4a (Fig. 4c), but this is not as unequivocally demonstrated as in the type material (Below 1987, pl. 24, figs 1–15). Below (1987) also noted that a small number of specimens lost their PR, 2’, 1a, and 2a plates during excystment. The Australian specimens of ?*Dapcodinium ovale* herein are considerably older than the Pliensbachian to Bajocian reports from the Arctic and Europe listed above. However, other than the marginally smaller size and greater variability in shape (i.e. spherical to ovoidal, rather than strictly ovoidal), the Australian forms are very closely comparable to the type material. The somewhat ‘hooded’ appearance suggested by the frequent loss of only the mediodorsal 3’, 4’, 3a and 4a plates is shared by all the illustrated records, as is the longitudinal alignment of fine grana that commonly gives the cyst surface a very finely wrinkled appearance. Unfortunately, it is difficult to compare the Australian specimens, which were studied with a transmitted light microscope, with the SEM images of the type material (Below, 1987). Thus, it is not clear if the much thinner epicystal plates, a very characteristic trait of the Australian assemblages, is a feature shared by their European and Arctic counterparts. Furthermore, the Australian specimens frequently exhibit some antapical cavation, and rarely circumcavation, that is not recorded in the type material. Thus, the Northern Carnarvon Basin specimens are questionably assigned to *Dapcodinium ovale* herein, but future investigations may find they justify elevation to a new species.

Dapcodinium polyedricum Below 1987

Plate 7, figs 13–15; Figure X

1987 *Dapcodinium polyedricum* Below 1987, p. 144–149; pl. 23, figs 1–5, 12–18; text-figs 74a–f, 75, 76a–k.

Dimensions (based on eight measured specimens): overall length (excluding the apical plates) 21 µm (26 µm) 30 µm; maximum width 20 µm (25 µm) 33 µm.

Local stratigraphical range: *Dapcodinium polyedricum* is very rare in the *H. balmei* and *R. rhaetica* zones (Norian–Rhaetian) of the Northern Carnarvon Basin.

Previous records: The type material of *Dapcodinium polyedricum* of Below (1987) is from the Norian of Buru, Maluku Islands and Misool, Raja Ampat archipelago, Indonesia.

Remarks: The Australian specimens of *Dapcodinium polyedricum* are very similar to the type material from Indonesia (Below, 1987); they are similar in size, have the same distinctive angular ambitus and polygonal appearance, and have more prominent sutural ridges or septa than other species of *Dapcodinium*. The sutural ridges/septa may extend into short (1–3 µm), distally blunt gonal spines. The 1', 2' and 5' apical plates commonly form a small, angular extension anterior of the remainder of the principal archaeopyle suture. Hence, *Dapcodinium polyedricum* does not have the 'hooded' appearance of *Dapcodinium ovale* or *Dapcodinium prolongata* sp. nov.

Dapcodinium priscum Evitt 1961 emend. Below 1987

Plate 7, figs 9, 10

1961 *Dapcodinium priscum* Evitt, p. 996–1001; pl. 119, figs 1–14; text-figs 1–20.

1987 *Dapcodinium priscum* Evitt 1961 emend Below 1987, p. 149; pl. 23, figs 6–11, 19.

Dimensions (based on 10 measured specimens): overall length (excluding the apical plates) 26 µm (29 µm) 32 µm; maximum width 27 µm (29 µm) 32 µm.

Local stratigraphical range: *Dapcodinium priscum* is rare to frequent in the *R. rhaetica* and *D. priscum* zones (Rhaetian–Pliensbachian) of the Northern Carnarvon Basin. It is most prominent in the Lower *D. priscum* Subzone. Very rare specimens may also occur in the *H. balmei* Zone (Norian). However, many of these forms are smaller than *Dapcodinium priscum sensu stricto,* and have a substantially less well-defined tabulation. These morphotypes are often best classified as *Dapcodinium* spp.

Previous records: Evitt (1961) first described *Dapcodinium priscum* from the Lower Jurassic of Denmark by Evitt (1961). Further very rare Norian, and common Rhaetian and Early Jurassic, European records include Riley (1972), Warrington (1974; 1997), Morbey (1975; 1978), Warrington et al. (1984), Below (1987), Riding and Thomas (1992), Courtinat et al. (1998), Courtinat and Piriou (2002), Lindström (2002), Bucefalo Palliani and Buratti (2006), Lindström and Erlström (2006), Yaroshenko (2007), Bonis et al. (2009), Ruckwied and Götz (2009), Vigran et al. (2014) and Cirilli et al. (2015). There are far fewer published records outside Europe; these include the Rhaetian and Early Jurassic of northern Australia (Helby et al., 1987a; Brenner, 1992; Burger, 1996; and Backhouse and Balme, 2002), the Godavari Basin, India (Aswal and Mehrotra, 2002), the Rhaetian of central-east Iran (Sabbaghiyan et al., 2015) and the Rhaetian of north-east Libya (Brugman and Visscher, 1988).

Remarks: the majority of specimens of *Dapcodinium* recorded herein do not accord with *Dapcodinium priscum sensu stricto*, especially below the Rhaetian. These are either smaller with less well-developed tabulation (*Dapcodinium* spp. herein), pear-shaped with rounded apical horns or protrusions and weaker tabulation (*Dapcodinium prolongata* sp. nov. herein), or are ‘hooded’, ovoidal to subspherical (rather than spheroidal) and commonly with a microrugulate surface ornament (?*Dapcodinium ovale* herein). Therefore, *Dapcodinium priscum sensu stricto* is only consistently present in the Rhaetian and Early Jurassic of the Northern Carnarvon Basin, and is not common in the Norian–Carnian Mungaroo Formation.

***Dapcodinium prolongatum* sp. nov.**

Plate 8, figs 6–25; Figure X

Derivation of name: *Dapcodinium prolongatum* sp. nov. is named after the Latin *prolongatus*, in regard to the elongate epicyst which may form a rounded protuberance.

Previous Australian usage:

Dapcodinium prolatum (Robin Helby informal industry name)

Dapcodinium prolongatum (MGP informal industry name)

Noricysta sp. D Backhouse & Balme 2002, p. 110–111; pl. 13, figs 9–12.

Holotype and type locality: Plate 8, fig. 20; Lynher-1 well at 7900 m to 7890 m, Browse Basin, Western Australia; slide xx, EF.Xx/x.

Paratype: Plate 8, fig. 15; Lynher-1 well at 7900 m to 7890 m, Browse Basin, Western Australia; slide xx, EF Xx/x.

Description: small, proximate, acavate or cavate, pyriform to ovoidal dinoflagellate cysts with a subrounded, lobate or flat-based hemispherical hypocyst and a variably tapered conate epicyst. The epicyst is much thinner walled, particularly the climactal plates, and thus superficially appears to be epicavate (there is no evidence of epicavation). Conversely, the endophragm and periphragm are frequently separated by 1–3 µm antapically (Plate 8, figs 24, 25). The surface ornament is typically scabrate to granulate or occasionally microreticulate or microrugulate. Low sutural ridges define an incomplete tabulation of n’, 4+a, 7’’, nc, 6/7’’’, n’’’’, ns. The relatively broad (3–5 µm) cingulum is largely undivided, with only rare hints of internal tabulation and typically is not indented. The compound combination archaeopyle involves the loss of the mediodorsal apical and anterior intercalary plates, most likely 3’, 4’, 2a and 3a (Fig. 4b). However, because the complete epicystal tabulation is not known, the exact plate equivalence of the operculum is unconfirmed.

Dimensions (based on 20 measured specimens): overall length (excluding the apical plates) 26 µm (32 µm) 43 µm; maximum width 21 µm (28 µm) 34 µm.

Local stratigraphical range: *Dapcodinium prolongatum* sp. nov. is rare to common from the *W. listeri* Zone to the Lower *D. priscum* Subzone (Norian–Rhaetian) in the Northern Carnarvon Basin. Extremely rare specimens have also been recorded from the uppermost *R. wigginsii* Zone (Norian). A similar stratigraphical range is known in the Browse and Bonaparte basins.

Remarks: the pear shaped or tear drop ambitus is the most diagnostic feature of *Dapcodinium prolongatum* sp. nov., and this trait is further emphasised by the substantially thinner walled climactal plates. The tabulation formula of n', 4+a, 7'', nc, 6/7''', n'''', ns for *Dapcodinium prolongatum* sp. nov. is apparently largely consistent with the tabulation of *Dapcodinium* as documented by Below (1987), i.e. PR, 5', 4–6a, 7'', 8c, 6–8''', 3'''', ns.

Comparisons: ?*Dapcodinium ovale* and *Dapcodinium priscum* both lack the diagnostic thin-walled apical horn and conate epicyst of *Dapcodinium prolongatum* sp. nov. Furthermore, ?*Dapcodinium ovale* is typically ovoidal, and may be more densely microrugulate or finely wrinkled than *Dapcodinium prolongatum* sp. nov. *Dapcodinium priscum* is generally much more strongly tabulate than *Dapcodinium prolongatum* sp. nov., and typically has a broader cingulum that may also be strongly indented.

Dapcodinium tabulodiniopsis sp. nov.

Plate 10, figs 1–11

Derivation of name: *Dapcodinium tabulodiniopsis* sp. nov. is named after the distinctly tabulate nature of this species, and in recognition of the earlier informal generic name used in Australia.

Previous Australian usage:

?*Dapcodinium* sp. 1117 (Robin Helby, informal industry name)

Tabulodiniopsis sp. (Robin Helby, informal industry name)

Holotype and type locality: Plate 10, figs 4a, b; ODP well 760B at 362.3.0 m, Northern Carnarvon Basin; slide 1761639GCR, EF Xx/x.

Paratype: Plate 10, figs 5a, b; ODP well 760B at 362.3.0 m, Northern Carnarvon Basin; slide 1761639GCR, EF Xx/x.

Description: small, proximate, acavate to cavate, flattened subspheroidal dinoflagellate cysts with an obtusely angular or rarely conate apex and a rounded or flat-based antapex. The epicysts and hypocysts are of similar length and both may exhibit weakly angular profiles at the boundary of the apical and precingular plates, and the transition between the postcingular and antapical plates. Although most specimens are acavate, poorly preserved cavate forms with very thin-walled endocysts are common. The separation of the endophragm and periphragm in these is greatest at the antapex, but rare specimens are strongly camocavate. The surface ornament of the endocyst is psilate with poorly or undefined tabulation. The periphragm (or autophragm) is psilate to scabrate, with coarser baculae, clavae and grana defining the sutures or surmounting low sutural ridges. These sutures define a typical dapcodinioid tabulation of ?4’, 4a, 7’’, 7–8c, 7’’’, 3’’’’, ns. The broad, moderately laevorotatory cingulum (4–7 µm) is divided into 8 plates, and is offset by a one half to two-thirds the cingular width; it has a flat or weakly indented profile. The archaeopyle is formed by the loss of apical and anterior intercalary plates. This appears to involve only the dorsal plates, probably 3’, 4’, 3a and 4a (Fig. 4d), but rare specimens appear to have also lost the 2’ and 1a plates.

