# A lifetime studying marine biodiversity and phytoplankton evolution

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I have spent over 40 years studying marine phytoplankton, particularly from polar and tropical environments. During that time I have described many new taxa of living and fossil haptophytes, parmales, diatoms and silicoflagellates. Most of these organisms are very small (<10  $\mu$ m), so the scanning electron microscope (SEM) has been an essential tool in my laboratory's research. These new taxa are often extremely rare, and so may appear insignificant, yet they provide valuable information on specialised habitats and evolutionary trends.

Turrilithus



# Why is biodiversity important?

It is essential that every niche is occupied by living organisms and that they contribute to the physical and chemical processes that support life on the planet.

#### What do we know about our planet's biodiversity?

The world's governments spend huge amounts of money on searching for extraterrestrial life, and yet we still know very little about what is on our own planet. In fact, a survey by UNESCO found that only 1% of the Earth's surface has been mapped.

#### How many living species are there on the Earth?

A recent article estimated that there are at least 8.75 million living species (80% of which are hypothetical), but the real number could range from 2 million-3 trillion (Wiens, 2023). Of those species, 1-10 million are protists (Adl et al., 2007).

#### Where should we look for hidden biodiversity?

For marine phytoplankton, the obvious places to look are extreme environments and remote areas (lower photic zone, marine lakes, coral reefs, polar regions), while for microfossils, almost everywhere is poorly investigated. In terms of geological time, the Oligocene, Paleocene and Early Cretaceous diatom assemblages, in particular, are not well documented.



BS, Simpson AGB et al. (2007). Diversity, nomenclature, and taxonomy of protists. Syst. Biol. 56: 684-689 How many species are there on Earth? Progress and problems. *PLoS Biol*. **21**: e3002388

# HAPTOPHYTES

My career began when I did a one-year internship at the Institute of Oceanographic Sciences in Wormley, UK (1982-1983). I was asked to investigate phytoplankton assemblages on membrane filters using an SEM. This was at a time when using filters and the SEM were unusual in marine plankton research. Later, this project was expanded to become my PhD, when I also conducted research in the temperate and subtropical regions of the North Atlantic Ocean during two scientific cruises of the RRS Discovery.

# The 'shade flora' of the Lower Photic Zone

Most scientists collected subtropical-tropical phytoplankton samples from the top 100m of the ocean, however, during my PhD (and thereafter), I sampled down to 300m. As a result, I encountered a lot of new and rare taxa of calcareous haptophytes (e.g., Jordan et al., 1991; Andruleit & Jordan, 2017). Subsequent work off Puerto Rico showed that the deep

# Wikipedia species

One new species has its own Wikipedia page, because it is the only species named after a TV programme ('The Blue Planet')

### Siliceous haptophytes

A global review of living haptophytes with siliceous scales revealed a new species of *Petasaria* (Jordan *et* al., 2016). In addition, two species of Hyalolithus were discovered in the fossil record (Abe *et al.*, 2016; 2022). This line of research could initiate a new branch of haptophyte science, which has traditionally been focused on calcite scales. We are now concentrating on other enigmatic siliceous microfossils which may be potential haptophytes.







Andruleit H & Jordan RW (