Dimensions (based on 20 measured specimens): maximum length 31 μm (38 μm) 46 μm; maximum width 21 μm (28 μm) 36 μm.

Local stratigraphical range: *Dapcodinium tabulodiniopsis* sp. nov. is very rare in the *R. wigginsii*, *W. listeri* and lowermost *H. balmei* zones (Carnian–Norian) of the Wombat Plateau, Northern Carnarvon Basin. The species has also been recorded from the Late Triassic of the Bonaparte Basin (Robin Helby, unpublished data).

Remarks: The broad cingulum, moderately narrow precingular plates, tabulation and compound AI archaeopyle all strongly support a generic assignment to *Dapcodinium*. As noted earlier, the labelling of the posterior plates herein (Figs 4d, e) follows that of Below (1987), thereby recognising three antapical plates (1–3'''') rather than a single antapical plate (1'''') and two posterior intercalary plates (1–2p).

Comparisons: The strongly tabulate appearance and squat subspherical ambitus of *Dapcodinium tabulodiniopsis* sp. nov. are most reminiscent of *Dapcodinium polyedricum* and *Dapcodinium priscum*. However, the sutural ornament of coarse grana, baculae or clavae impart a strongly denticulate edge to the sutures, and this readily distinguishes *Dapcodinium tabulodiniopsis* sp. nov. from these and all other species of *Dapcodinium*. Note that some of the paratypes of *Dapcodinium priscum* illustrated by Evitt (1961, pl. 119, figs 7, 9, 10, 13) appear to exhibit short baculae or grana along sutural boundaries, but these are never as coarse or as persistent as in *Dapcodinium tabulodiniopsis* sp. nov.

***Dapcodinium* spp.**

Plate 7, figs 1–8, 11, 12, Plate 8, figs 1–5

Remarks: small dapcodinioid dinoflagellate cysts, such as Plate 7, figs 1–8, with probable combination (apical-anterior intercalary) archaeopyles and pronounced to weak cingulums are lumped together herein as *Dapcodinium* spp. These morphotypes are deliberately not forced into fitting into a broader definition of *Dapcodinium priscum*. They are often smaller, and lack the full tabulation and very broad cingulum of *Dapcodinium priscum sensu stricto*. Intergradational forms of this genus, such as *Dapcodinium priscum–polyedricum* (Plate 7, fig. 11), are also recorded as *Dapcodinium* spp. herein.

Genus *Rhaetogonyaulax* Sarjeant 1966 emend. Below 1987

1966 *Rhaetogonyaulax* Sarjeant, p. 152–153.
1973 *Shublikodinium* Wiggins, p. 2–4.
1975 *Rhaetogonyaulax* Sarjeant 1966 emend. Harland et al., p. 860.
1979 *Rhaetogonyaulax* Sarjeant 1966 emend. Fisher and van Helden, p. 270, 272.
1987 *Shublikodinium* Wiggins 1973 emend. Stover and Helby, p. 118–119.
1987 *Rhaetogonyaulax* Sarjeant 1966 emend. Below, p. 101–102.

Type: *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jr and Loeblich III 1968 emend. Below 1987, p. 105–106.

Remarks: *Rhaetogonyaulax* has a relatively long and moderately complex taxonomic history. This important genus was first erected by Sarjeant (1966) to better accommodate his species *Gonyaulax chaloneri* and *Gonyaulax rhaetica* (see Sarjeant 1963). The latter author considered the elongate spindle shaped ambitus of these Rhaetian forms to be significantly unique to warrant the erection of a new genus. However, his interpretation of a standard gonyaulacacean tabulation substantially underestimated the number of climactal plates, amongst other misinterpretations of the tabulation. Successive emendations by Harland et al. (1975) and Fisher and van Helden (1979) perceptively noted the relatively large number of apical and anterior intercalary plates, although they differed significantly in their interpretation of the archaeopyle. Harland et al. (1975) considered that the archaeopyle formed by the ‘progressive loss of all paraplates anterior to the precingular paraplates’. By contrast, Fisher and van Helden (1979) suggested that there are two distinct archaeopyle types, i.e. a simple 6A5I operculum and compound $A_{4'}$5I opercula. The latter proposition has not been widely accepted, at least not as a trait to distinguish different species, and the three new taxa erected by Fisher and van Helden (1979) were subsequently all synonymised with *Rhaetogonyaulax rhaetica* by Below (1987). In the latter ground-breaking study, Below (1987) provided exceptional scanning electron microscope images of *Rhaetogonyaulax rhaetica* that revealed the full tabulation formula of PR, 5’, 4a, 7’’, 8c, 7–8’’’, 3’’’’, ns, as. Below (1987) also considered that archaeopyle formation may involve all the climactal plates (PR + 5A4I) in various simple or compound arrangements; commonly with the preapical and most of the apical plates ($A_{1', 2', 4'}$) forming a single simple opercular piece, which is either free or adnate. Alternatively, the excystment aperture of *Rhaetogonyaulax* involves only the intercalary plates; the subsequent loss of apical and preapical plates being simply due to mechanical damage. Below (1987) also recognised a small ‘cap’ (canal) plate) between the 1’ and 4’ plates; therefore he considered the plate immediately anterior of the 7’’ plate to be the 5’ plate (Fig. 5a). Wiggins (1973) and Stover and Helby (1987) previously regarded the latter plate to be 5a, and the ‘cap’ plate of Below (1987) to be a further apical plate.

When Wiggins (1973) erected the genus *Shublikodinium* for ten new Carnian species from the Arctic North Slope in Alaska, the original tabulation formula of *Rhaetogonyaulax* by Sarjeant (1963) had not been emended. Hence these two genera were still considered to be separate, and interpreted to have different archaeopyle types and tabulation formulae. Subsequently, Stover and Evitt (1978) synonymised these two genera, prior to Below (1987) confirming they have the same tabulation formulae and variability in archaeopyle formation. Stover and Evitt (1978) also rationalised the ten species of *Shublikodinium* of Wiggins (1973) into just two species of *Rhaetogonyaulax*. Wiggins (1973) largely subdivided his ten *Shublikodinium* species on the basis of surface ornament. These minor variations are considered to be within the boundaries of intraspecific variability, and the reorganisation by Stover and Evitt (1978) was unequivocally justified. Stover and Helby (1987) maintained *Shublikodinium* (for *Shublikodinium wigginsii*), citing stratigraphic separation as an important distinction. However, Stover and Helby (1987) were not aware of Below (1987), and the temporal overlap of *Rhaetogonyaulax* and *Shublikodinium wigginsii* in the Rhaetian of Australia (Fig. X). It should also be noted that *Rhaetogonyaulax rhaetica* ranges into the Norian (and possibly into the Carnian) in Arctic

Canada (Bujak and Fisher 1976) and the Barents Sea region (Paterson and Mangerud 2015, Paterson et al. 2018).

As currently accepted, *Rhaetogonyaulax* encompasses a wide variety of shapes and sizes. These range from moderately large, elongate, spindle-shaped taxa such as *Rhaetogonyaulax rhaetica*, to small, squat, biconical forms, often with only a rudimentary antapical horn or an acuminate antapex, for example *Rhaetogonyaulax arctica*. Furthermore, some forms have sub-rounded hypocysts. This trait is best developed in *Rhaetogonyaulax nagelii* sp. nov. from Australia, but also rarely occurs in the Arctic and Indonesian populations of *Rhaetogonyaulax arctica*. Below (1987) allowed for this in his generic emendation. He included 'rounded poles' within his circumscription of *Rhaetogonyaulax,* and also noted that *Rhaetogonyaulax arctica* may have a 'hemispheroid or flattened coniform hypocyst'. Therefore, the presence of an antapical horn is not considered to be a critical morphological criterion in *Rhaetogonyaulax*.

Rhaetogonyaulax dilatata **(Wiggins 1973) Stover & Evitt 1978**

Plate 11, figs 13–20

1973 *Shublikodinium dilatata* Wiggins, p. 6; pl. 5, figs 3–4.

1973 *Shublikodinium echinoverrucatum* Wiggins, p. 6–7; pl. 5, figs 5–6 [junior synonym according to Stover and Evitt 1978, p. 219].

1973 *Shublikodinium granulatum* Wiggins, p. 6; pl. 5, fig. 2 [junior synonym according to Stover and Evitt 1978, p. 219].

1973 *Shublikodinium scaberrimum* Wiggins, p. 7; pl. 5, fig. 7 [junior synonym according to Stover and Evitt 1978, p. 219].

1978 *Rhaetogonyaulax dilatata* (Wiggins 1973) Stover and Evitt, p. 219.

Description: small to medium, proximate, acavate, ovoidal to biconical dinoflagellate cysts with distinctly larger hypocysts than epicysts. The hypocyst is semi-hemispherical or rarely conate, and lacks antapical horns; vestigial horns or protuberances may be occasionally present. The autophragm is scabrate to granulate, whereas the sutural ornament is often coarser, particularly on the cingular sutures, and varies from granae and verrucae to short baculae and spinae. The tabulation is weakly indicated or unexpressed, with more sutures visible on the hypocyst than the epicyst. Consequently the tabulation formula is not fully resolved, and can be summarised as ?PR, x', xa, 7'', xC, ?7''', 2–3''''. The archaeopyle frequently involves the loss of all climactal plates with only very rare specimens retaining their preapical or apical plates. This often leaves the tall, tapering, commonly flat-topped 1'' plate protruding distinctively above the remaining, shorter precingular plates.

Dimensions (based on 10 measured specimens): overall length (excluding opercula) 33 µm (38 µm) 41 µm; maximum width 42 µm (47 µm) 52 µm; length of sutural spines 0.5–2.0 µm.

Local stratigraphical range: *Rhaetogonyaulax dilatata* is very rare in the *R. wigginsii* and *W. listeri* zones (Carnian–Norian) of the Wombat Plateau, Northern Carnarvon Basin.

Previous records: Wiggins (1973) originally documented *Rhaetogonyaulax dilatata* from the upper Carnian Shublik Formation of the North Slope, Alaska. There are no other published records of this species, however, Suneby and Hills (1988) recorded *Rhaetogonyaulax* sp. cf. *R. dilatata* from the Norian of Ellesmere Island, Sverdrup Basin.

Remarks: Although all *Rhaetogonyaulax* may lose their full complement of climactal plates during archaeopyle formation, most individuals only shed 2–4 anterior intercalary plates or a combination of anterior intercalary and apical plates. Thus, *Rhaetogonyaulax dilatata* is unique in commonly shedding all the climactal plates. None of the Australian specimens were found with all the apical and preapical plates attached; only very rare specimens retained any of these plates. Wiggins (1973) did not comment on the archaeopyle type of *Rhaetogonyaulax dilatata* outside of his generic discussions, but did note that the 'epitract characteristics are unknown' for this species and his other later synonymised taxa. This suggests that these specimens also commonly lost all their climactal plates. Wiggins (1973, pl. 5, fig. 5) figured one specimen of *Shublikodinium echinoverrucatum* [now *Rhaetogonyaulax dilatata*]) that had retained some of the climactal plates; this is similar to pl. 11, fig. 19 herein. The protruding 1’’ plate noted in the description above is also apparent in three of the specimens of Wiggins (1973, pl. 5, figs 2–4). Wiggins (1973) also noted vestigial horns or protuberances on the hypocysts of some specimens of *Rhaetogonyaulax dilatata* from Alaska.

Comparison: *Rhaetogonyaulax dilatata* is larger and substantially broader than *Rhaetogonyaulax arctica*, and has a less indented cingulum. The cingulum is also wider, with a much reduced intratabular ornament. Furthermore, it lacks the inflated precingular and postcingular bulges that may be present on *Rhaetogonyaulax arctica,* and typically loses all of the climactal plates during excystment. The delicate sutural spines are also markedly finer than their counterparts on *Rhaetogonyaulax arctica*.

The assemblages from the Wombat Plateau containing *Rhaetogonyaulax dilatata* also include some superficially similar ?*Noricysta* species (pl. 11, figs 1–12). Well preserved specimens of the latter are readily distinguished by the presence of a thin periphragm. However, when this is not preserved, the two taxa are similar in size and of broadly comparable shape, although the questionable *Noricysta* specimens are still typically more semi-hemispherical and lack a conate antapex. The tabulation of these questionable *Noricysta* specimens is also poorly expressed, but appears to involve more precingular plates than *Rhaetogonyaulax dilata*.

Rhaetogonyaulax nagelii sp. nov.

Plate 12, figs 1–15

Derivation of name: this species is named after the eminent Australian geologist Jim Nagel.

Holotype and type locality: Plate 12, fig. 6; Galahad-1 well at between 2460 m and 2455m, Northern Carnarvon Basin; slide ox1, EF X56/3.

Paratype: Plate 12, fig. 10, Galahad-1 well at between 2460 m and 2455m, Northern Carnarvon Basin; slide ox2, EF E52/4.

Description: small, proximate, acavate, ovoidal to rarely biconical dinoflagellate cysts with roughly equant epicysts and hypocysts. The epicyst is conical, narrowing to a short, triangular apical horn. The hypocyst is hemispherical with a rounded, sub-rounded or lobate antapex; very rare specimens have a conate antapex or a short stubby antapical horn. A rudimentary second hypocystal horn or protuberance, offset from the antapex, is developed in <10% of specimens. The broad cingulum varies from having a flat profile to being weakly concave and is less densely ornamented than the rest of the cyst. The autophragm ranges from scabrate to comprehensively granulate or verrucate with coarser clusters sometimes forming on the precingular and postcingular plates. Coarser grana or verrucae may also be aligned along the sutural ridges, particularly bordering the cingulum, and along the precingular and postcingular plate boundaries, often imparting a weakly serrated appearance to these plate margins. The precingular and postcingular plates are commonly inflated, forming irregular nodes extending out from each side of the cingulum. The tabulation formula is not known in full, but appears to be ?PR, 4+’, 4–5a, 6’’, nc, 6+’’’, n’’’’, ns. The archaeopyle is commonly formed by the loss of 3–4 anterior intercalary plates, however this disintegrative plate loss may also continue until all the climactal plates are lost. However, the loss of the apical and preapical plates may be solely due to mechanical damage. The operculum is mostly compound via the loss of individual anterior intercalary plates, however the apical and preapical plates may be lost as single piece.

Dimensions (based on 20 measured specimens): overall length (including the attached opercula) 30 µm (38 µm) 51 µm; maximum width 24 µm (31 µm) 41 µm; length of antapical horn (present in <20% of specimens) 1.0 µm (1.6 µm) 2.5 µm.

Local stratigraphical range: The inception of *Rhaetogonyaulax nagelii* sp. nov. is in the previously unzoned early Carnian interval, and marks the base of the new *R. nagelii* Zone. The species extends to the top of the *H. balmei* Zone (late Norian). Therefore, the *R. nagelii* Zone partially fills the apparent hiatus in the Australian dinoflagellate cyst record between the *S. ottii* Range Zone (Ladinian–earliest Carnian) of the Bonaparte Basin and the *R. wigginsii* Zone (late Carnian). A small acme of *Rhaetogonyaulax nagelii* sp. nov. was also noted in the Hb6 marine event in the upper *H. balmei* Zone (late Norian) of several wells in the Northern Carnarvon Basin.

Previous records: There are no previous records of *Rhaetogonyaulax nagelii* sp. nov. However, because *Rhaetogonyaulax arctica* is clearly very closely related, the existing reports of that species are noted here. Wiggins (1973) described *Rhaetogonyaulax arctica* from the Shublik Formation (upper Carnian) of the North Slope, Alaska, whilst Felix and Burbridge (1978) noted it was abundant in the Carnian Schei Point Formation of the Sverdrup Basin of Arctic Canada. A further Arctic record was published by Paterson and Mangerud (2015) from Hopen Island in the Svalbard Archipelago. This followed Bjaerke and Manum (1977), who illustrated *Rhaetogonyaulax* sp. cf. *R. rhaetica*, also from Hopen Island, that appears to be *Rhaetogonyaulax arctica*. The latter authors noted some specimens were similar to *Shublikodinium armatum* (now *Rhaetogonyaulax arctica*). The specimens of Bjaerke and Manum (1977) and Paterson and Mangerud (2015) are predominantly from the Flatsalen Formation. The former authors attributed a ?Rhaetian age for this unit, however Paterson and Mangerud (2015) revised this to an early Norian age based on ammonoids and magnetostratigraphy. This is consistent with the Carnian to Norian range noted by Hochuli et al. (1989) for *Rhaetogonyaulax arctica* from the Barents Sea region. Below (1987) illustrated this species from the Norian of Buru, Maluku Islands and Misool, Raja Ampat archipelago, Indonesia. The only Australian records are of those of Helby (1976) who illustrated *Shublikodinium* sp. 270 [=*Shublikodinium setigerum* (now *Rhaetogonyaulax arctica*)] from the lower Norian of the Bonaparte Basin. Overall, the Carnian to Norian global range of *Rhaetogonyaulax arctica* is very similar to that of *Rhaetogonyaulax nagelii* sp. nov. and they are likely very closely related.

Remarks: Smaller or poorly preserved specimens of *Rhaetogonyaulax nagelii* sp. nov. are often not easy to identify as rhaetogonyaulacaceans. The examination of the entire assemblage is frequently required before their identification can be confirmed. Specifically, the lack of an antapical horn, a biconical shape or an obvious archaeopyle on many specimens makes identification particularly difficult. However, even these specimens usually exhibit some typical rhaetogonyaulacacean traits. These are a prominent and broad cingulum (often less coarsely ornamented than the rest of the cyst), an apical horn, very short precingular plates and sutural grana or verrucae. These smaller forms are commonest in the early–middle Carnian, and probably represent the first moderately common rhaetogonyaulacaceans, which later evolved into larger, more elongate and more clearly tabulate taxa (Fig. X). *Sahulidinium ottii*, of the Ladinian–early Carnian, is the oldest unequivocal dinoflagellate cyst and also exhibited weak rhaetogonyaulacacean tabulation but is incredibly rare.

Comparisons: *Rhaetogonyaulax nagelii* sp. nov. is very closely related to *Rhaetogonyaulax arctica* and it was only after careful consideration that this new taxon is erected. This new Australian species is broadly ovoidal with a rounded or subrounded antapex, and thus differs from the predominantly biconical *Rhaetogonyaulax arctica* as described from Alaska (Wiggins, 1973) and well-illustrated specimens from Indonesia (Below, 1987). Furthermore, *Rhaetogonyaulax nagelii* sp. nov. is marginally smaller and generally has a much less indented cingulum.

Larger specimens of *Rhaetogonyaulax nagelii* sp. nov. show some gradation towards *Rhaetogonyaulax wigginsii,* and poorly preserved specimens are best recorded as *Rhaetogonyaulax* spp. However, the denser surface ornament, frequently inflated hypocystal plates and unclear tabulation of *Rhaetogonyaulax nagelii* sp. nov. all contribute to a somewhat incoherent overall appearance.

Rhaetogonyaulax rhaetica (Sarjeant 1963) Loeblich Jr & Loeblich III 1968

Plate 13, figs 1–9

1963 *Gonyaulax rhaetica* Sarjeant, p. 353, text-figs 1–2.

1968 *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jr & Loeblich III, p. 212.

1975 *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jr & Loeblich III 1968 emend. Harland et al., p. 862; pl. 100, figs 1–8; pl. 101, figs 1–12; pl. 102, figs 1–9; pl. 103, figs 1–14; pl. 104, figs 1–12; text-figs 1A, B, 2A–E.

1979 *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jr & Loeblich III 1968 emend. Fisher & van Helden, p. 270; pl. 2, figs 1, 2; pl. 4, figs 9, 10; text-figs 1A–D, 3A.

1979 *Rhaetogonyaulax testacea* Fisher & van Helden, p. 272; pl. 1, figs 1–6; text-fig. 1E; [junior synonym according to Below 1987, p. 105].

1979 *Rhaetogonyaulax tortuosa* Fisher & van Helden, p. 274, 276; pl. 2, fig. 7; pl. 3, figs 2, 6, 7; pl. 4, figs 1–8; [junior synonym according to Below 1987, p. 105].

1979 *Rhaetogonyaulax uncinata* Fisher & van Helden, p. 274; pl. 2, figs 3–8; pl. 3, figs 1, 3–5; [junior synonym according to Below 1987, p. 105].

1987 *Rhaetogonyaulax rhaetica* (Sarjeant 1963) Loeblich Jr & Loeblich III 1968 emend. Below, p. 105–106; pl. 9, figs 1–18; pl. 10, figs 1–18; text-figs 60, 61.

Dimensions (based on 20 measured specimens): overall length including attached opercula 69 µm (77 µm) 87 µm; overall length excluding attached opercula 48 µm (53 µm) 59 µm; maximum width 30 µm (43 µm) 53 µm.

Local stratigraphical range: *Rhaetogonyaulax rhaetica* is rare to common in the Rhaetian Brigadier Formation of the Northern Carnarvon Basin (Helby et al., 1987a; Brenner, 1992; Burger, 1994, 1996; Backhouse and Balme, 2002; Backhouse et al., 2002; herein). It is restricted to the *R. rhaetica* Zone and the Lower *D. priscum* Subzone (Rhaetian). This species is also frequent in other Rhaetian strata such as the Nome and Lower Malita formations of the Bonaparte and Browse basins (Helby, 1976), and rarely in the Lower Bedout Formation of the Roebuck Basin (e.g. Burger, 1994, 1996 and unpublished industry reports). Rare occurrences of *Rhaetogonyaulax rhaetica* in Lower Jurassic strata from Australia are all considered to represent reworking. However, as rare occurrences of this species are also recorded above the Triassic–Jurassic transition in

Europe (Ruckwied and Götz, 2009; Lindström et al., 2017), it is possible that this species occasionally ranges into the lowermost Jurassic, assuming the European occurrences are not reworked.

Previous records: Sarjeant (1963) first described *Rhaetogonyaulax rhaetica* from the Rhaetian successions in the Stowell Park borehole in Gloucestershire, England. *Rhaetogonyaulax rhaetica* has subsequently proved to be the most cosmopolitan Rhaetian dinoflagellate cyst. These include many records from European Rhaetian successions (e.g. Fisher, 1972; Orbell, 1973; Morbey and Neves, 1974; Harland et al., 1975; Morbey, 1975; Warrington, 1977, 1978; Fisher and Dunay, 1981; Woollam and Riding, 1983; Karle, 1984; Courtinat et al., 1998; Courtinat and Piriou, 2002; Lindstöm, 2002; Holstein, 2004; Bucefalo Palliani and Buratti, 2006; Lindstöm and Erlström, 2006; Bonis et al., 2009; Ruckwied and Götz, 2009; Vigran et al., 2014; and Paterson and Mangerud, 2015) along with several early Norian recoveries from Hopen Island, Svalbard and the Sentralbanken High, Barents Sea (Vigran et al., 2014; Paterson and Mangerud, 2015; and Paterson et al., 2018a). Furthermore, Paterson and Mangerud (2015) and Paterson et al. (2018b) documented even older occurrences of *Rhaetogonyaulax rhaetica* from the middle–upper Carnian De Geerdalen Formation, Barents Sea. These significantly older records fit with the observations of Bujak and Fisher (1976; pl. 9, figs 18–20), who also recorded a Carnian *Rhaetogonyaulax* sp. from Arctic Canada that looks remarkably similar to *Rhaetogonyaulax rhaetica*. It would thus seem that *Rhaetogonyaulax rhaetica* first appears in much older successions in the high latitudes of the Northern Hemisphere than its more global distribution in the Rhaetian. Non-European records of *Rhaetogonyaulax rhaetica* include the Late Triassic (possibly reworked) of the Andaman Islands, Bay of Bengal (Sharma and Sarjeant, 1987), the Norian–Rhaetian of Arctic Canada (Felix, 1975; Felix and Burbridge, 1978; Fisher and van Helden, 1979), the Norian of Seram, Indonesia (Martini et al., 2004), the ?late Norian–Rhaetian of Iran (Ghasemi-Nejad et al., 2004; Sabbaghiyan et al., 2015) and the Norian–Rhaetian of Israel (Eshet, 1990).

Remarks: As currently accepted, *Rhaetogonyaulax rhaetica* encompasses a broad morphological range, varying considerably in surface ornament, overall shape and the length of the apical and antapical horns. As much of this variation is seen within single populations and the stratigraphic range of these forms is very consistent, a wide scope for diagnosing the taxa seems reasonable. The tabulation (PR, 5’, 4a, 7’’, 8c, 7–8’’’, 3’’’, ns, as; Below 1987) and archaeopyle formula are consistent across all forms (though the former is typically only partially discernable without detailed scanning electron microscopy).

Harland et al. (1975) were the first to include this broader species concept in their emended diagnosis and considered *Rhaetogonyaulax chaloneri* Sarjeant 1963 to represent a variety of *Rhaetogonyaulax rhaetica* rather than a distinct species; the minor differences in surface ornament were deemed insufficient for speciation. Similarly, Below (1987) reassigned Fisher and van Helden’s (1979) three new *Rhaetogonyaulax* species to *Rhaetogonyaulax rhaetica*, thus further expanding the range of surface ornament exhibited by this taxon (smooth, scabrate, granulate, punctate, reticulate, or spinose with simple or bifurcate tips). Below (1987) also disputed the differing archaeopyle types that Fisher and van Helden proposed for these species; preferring a variable archaeopyle formation that can progress from the loss of 1–4 intercalary plates through to the loss of all climactal plates. As the majority of specimens only lose intercalary plates, it is possible that the loss of preapical and apical plates is due solely to mechanical damage rather than any excystment process.

Rhaetogonyaulax wigginsii **(Stover & Helby 1987) Lentin & Williams 1989**

Plate 12, figs 16–25

Remarks: On the basis of the nature of the ornamentation of the autophragm, we propose the subdivision of *Rhaetogonyaulax wigginsii* into two subspecies.

Rhaetogonyaulax wigginsii **(Stover & Helby 1987) Lentin & Williams 1989 subsp. *wigginsii*** **(autonym)**

Plate 12, figs 16–22

1987 *Shublikodinium wigginsii* Stover & Helby, p. 120; figs 19A–I; text-figs 18A–B, 20.

1989 *Rhaetogonyaulax wigginsii* (Stover & Helby 1987) Lentin & Williams, p. 316.

Dimensions (based on 20 measured specimens): overall length including apical horn 38 µm (48 µm) 60 µm; maximum width 32 µm (44 µm) 52 µm.

Local stratigraphical range: *Rhaetogonyaulax wigginsii* subsp. *wigginsii* is rare to common in the Mungaroo Formation, and rare to very rare in the Brigadier Formation of the Northern Carnarvon Basin. This subspecies ranges from the *R. wigginsii* to the *R. rhaetica* zones (latest Carnian–Rhaetian). *Rhaetogonyaulax wigginsii* subsp. *wigginsii* is most prominent in the more open marine successions in the *R. wigginsii* Zone and the lower part of the *W. listeri* Zones (latest Carnian–middle Norian). Similar ranges are noted in the Bonaparte and Browse basins for this subspecies.

Previous records: *Rhaetogonyaulax wigginsii* subsp. *wigginsii* was described by Stover and Helby (1987) from the late Carnian of the Bonaparte Basin. It is much less widespread than *Rhaetogonyaulax rhaetica* with relatively few records outside Australia (Burger, 1996; Backhouse and Balme, 2002; Backhouse et al., 2002). There are no confirmed records of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* from the Arctic, despite Bucefalo Palliani and Buratti (2006) attributing occurrences to Wiggins (1973). All the species of *Shublikodinium* established by Wiggins (1973) were transferred to *Rhaetogonyaulax arctica* or *Rhaetogonyaulax dilatata*. European records of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* are limited to those from the Rhaetian Blue Anchor Formation in south-west England (Bucefalo Palliani and Buratti, 2006; and pers. comm. Woollam in Powell, 1992). Hochuli and Frank (2000) also recorded *Rhaetogonyaulax* sp. cf. *R. wigginsii* from the Raibl Group (lower Carnian) of Switzerland. Further Northern Hemisphere records of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* are from the upper Carnian of the Alborz Mountains, Iran (Ghasemi-Nejad et al., 2004) and the Krishna Godavari Basin, India (Aswal and Mehrotra, 2002).

Remarks: Without scanning electron microscopy, it would be difficult to unequivocally confirm the tabulation formula of *Rhaetogonyaulax wigginsii* subsp. *wigginsii*, however the generic formula of Below (1987) (PR, 5’, 4a, 7’’, 8c, 7–8’’’, 3’’’’, ns, as) appears to be consistent for this subspecies. The latter formula differs slightly from that of Stover and Helby (1987), which is 1–2PR, 6’, 5a, 7’’, Xc, 7’’’, 3’’’’, 2–3S, 1PPL. The key differences pertain to the number and configuration of the preapical and apical plates, and the labelling of the plate immediately anterior to the 7’’ plate. Below (1987) considered that *Rhaetogonyaulax* has a small canal (‘cap’) plate inserted between the 1’ and 4’ plates; previous authors interpreted this as a small apical plate. Thus the 5’ plate of Below (1987), which is anterior to the 7’’ plate, was interpreted by other researchers as the 5a plate (Fig. XA).

Stover and Helby (1987) interpreted the excystment aperture of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* to be a type I to 5I anterior intercalary archaeopyle. This is consistent with the commonest archaeopyles noted herein. These typically involved the loss of 2 to 4 anterior intercalary plates, with or without the loss of the 3” plate (Figs 5A, B). However, rare specimens were also observed which have lost their apical and preapical plates (Fig. 5D). This situation is far rarer for *Rhaetogonyaulax wigginsii* subsp. *wigginsii* than for *Rhaetogonyaulax rhaetica* and, in both these species, may be related to mechanical damage rather than excystment. When the apical and preapical plates are also shed, they may detach as a simple operculum. Smaller forms of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* are especially common in the upper Carnian, where they may grade towards the early forms of *Rhaetogonyaulax nagelii* sp. nov.

***Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov.**

Plate 12, figs 23–25

Derivation of name: From the Latin *claviger*, after the cluster of spines on the antapical horn that are reminiscent of a medieval club or mace.

Holotype and type locality: Plate 12, fig. 24; North Gorgon-6 well at between 3840 m and 3830 m, Northern Carnarvon Basin; slide x, EF xxx/x.

Paratype: Plate 12, fig. 23; North Gorgon-6 well at between 3840 m and 3830 m, Northern Carnarvon Basin; slide x, EF xxx/x.

Description: medium, proximate, biconical dinoflagellate cysts with a short pyramidal apical horn and more elongate, mace-like antapical horn. A second rudimentary hypocystal horn or short protuberance is only very rarely evident, protruding from the adjacent antapical plate. The autophragm is scabrate to coarsely granulate with numerous short, acuminate to capitate spines (1–4 µm) surmounting the sutures, particularly bordering the cingulum and sulcus. A further cluster of spines on the antapical horn is particularly characteristic. The tabulation is indicated by low ridges that are notably thicker along the cingular and sulcal boundaries. These ridges clearly express the strongly laevorotatory nature of the cingulum, which is offset by two-thirds to a full cingular width. The full tabulation formula is unknown, but can be summarised as ?PR, 4+', 4–5a, 7'', nc, n''', n'''', ns. The archaeopyle is formed by the compound loss of 1 to 5 anterior intercalary plates (the commonest type), the loss of a combination of apical and anterior intercalary plates or all the climactal plates.

Dimensions (based on 10 measured specimens): overall length including the apical horn 52 µm (61 µm) 70 µm; maximum width 39 µm (46 µm) 52 µm.

Local stratigraphical range: *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov. is rare in the *R. wigginsii*, *W. listeri* and lower *H. balmei* zones (latest Carnian–middle Norian). It is most prominent in the Wl 1 marine event in the *E. vigens* Subzone of the *M. crenulatus* pollen/spore Zone.

Remarks: most of the species of *Rhaetogonyaulax* exhibit a wide variety of surface ornament, and this is generally accepted as reasonable for species level variation. The 16 described species of *Rhaetogonyaulax* have been synonymised into four (Williams et al., 2017). However, *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov. is considered to be best classified as a subspecies of *Rhaetogonyaulax wigginsii* rather than a new species. It differs substantially in surface ornament from the type material of Stover and Helby (1987), but it remains within the original core concept and description of that species. The tabulation formula is likely to be fully consistent with those of Below (1987) and Stover and Helby (1987), however there are differences in how these authors labelled the apical and anterior intercalary plates.

Comparison: Stover and Helby (1987) noted the morphological variability, particularly in the ornamentation of the autophragm, of *Rhaetogonyaulax wigginsii* in their original description. These authors stated that this species may have 'solid, often distally expanded processes (up to 4 μm long, 0.5–1 μm diameter)'. However the specimens illustrated by Stover and Helby (1987) all have notably broader based verrucae and other projections, in marked contrast with the more slender, elongate spines of *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov. The type material of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* also exhibit much rounder hypocysts with only vestigial antapical horns. They also typically lack the well-developed antapical horn of *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov., and thus the sharply biconical outline of this subspecies. There is much gradation between these end members however, and most of the specimens of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* herein (Plate 12, figs 16–22) have more conical hypocysts and longer antapical horns than the type material. The present material of *Rhaetogonyaulax wigginsii* subsp. *wigginsii* also frequently exhibit several short spines close to the antapical horn, but not the cluster of antapical spines typically developed in *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov.

Rhaetogonyaulax wigginsii subsp. *clavigerii* subsp. nov. also has a more strongly developed antapical horn than *Rhaetogonyaulax wigginsii* subsp. *wigginsii*. Therefore, the former subspecies is superficially more similar in shape to *Rhaetogonyaulax rhaetica*. However, *Rhaetogonyaulax rhaetica* is larger, is longer, has a more elongate spindle-shaped ambitus and lacks the concentration of coarser or longer ornament along the cingular and sulcal borders. *Rhaetogonyaulax rhaetica* is also a more cosmopolitan taxon; it has been recorded from Rhaetian shallow marine sections, particularly carbonates, from the Arctic to Gondwana. There are few published images of *Rhaetogonyaulax rhaetica sensu stricto* from the Norian (see above). It is possible that the significant morphological variability in *Rhaetogonyaulax wigginsii sensu lato* outlined herein may account for some of the pre-Rhaetian records of '*Rhaetogonyaulax rhaetica*'.

Subclass PERIDINIPHYCIDAE Fensome et al. 1993

Order UNCERTAIN

Family UNCERTAIN

Genus *Hebecysta* Bujak & Fisher 1976

1976 *Hebecysta* Bujak & Fisher, p. 64.

Type: *Hebecysta brevicornuta* Bujak & Fisher 1976

Hebecysta balmei (Stover & Helby 1987) Below 1987

Plate 14, figs 1–16

1987 *Heibergella balmei* Stover & Helby, p. 109–110, figs 7A–H.

1987 *Hebecysta balmei* (Stover & Helby 1987) Below, p. 126, pl. 12, figs 1–5, 10–18; text-fig. 67.

2002 *Hebecysta* sp. A Backhouse & Balme, p. 108, pl. 16, figs 7–10.

Dimensions (based on 20 measured specimens): overall length 36 µm (44 µm) 56 µm; maximum width 29 µm (36 µm) 47 µm.

Local stratigraphical range: *Hebecysta balmei* is restricted to the middle–upper Norian Mungaroo Formation (*H. balmei* Zone) in the Northern Carnarvon Basin. It is typically quite rare in these predominantly deltaic deposits, but can be abundant in the Hb4 main marine spike or common in the Hb6 marine event. The species has a similar range in the Bonaparte and Browse basins.

Previous records: Stover and Helby (1987) described *Hebecysta balmei* (as *Heibergella balmei*) from the Norian of the Bonaparte Basin, northern Australia. It has subsequently been found to be common in middle–upper Norian strata across the North West Shelf of Australia (Brenner, 1992; Backhouse and Balme, 2002; Backhouse et al., 2002), whilst Below (1987) recorded it further north in the Norian successions of Buru, Maluku Islands, Indonesia. *Hebecysta balmei* has not been positively identified from the more widely studied Upper Triassic successions of the Northern Hemisphere. However, Ghasemi et al. (2008) recorded *Hebecysta* cf. *balmei* from the Norian of northeastern Iran, but the poor preservation of this material makes close comparisons difficult.

Remarks: Most specimens of *Hebecysta balmei* from the Northern Carnarvon Basin are acavate, as originally described by Stover and Helby (1987, p. 109, as *Heibergella balmei*). However, because very rare specimens herein are marginally epicavate, we accept the transfer to *Hebecysta* of Below (1987). Furthermore, there is an increase in the proportion of cavate specimens in the Hb4 main marine spike; these assemblages contain commonly epicavate forms together with rare bicavate, cingulocavate and circumcavate individuals. Many of these Hb4 variants also display much reduced surface ornamentation, i.e. the ‘mesh reticulum’ of Stover and Helby (1987) or the ‘crude rugulae’ of Below (1987). These specimens may be almost smooth, but the majority retain some reticulation on the apical plates (Plate 14, figs 10–12) or around the cingulum (Plate 14, fig. 9). This reticulation is frequently restricted to the periphragm on these smoother variants of *Hebecysta balmei*. Backhouse and Balme (2002, p. 108) recorded these almost psilate and consistently cavate forms as *Hebecysta* sp. A. These authors stated that most of the specimens they studied are not *Hebecysta balmei sensu stricto,* but are considered to be intermediate morphotypes. This situation was also noted herein and, as no clear end-members are apparent, these forms are all included within the accepted intraspecific variation of *Hebecysta balmei*. They are of comparable size and shape to the type material, and also possess similar reticulate ornament albeit not as pervasively. These smoother variants also share the same stratigraphical range and are similarly commonest in the Hb4 main marine spike. There is also a huge variation in the coarseness of the reticulation in all the associations studied here. The lumina may vary from 2–10 µm wide on a single specimen. More commonly the reticulation is moderately consistent across each cyst but varying from one cyst to another, e.g. finely reticulate forms (lumen width, 1–3 µm; Plate 14, figs 1, 3) and coarsely reticulate forms (lumen width, 5–10 µm; Plate 14, figs 15, 16).

***Hebecysta* sp. cf. *H. brevicornuta* Bujak & Fisher 1976**

Plate 15, figs 11–17

1976 *Hebecysta brevicornuta* Bujak & Fisher, p. 64, pl. 9, figs 11–15; text-figs 6A–B.

Dimensions (based on 10 measured specimens): overall length 34 µm (37 µm) 40 µm; maximum width 30 µm (33 µm) 38 µm.

Local stratigraphical range: *Hebecysta* sp. cf. *H. brevicornuta* is a very rare component of assemblages from the uppermost Carnian to Norian Mungaroo Formation (upper *R. wigginsii* Zone to *H. balmei* Zone) in the Northern Carnarvon Basin.

Previous records: *Hebecysta brevicornuta* was described from the Norian of Melville Island and the surrounding area in Arctic Canada (Bujak and Fisher, 1976). Additional records from the Carnian and Norian include those from Alaska (Witmer, 1981), the Barents Sea (Vigran et al., 2014) and other studies from Arctic Canada (Felix and Burbridge, 1978; Ford, 1979; Suneby and Hills, 1988). There are also rare Rhaetian records from St Audrie’s Bay, southwest England (Bonis et al., 2010) and the Tabas Block, east-central Iran (Sabbaghiyan et al., 2015).

Remarks: the Australian specimens of *Hebecysta* sp. cf. *H. brevicornuta* herein are markedly smaller than the type material, but otherwise are broadly comparable. They are ovoidal to sub-rhomboidal, cornucavate dinoflagellate cysts with a strongly granulate periphragm, a broad cingulum and an anterior intercalary archaeopyle which possibly involves two or three plates. However as only three specimens were figured by Bujak and Fisher (1976), and the paratype appears to be similar to some forms of *Noricysta* (e.g. spherical, cristate, possibly circumcavate and constructed of a larger number and series of plates), the morphology of *Hebecysta brevicornuta sensu stricto* is somewhat obscure.

***Hebecysta* spp.**

Plate 15, fig. 10, Plate 16, figs 16, 17, Plate 16, figs 18–25 as ?*Hebecysta* spp.

Remarks: many small spherical to ovoidal, cavate or questionably cavate dinoflagellate cysts were recorded as *Hebecysta* sp. or ?*Hebecysta* sp. herein. Most of these have no definite archaeopyle (which is typical of this genus), lack tabulation or have only faint cingular ridges. However, the two wall-layers, lack of suessioid features (e.g. multiserial tabulation) and no apparent loss of apical plates (suggesting that the archaeopyle is probably intercalary) make *Hebecysta* the most suitable dinoflagellate cyst genus for these specimens.

Genus *Heibergella* Bujak & Fisher 1976

1976 *Heibergella* Bujak & Fisher, p. 52, 54.

Type: *Heibergella asymmetrica* Bujak & Fisher 1976

Remarks: *Heibergella* Bujak & Fisher 1976 is a rather poorly defined genus: 'apparently single-walled dinoflagellate cysts without reflected tabulation', with the 'cingulum and sulcus well or poorly defined' and with an apical horn and one, two or no antapical horns. The anterior intercalary archaeopyle is 'formed by the loss or displacement of one to three plates'. This rather broad description covers a wide range of possible cysts and confusingly promotes the lack of reflected tabulation (Bujak and Fisher, 1976, p. 54) as a key generic feature. This contrasts with the well-defined cingulum and sulcus on most of their illustrated types and the strong suggestions of further tabulation (including aligned sutural spines on *Heibergella aculeata*). Without further study of well-preserved assemblages (ideally including scanning electron microscopy to fully elucidate the tabulation) the relationship of *Heibergella* to other Late Triassic dinoflagellate genera remains highly uncertain. The type species, *Heibergella asymmetrica* Bujak & Fisher 1976, looks structurally very similar to some *Hebecysta* spp. and if proven to have two wall layers, albeit typically closely appressed, these genera may be synonymous (assuming similar tabulation formulae). The other Bujak and Fisher (1976) *Heibergella* species both have one or two antapical horns (e.g. the two antapical horns of *Heibergella aculeata*) and are somewhat reminiscent of *Rhaetogonyaulax*. Furthermore, both genera lose intercalary plates during excystment and although the *Rhaetogonyaulax* archaeopyle may also involves detachment of the PR and apical plates, it is the intercalary plates that are consistently lost first.

Heibergella? *obelixi* sp. nov.

Plate 15, figs 1–9

Derivation of name: after Obelix, the portly cartoon character from the French Asterix comics by René Goscinny and Albert Uderzo. Obelix, an artisan who is the best friend of Asterix, habitually wears a broad belt that is comparable to the wide cingulum of this rotund, squat dinoflagellate cyst species.

Holotype and type locality: Plate 15, figs 6a, b; ODP 760B well at 398.0 m, Northern Carnarvon Basin; slide 1761766GCR, EF L63/1.

Paratype: Plate 15, figs 5a, b; ODP 760B well at 398.0 m, Northern Carnarvon Basin; slide 1761766GCR, EF F41/0.

Description: small, proximate, acavate, ovoidal to biconical dinoflagellate cysts with a very short conate apical horn or bluntly rounded apex and a broadly hemispherical hypocyst. The autophragm is scabrate to coarsely granulate and some areas of denser ornamentation may appear spongy. The very broad cingulum (8–12 µm) and posterior sulcal margin are highlighted by the alignment of coarser grana, frequently conferring a weakly serrated edge to these sutures. The cingular margins may also be marked by low folds or ridges. The tabulation is typically only indicated by these cingular and sulcal boundaries, or by the archaeopyle margin and accessory archaeopyle sutures. However, rare clusters of coarser, intratabular grana may also denote some of the precingular and intercalary plates, along with the rare alignment of sutural grana distal to the cingulum and sulcus. The cingulum is moderately laevorotary and is undivided. The full tabulation formula is undetermined (?PR, n', 4–5a, 6+'', nc, n''', n'''', ns). The archaeopyle is formed through the compound loss of one to three anterior intercalary plates.

Dimensions (based on 20 measured specimens): overall length 37 µm (43 µm) 49 µm; maximum width 30 µm (38 µm) 43 µm.

Local stratigraphical range: *Heibergella*? *obelixi* was recovered only from the upper Carnian and lowermost Norian successions (*R. wigginsii* and *W. listeri* zones) in the more distal ODP wells drilled on the Wombat Plateau, Northern Carnarvon Basin.

Remarks: the ovoidal to biconical shape, very broad cingulum with aligned coarser grana, well-defined posterior sulcal margin and the loss of up to three anterior intercalary plates in *Heibergella*? *obelixi* sp. nov. invites comparison to *Rhaetogonyaulax nagelii* sp. nov. and *Rhaetogonyaulax wigginsii*. However, as there is no suggestion of further plate loss in archaeopyle formation, and the epicyst is conate rather than forming a true apical horn, this new species is questionably placed in *Heibergella* herein.

Comparison: *Heibergella*? *obelixi* sp. nov. is smaller than all previously published species of this genus, and it has a notably broader cingulum which is reminiscent of *Rhaetogonyaulax*. It differs further from the type species, *Heibergella asymmetrica* Bujak & Fisher 1976, in possessing a coarsely granulate autophragm and lacking a pronounced apical horn. The other species of *Heibergella* described by Bujak and Fisher (1976) from the Canadian Arctic, i.e. *Heibergella aculeata* and *Heibergella salebrosacea*, are strongly biconical with longer apical horns and have short, acuminate antapical horns. Thus, these differ substantially from the hemispherical to flat-based antapex of *Heibergella*? *obelixi* sp. nov. The dense covering of spines and the frequent second antapical horn further distinguish *Heibergella aculeata*. Morbey (1975) considered *Rhombodella kendelbachia* to have an apical archaeopyle. However, this feature was not proved; this author illustrated a specimen with mechanical damage around the apex (Morbey, 1975, pl. 14, fig. 2). Thus, Lentin and Williams (1981) transferred the species to *Heibergella*. However, *Heibergella kendelbachia* is more strongly rhomboidal, with a far less pronounced cingulum or sulcus than *Heibergella*? *obelixi* sp. nov., and may have short (up to 2 µm) processes that are ‘tapered, cylindrical, and slender hair-like stems and simple or bifurcate terminations’. However, these processes are also not readily discernable in the type material (Morbey (1975, pl. 14, figs 1-4, pl. 17, figs 1-3).

?*Heibergella obscura* sp. nov.

Plate 16, figs 1–15

Derivation of name: From the Latin *obscurus*, after the small, unobtrusive appearance of this species.

Holotype and type locality: Plate 16, fig. 7; Geryon-2 well at 3134.3 m, Northern Carnarvon Basin; slide 1, EF G61/1.

Paratype: Plate 16, fig. 10; Geryon-2 well at 3134.3 m, Northern Carnarvon Basin; slide 1, EF M61/1.

Description: small, proximate, mostly acavate, ovoidal to subspherical dinoflagellate cysts with a very short conate apex or stubby apical horn (3–5 µm long) and a broadly rounded or hemispherical hypocyst. The autophragm is scabrate to granulate, and typically lacks indications of tabulation; very rarely grana may align along presumed sutures. The cingulum and sulcus are not discernible. Very rare specimens may show minor cavation at the apical horn. The archaeopyle involves the loss of multiple anterior intercalary plates, but the number of plates, or the compound or simple nature of the opercula, are unknown. A dark brown, subcircular accumulation body, 4–7 µm in diameter, is present in most specimens, and is positioned equatorially.

Dimensions (based on 20 measured specimens): overall length 32 µm (36 µm) 40 µm; maximum width 28 µm (32 µm) 41 µm.

Local stratigraphical range: *Heibergella*? *obscura* sp. nov. is rare to frequent in the *W. listeri* and *H. balmei* zones, and the Lower *R. rhaetica* Subzone (middle Norian to early Rhaetian) in the Northern Carnarvon Basin. A notable spike in abundance was noted in the *D. harrisii* Spore-Pollen Subzone (*M. crenulatus* Spore-Pollen Zone) in the uppermost Mungaroo Formation in the Geryon-2 well.

Remarks: The lack of tabulation makes *Heibergella*? *obscura* sp. nov. very difficult to confidently identify, or to even recognise, in rich palynomorph assemblages. It is most commonly preserved in various lateral orientations, but it is also frequently observed in polar orientation due to the short, ovoidal or subspherical shape. These specimens in polar orientation typically appear to be little more than granulate spheres. The darker brown accumulation body is often the only hint of their dinoflagellate affinity, though the anterior intercalary archaeopyle is occasionally evident. Typically, it is only by examining the whole assemblage that the species identification can be confirmed. This species is questionably placed in *Heibergella* as very rare specimens exhibit minor apical cavation. *Heibergella* is an acavate genus, but as most dinoflagellate walls are formed from multiple wall layers which are frequently closely appressed, occasional separation of these wall layers, particularly apically, may not be a particularly useful generic distinction. Thus, it is possible that *Heibergella* (ovoidal, proximate, acavate dinoflagellate cysts with an anterior intercalary archaeopyle) is very closely related, and possibly congeneric with *Hebecysta* (ovoidal, proximate, cavate dinoflagellate cysts with an anterior intercalary archaeopyle). *Hebecysta balmei* was originally described as acavate, however Below (1987) noted that it may also be epicavate and transferred it to *Hebecysta*.

Comparison: *Heibergella*? *obscura* sp. nov. is most similar to *Heibergella asymmetrica,* but is considerably smaller, has a more densely granulate surface and a less pronounced apical horn. It is also slightly smaller than *Heibergella*? *obelixi* sp. nov., and lacks the broad cingulum and commonly well-defined sulcus of that species. *Heibergella*? *obscura* sp. nov. is also smaller than most species of *Hebecysta* and differs in being typically acavate.

***Heibergella* spp.**

Plate 17, figs 1–4

Remarks: small to medium sized, acavate, proximate, ovoidal, subspherical or rhomboidal dinoflagellate cysts with anterior intercalary archaeopyles were recorded as *Heibergella* spp. herein. The anterior intercalary archaeopyle was not evident on many specimens but, more importantly, there was no loss of the apical plates in any of them. The surface ornament varies from smooth to scabrate to granulate or, very rarely, sparsely spinose forms were noted (e.g. Plate 17, fig. 1). The latter specimen is thus very similar to the description of *Heibergella kendelbachia* that allows for comparable slender, blunt-tipped spines. However, as these spines are notably more prominent than in the type material of Morbey (1975), it is not specifically identified as such herein. These specimens are very rare in the Northern Carnarvon Basin assemblages.

Genus *Sverdrupiella* Bujak & Fisher 1976

1976 *Sverdrupiella* Bujak & Fisher, p. 45–48.

Type: *Sverdrupiella septentrionalis* Bujak & Fisher 1976

Remarks: *Sverdrupiella* spp. are very rare to occasionally frequent in the middle–upper Norian part of the Mungaroo Formation in the Northern Carnarvon Basin. The genus is also rare in the overlying Rhaetian Brigadier Formation, where *Sverdrupiella rhaetica* sp. nov. is present. This is consistent with most Northern and Southern Hemisphere records of *Sverdrupiella* which indicate that it is a largely Norian, or possibly Carnian–Norian, genus. Bujak and Fisher (1976, p. 45) characterised this genus as ‘cavate to bicavate dinoflagellate cysts, ovoidal to polygonal in shape, with or without one apical and one or two antapical horns’. They described 11 species, later reduced to nine by Below (1987), that demonstrated the highly variable shape and size of the pericyst from squat polygonal forms to highly elongate forms with pronounced apical and antapical horns. The tabulation is weakly expressed, thus the relationship to other Triassic genera is uncertain. Below (1987, p. 100) suggested that the apparent multiplate tabulation of *Sverdrupiella mutabilis* is similar to the multiserial plate configuration of *Suessia swabiana* (see Bujak and Fisher, 1976, pl. 4, fig. 10). However, even with SEM images of *Sverdrupiella sabinensis,* Below (1987) could not elucidate the tabulation formula for this genus. Both *Sverdrupiella* and *Suessia* also initiate archaeopyle formation through the loss of the mid-dorsal anterior intercalary and/or postapical plates. However, the disintegrative loss of further climactal plates appears to be much more typical of *Suessia*, although Bujak and Fisher (1976; p. 45) noted that ‘some or all remaining epitractal plates may also be displaced or lost’ by *Sverdrupiella*. Alternatively, comparisons can be made to *Rhaetogonyaulax*, which also has a complex combination archaeopyle formed by the loss of intercalary and apical plates, although the latter may be partly lost due to mechanical damage. *Rhaetogonyaulax* and *Sverdrupiella* both have characteristically short precingular plates (Bujak and Fisher, 1976, fig. 3; Dörhöfer and Davies, 1980, p. 11; Helby and Wilson, 1988, figs 3, 4, 11).

Sverdrupiella rhaetica **sp. nov.**

Plate 17, figs 6–8, 10–12, 15, 16

Derivation of name: this species is most prominent in the Rhaetian, in contrast with most other forms of *Sverdrupiella* spp. which are more typical of the Norian.

Holotype and type locality: Plate 17, fig. 12; GWA-06 well at 4782.5 m, Northern Carnarvon Basin; slide 2, EF S51/3.

Paratype: Plate 17, fig. 6; GWA-06 well at 4782.5 m, Northern Carnarvon Basin; slide 3, EF Q31/1.

Description: small, proximate, cavate to bicavate dinoflagellate cysts with a relatively dark, ovoidal endocyst and a thin-walled periphragm that forms a short, conate apical horn (2–10 µm long) and encloses an irregular antapical pericoel (3–11 µm in diameter). The antapical periphragm may form a rounded protuberance, or a larger angular pericoel, often with a broadly serrated or pyramidal posterior margin, that is commonly asymmetrically offset from the midline. The endophragm is smooth to scabrate, with many broad folds and a conspicuous dark accumulation body close to the cingulum. The periphragm is scabrate, finely granulate or irregularly microreticulate with numerous finer folds and rugulae. The extensive folds in the periphragm largely obscure the very sparse low sutural ridges (where present); only the cingulum is commonly identifiable. The tabulation formula is undetermined. The archaeopyle is typically not clear, but very rare specimens exhibit mid-dorsal intercalary or postapical plates with angular anterior margins that likely represent opercular plates.

Dimensions (based on 20 measured specimens): overall length of the pericyst 37 µm (41 µm) 60 µm; maximum width 23 µm (28 µm) 44 µm.

Local stratigraphical range: *Sverdrupiella rhaetica* sp. nov. is very rare to frequent in the Rhaetian Brigadier Formation (*R. rhaetica* Zone) in the Northern Carnarvon Basin. This species is notably common in the Lower *R. rhaetica* Subzone in the GWA-06 well, where it co-occurs with *Wanneria misolensis*.

Remarks: this species is attributed to *Sverdrupiella* because it is distinctively cavate to bicavate with a weakly expressed tabulation and a probable anterior intercalary archaeopyle. Although *Hebecysta* also displays some separation of the periphragm and endophragm, the cavation is not as well-developed as in *Sverdrupiella*.

Comparisons: *Sverdrupiella rhaetica* sp. nov. is significantly smaller than all other species of the genus. It is also present in the Rhaetian, as opposed to the predominantly Norian age of most other species of *Sverdrupiella*. Furthermore, *Sverdrupiella rhaetica* sp. nov. lacks the prominent spines and verrucae of many of the Norian species. It is most similar to the smooth, less elongate forms of *Sverdrupiella mutabilis* Bujak & Fisher 1976, but is still notably shorter, less biconical and with substantially smaller cavation and horn development.

Sverdrupiella sp. cf. *S. sabinensis* Bujak & Fisher 1976

Plate 18, figs 6–8

1976 *Sverdrupiella sabinensis* Bujak & Fisher, p. 49, pl. 3, figs 1–3, text-fig. 2E.

Dimensions (based on six measured specimens): maximum length of the pericyst 40 µm (51 µm) 59 µm; maximum width 41 µm (47 µm) 52 µm.

Local stratigraphical range: *Sverdrupiella* sp. cf. *S. sabinensis* is a very rare component of the middle–upper Norian Mungaroo Formation (*H. balmei* Zone) in the Northern Carnarvon Basin. A minor influx is present in the Hb1 marine event, between 4030–4020 m and 4000–3990 m, in the Pontus 1ST1 well.

Previous records: *Sverdrupiella sabinensis* was described by Bujak and Fisher (1976) from the Carian–Norian of the western Queen Elizabeth Islands of the Sverdrup Basin, Canada. Further Carnian–Norian records from this locality were published by Ford (1979), Dörhöfer and Davies (1980) and Suneby and Hills (1988). The only previous record from the Southern Hemisphere is the single specimen figured by Below (1987) from the Norian of Buru, Maluku Islands, Indonesia.

Remarks: The Northern Carnarvon Basin specimens of *Sverdrupiella* sp. cf. *S. sabinensis* herein are, on average, smaller than those of *Sverdrupiella sabinensis sensu stricto* from the Sverdrup Basin in Arctic Canada although there is some overlap. Several of the specimens of the former are more pentagonal (e.g. Plate 18, figs 6, 7). However, others exhibit similar shapes to *Sverdrupiella sabinensis sensu stricto*, i.e. a short, rounded or broadly conate epicyst and a marginally longer, slightly tapering hypocyst with a narrow antapex (Plate 18, fig. 8). The Australian forms also have a more strongly granulate periphragm rather than the sparse covering of verrucae and short spines exhibited by the type material from the Sverdrup Basin.

Sverdrupiella usitata Bujak & Fisher 1976

Plate 18, figs 14–16

1976 *Sverdrupiella usitata* Bujak & Fisher, p. 49, pl. 2, figs 1–12, text-fig. 2H.

Dimensions (based on three measured specimens): maximum width 52 µm (54 µm) 57 µm.

Local stratigraphical range: *Sverdrupiella usitata* is a very rare component in the middle–upper Norian Mungaroo Formation (*H. balmei* Zone) of the Northern Carnarvon Basin. It was only recorded from the Hb4 main marine spike in core from the Yodel-1 well.

Previous records: *Sverdrupiella usitata* was described by Bujak and Fisher (1976) from the Carian–Norian of the western Queen Elizabeth Islands of the Sverdrup Basin, Canada. It has been further recorded from the Norian successions in this basin by Felix and Burbridge (1977, 1978), Ford (1979) and Suneby and Hills (1988). It was also noted reworked into the Lower Cretaceous (Aptian–Albian) of northeast Alaska by Reifenstuhl and Plumb (1993).

Remarks: The specimens of *Sverdrupiella usitata* from the Northern Carnarvon Basin are relatively small and are barely within the size range of the Sverdrup Basin material (Bujak and Fisher, 1976). In most other respects, they conform to the original diagnosis; the periphragm is broader than long and all the Australian specimens present in polar view. The baculate or clavate spines, 0.5–2.5 µm long, surmounting the cingular ridges are the most distinctive feature of this species and are well developed on the Australian specimens. Two of the Northern Carnarvon Basin specimens appear to have lost anterior intercalary plates, or to have mechanical damage in this area (Plate 18, figs 14, 15).

Comparison: *Sverdrupiella usitata* is morphologically similar to *Sverdrupiella warepaensis* Helby & Wilson 1988 from the Norian of New Zealand. The former has a greater breadth to length ratio and is therefore typically preserved in polar view. Further differences include the more extensive posterior pericoel and the strongly concave indentation of the sulcus in *Sverdrupiella warepaensis*. All other species of *Sverdrupiella* are considerably longer, with a greater length to width ratio, or lack the prominent cingular spines of *Sverdrupiella usitata*.

Sverdrupiella spp.

Plate 17, figs 5, 9, 13, 14, Plate 18, figs 1–5, 9–13

Remarks: a variety of largely squat specimens of *Sverdrupiella* spp. were encountered in the middle–upper Norian, and rarely the lower Rhaetian, successions of the Northern Carnarvon Basin. None of these exhibit the characteristic elongate pericysts or the extremely long antapical horns of many of the Arctic Canadian species of Bujak and Fisher (1976) such as *Sverdrupiella baccata*, *Sverdrupiella manicata*, *Sverdrupiella ornaticingulata* and *Sverdrupiella septentrionalis*. However, some Australian specimens, such as Plate 18, figs 11, 12, are reminiscent of varieties of *Sverdrupiella mutabilis* with acutely conate hypocysts and rounded antapices (Bujak and Fisher, 1976, pl. 4, fig. 7, pl. 5, fig. 10). Many of the less elongate Australian forms, e.g. Plate 18, figs 5, 9, 10, are also closely comparable with material illustrated by Bujak and Fisher (1976; pl. 7, figs 7–9). Helby and Wilson (1988, p. 122) also noted similar forms from New Zealand.

Subclass UNCERTAIN

Order UNCERTAIN

Family UNCERTAIN

Genus *Goodwynia* gen. nov.

Derivation of name: after the Goodwyn Field in the North West Shelf of Australia, where this genus was first recorded by the Australian palynologist Robin Helby.

Type: *Goodwynia spinosa* sp. nov.

Description: small, acavate, chorate to proximochorate, ovoidal to subspherical dinoflagellate cysts with numerous spines or short, furcate processes. There are slender spines which are mostly clustered in small groups in plate-centred positions, and broader processes which are typically restricted to a single element per plate. These larger processes vary considerably from flattened to hollow projections with branched, denticulate or digitate terminations. The compound, heteromorphic branching ranges from simple first order bifurcation to third order multi-furcate terminations. The cingulum may lack processes or contain fewer, simpler processes than the rest of the cyst. The antapical process may be broader and/or longer than the surrounding hypocystal projections. The surface of the autophragm varies from scabrate to granulate. The tabulation is indicated only by the plate-centred positions of the processes and the poorly defined principal archaeopyle suture. The tabulation formula is not fully known, but can be summarised as: 2+’, xa, ?5–6’’, xc, ?5–8’’’, xp, ?1+’’’’. The archaeopyle type is also uncertain, but appears to involve the loss of the apical and anterior intercalary plates.

Remarks: the dinoflagellate affinity of these tiny dinoflagellate cysts is not easily proven. However, the consistent presence of an angular, straight-edged, opening with six or more sides, in an anterior position, strongly suggests a dinoflagellate cyst archaeopyle in *Goodwynia* gen. nov. This feature formed by the loss of multiple plates, probably both apical and intercalary plates. Furthermore, the regular distribution and clustering of small spines, and/or the regular distribution of the larger processes, strongly suggests that these are plate-centred positions on a tabulate dinoflagellate cyst. Although the tabulation formula cannot be fully elucidated, the apparent presence of five or more precingular plates and six or more postcingular plates is again strong evidence of a dinoflagellate cyst affinity. The equatorial area either lacks processes, or has notably smaller spines, and is interpreted as the cingulum.

Comparisons: The very small size of *Goodwynia* gen. nov. (typically <20 μm in diameter, excluding the spines) makes it very difficult to separate from *Micrhystridium* or other small Late Triassic acanthomorph acritarchs. However, when examined at high magnifications, the consistent anterior position of the archaeopyle, the plate-centred processes or spines and the apparently prominent cingulum all readily distinguish *Goodwynia* gen. nov. from all spinose acritarchs. The largely Palaeozoic acritarch genus *Multiplicisphaeridium* is the most closely comparable. This genus possesses similar compound heteromorphic processes with multi-order furcate branches and distal terminations. However, it has a markedly different excystment aperture, often a split-like pylome rather than the large, broad multiplate archaeopyle of *Goodwynia* gen. nov. *Multiplicisphaeridium* also lacks the other dinoflagellate features of *Goodwynia* gen. nov., namely a cingulum and plate-centred processes. There are no comparable Triassic dinoflagellate cysts except the proximochorate to chorate genus *Beaumontella*. The latter has substantially simpler processes and more plate series which strongly suggest close affinities to the suessioids.

Goodwynia dendroidea **(Morbey 1975) comb. nov.**

Plate 19, figs 9–14

1975 *Multiplicisphaeridium dendroidium* Morbey, p. 50–52, pl. 16, figs 21–22, text-fig. 24.

Description: very small, acavate, chorate to proximochorate, ovoidal to subspherical dinoflagellate cysts with a diverse array of furcate processes. The thin autophragm is typically scabrate, however rare specimens are granulate. The plate-centred processes are mostly hollow although some appear flattened, and are 1–5 μm in width. The hollow processes may be relatively simple with denticulate or digitate distal terminations; more commonly they are variably furcate. These branched processes vary from relatively simple bifurcate projections to those with three or more orders of branching and bifurcate, trifurcate or quadrifurcate distal terminations. The process tips may be blunt or pointed, and vary from stout to very delicate and slender. The main process trunk is commonly weakly fibrous or ribbed. The cingulum is marked by an absence of spines or by much simpler, blunt, unbranched processes. The antapical process may be broader and/or longer than the surrounding hypocystal projections. The full tabulation formula is unclear, but appears similar to: 2+’, xa, ?5–6+’’, xc, ?6–8’’’, xp, ?1+’’’’. The archaeopyle is uncertain, but appears to involve the loss of the apical and anterior intercalary plates.

Dimensions (based on 10 measured specimens): overall length (excluding spines) 16 µm (18 µm) 20 µm; maximum width (excluding spines) 14 µm (17 µm) 19 µm; length of spines 2–8 µm; width of spines <1–5 µm.

Local stratigraphical range: *Goodwynia dendroidea* is rare to frequent in the *H. balmei* Zone and the Lower *R. rhaetica* Subzone (late Norian to early Rhaetian), and very rare in the Upper *R. rhaetica* Subzone (late Rhaetian) in the Northern Carnarvon Basin.

Previous records: *Goodwynia dendroidea* was described by Morbey (1975) from the Westbury Formation of the Penarth Group (Rhaetian) in the Bunny Hill Borehole, Nottinghamshire, central England, and from the Swabian Facies to the Pre-*planorbis* Beds (Rhaetian) in the Kendlebachgraben of central Austria. Various Cambrian and Ordovician records of this species, such as Eisenack (1976), Volkova (1979), Downie (1982), and Hagenfeldt (1988) undoubtedly relate to superficially similar acritarchs with comparable processes but clearly lacking any dinoflagellate characteristics.

Remarks: Morbey (1975) noted that *Goodwynia dendroidea* (as *Multiplicisphaeridium dendroidium* occasionally possesses an ‘apical split-like pylome’. Although the apical position of this excystment aperture is consistent with the interpretation as an archaeopyle herein, the ‘split-like’ structure of this opening is not so definitive. However, some dinoflagellate cysts do have ‘split-like’ archaeopyles (Norris and Hedlund 1972). Despite this, it is only rare specimens (from the many observed herein) that show an apparently multi-sided, straight-edged archaeopyle. This is more easily observed on specimens in polar view. The archaeopyle could easily appear to be ‘split-like’ in lateral view as is the case for most specimens.

Comparisons: Although *Goodwynia dendroidea* is closely comparable in morphology to *Goodwynia spinosa* sp. nov., it is distinguished by the consistent differences in the length, number, and shape of the processes, and the marginally larger cyst size. *Goodwynia spinosa* sp. nov has numerous simple spines (up to eight per plate), rather than the usual single process per plate of *Goodwynia dendroidea*. The single processes of the latter are broader, more complex (commonly branched), more varied and longer than the dominantly distally blunt spines of *Goodwynia spinosa* sp. nov.

***Goodwynia spinosa* sp. nov.**

Plate 19, figs 1–8

Derivation of name: From the Latin *spinosa*, after the thorny or spinose ornament which covers the autophragm of this species.

Holotype and type locality: Plate 19, figs 4a–c; ODP well 760A at 205.09 m, Northern Carnarvon Basin; slide 1761641GCR, EF E35/3.

Paratype: Plate 19, figs 2a–c; ODP well 760A at 205.09 m, Northern Carnarvon Basin; slide 1761641GCR, EF O26/0.

Description: Very small, acavate, chorate to proximochorate, ovoidal to subspherical dinoflagellate cysts. The thin autophragm is scabrate with a covering of numerous very slender spines. The majority of the spines are loosely clustered in plate-centred positions; the remainder are nontabular. These simple spines are mostly distally blunt, but they may also be acuminate, pilate, or have finely furcate tips. Rarely the bases of adjacent spines are fused, while several specimens also have marginally broader flattened processes up to 2 μm wide, with bifurcate or trifurcate branching. The cingulum is marked by reduced numbers, or the entire absence, of spines and is commonly distinctly concave in lateral profile. The full tabulation formula is unknown, but may be summarised as: 2+’, xa, ?5–6+’’, xc, ?5–6+’’’, xp, ?1+’’’’. The archaeopyle type is also uncertain but appears to involve the loss of the apical and anterior intercalary plates.

Dimensions (based on 10 measured specimens): overall length (excluding spines) 14 µm (17 µm) 20 µm; maximum width (excluding spines) 13 µm (15 µm) 17 µm; length of spines 1–5 µm; width of spines <1–2 µm.

Local stratigraphical range: *Goodwynia spinosa* sp. nov. is typically very rare in the upper *W. listeri* and *H. balmei* zones (middle–upper Norian) of the Northern Carnarvon Basin. However, it appears to be more common in coeval strata from the more distal settings such as the ODP wells drilled on the Wombat Plateau.

Remarks: Although there is some intergradation between the highly cryptic, minute dinoflagellate cysts *Goodwynia dendroidea* sp. nov. and *Goodwynia spinosa* sp. nov. the majority of specimens of these two species are readily distinguishable. Therefore, it was considered appropriate to erect a new species, *Goodwynia spinosa* sp. nov. The latter has up to eight simple spines per plate, rather than the equivalent typically single, branched processes of *Goodwynia dendroidea* and is also marginally smaller.

Comparisons: *Goodwynia spinosa* sp. nov. is even harder to separate from the common *Micrhystridium* spp. in the Norian marine successions of the distal reaches of the Northern Carnarvon Basin than *Goodwynia dendroidea*, due to the numerous morphologically similar spines. However, unlike the predominantly distally acuminate spines of *Micrhystridium* and other small Triassic acanthomorph acritarchs, the slender processes of *Goodwynia spinosa* sp. nov. may be acuminate, blunt, pilate or rarely furcate, and they occur in discrete clusters. These plate-centred groupings of spines, the reduced distribution of spines across the cingulum and the combination archaeopyle (apical/anterior intercalary) further distinguish well-preserved specimens of *Goodwynia spinosa* sp. nov. from all small, acanthomorph acritarchs.

6. Overview and conclusions

This investigation has documented the presence of highly unusually diverse dinoflagellate cyst assemblages from the Upper Triassic successions of the Northern

Carnarvon Basin, Western Australia. Ten genera were documented, one of which (*Goodwynia*) is new. Fifteen existing species were observed, and 14 new species have been established herein. Furthermore, one new subspecies, *Rhaetogonyaulax wigginsii* subsp. *clavigerii* subsp. nov., is described. These relatively species-rich associations exhibit significant apparent evolutionary change that allows for a high-resolution biostratigraphy (Fig. 2).

This taxonomic diversity in the Northern Carnarvon Basin, i.e., 29 species and one subspecies plus undifferentiated forms of five genera, means that the associations documented herein are, by a considerable margin, the richest Triassic dinoflagellate cyst assemblages ever described. The closest comparable study is that of Bujak and Fisher (1976), who described 16 new species from the Carnian and Norian of the Sverdup Basin in Arctic Canada. The four new genera described by Bujak and Fisher (1976) were *Hebecysta, Heibergella, Noricysta* and *Sverdrupiella*. This association, the *Sverdrupiella* complex, is extremely characteristic of the high northerly palaeolatitudes. *Sverdrupiella* is also present elsewhere in the Canadian Arctic and in Alaska (Felix and Burbridge, 1978; Staplin, 1978; Wiggins, 1987; Suneby and Hills, 1988; Embry and Suneby, 1994; JBR, unpublished data). After observing *Sverdrupiella* from Australia, Helby et al. (1987b) invoked a circum-Pacific distribution for this genus and its relatives. *Sverdrupiella* and its relatives are extremely rare in subequatorial palaeolatitudes in the Western Tethys region, i.e. Europe and the Middle East (e.g. Powell, 1992; Bucefalo Palliani and Buratti, 2006; Ghasemi-Nejad et al., 2008). Most contributions on Triassic dinoflagellate cysts record much lower species richnesses. The majority of these are of the species *Dapcodinium priscum* and *Rhaetogonyaulax rhaetica* (see, for example, Woollam and Riding, 1983; Mangerud et al., 2019).

Therefore it seems that there are two areas with diverse Late Triassic dinoflagellate cysts, i.e. Arctic North America (~50° N) in the northern hemisphere and the Northern Carnarvon Basin (~30° N) of the southern hemisphere. By contrast, the subequatorial palaeolatitudes are normally characterised by very low diversity floras (Fig. 3). The two dinoflagellate cyst diversity hotspots, and the low diversity region illustrated in Fig. 3, are all in extensive regions of open shelf seas. These areas are all theoretically ideal for dinoflagellates in ecological terms compared with today (Wall et al., 1977). The major difference between them appears to be palaeoclimate. Arctic North America and the Northern Carnarvon Basin are in temperate and cool temperate palaeolatitudes, whereas much of Western Tethys is within the warm temperate/subtropical/tropical zone (Fig. 3). Palaeolatiude, and hence palaeoclimate, is hence considered to have been the prime environmental factor controlling the distribution of these palynomorphs, as opposed to sea level variations (Bucefalo Palliani and Buratti, 2006), particularly in the northern hemisphere. The palaeoclimate during the Triassic was, on average, ~6°C warmer than today. Furthermore, there were no polar icecaps, there was a very strong monsoonal regime and palaeotemperatures exhibited relatively little latitudinal variation (Preto et al., 2010 and references therein). This means that the dinoflagellate cyst diversity gradient appears to have reacted to relatively subtle palaeotemperature changes. Hence, it is conceded that there may be a eustatic overprint on this scenario. Also it is possible that phenomena such as nutrient/salinity gradients and **adverse** ocean currents prevented the migration south of the *Sverdrupiella* complex migrating south through the Viking Corridor in substantial numbers. By contrast, it is possible that this plexus could have migrated between the hemispheres around the western and southern margins of Pangaea as suggested by Helby et al. (1987b).

There are substantial number of dinoflagellate cyst range bases in the Norian and Rhaetian. However, it is noted that the initial apparently evolutionary burst of these palynomorphs was during the late Carnian (Figure 2). This emergence of dinoflagellate body fossils, which represents the dawn of the modern phytoplankton with the dominance of the "red" eukaryotic algal lineage (Martin et al., 2008, fig. 1) may have been partially triggered by a much delayed recovery from the end Permian mass extinction and/or by the Carnian Pluvial Event (CPE; Simms and Ruffell, 1989). Of these two causal mechanisms, the latter seems to have been the most significant, **perhaps due to the greatly increased nutrient levels because of the elevated runoff from the land areas at this time (Jeppsson, 1990)**. Other major evolutionary innovations which followed the CPE included dinosaurs, and diversifications in calcareous nannofossils, conifers, and scleractinian corals (e.g. Furin et al., 2006). These apparently exploited substantial levels of ecospace vacated by many representatives of groups such as ammonoids, bryozoans and crinoids (Simms and Ruffell, 1989).

Later, during the Early Jurassic, similar patterns are evident. For example, in the Toarcian, dinoflagellate cyst assemblages in the northern hemisphere become significantly more diverse with increasing palaeolatitude (Riding, 1984b; Riding et al., 1999; Bucefalo Palliani and Riding, 2003b).

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Fig. 1. The location of the Northern Carnarvon Basin and adjacent depocentres at the southwestern end of the North West Shelf of Australia, and the wells studied herein.

Fig. 2. The semi-quantitative stratigraphical distribution of dinoflagellate cysts throughout the Upper Triassic (Carnian–Rhaetian) successions of the Northern Carnarvon Basin and immediately adjacent areas. The dinoflagellate cyst ranges are calibrated to the current Geologic Time Scale (Gradstein et al., 2012), the spore-pollen biozones (reference/s), the dinoflagellate cyst biozones, subzones and events (Riding et al., 2010 ?plus others?), and regional hydrocarbon play intervals and regional sequences (Marshall and Lang, 2013). The data in this chart have been compiled from the author's unpublished databases on the wells illustrated in Fig. 1

Fig. 3. A palaeogeographic map for the Late Triassic Epoch adapted from Scotese (2004) and Preto et al. (2010). The two dinoflagellate cyst diversity hotspots referred to in section 6 are marked as 1 (Arctic North America) and 2 (the Northern Carnarvon Basin). The low diversity region in the Western Tethys is also indicated as 3.

Species mentioned:

Pollen and spores:

Aulisporites astigmosus

Camerosporites secatus

Ephedripites macistriatus

Minutosaccus crenulatus

Rimaesporites aquilonalis

Samaropollenites speciosus

Dinoflagellate cysts:

Rhaetogonyaulax arctica

Sahulidinium ottii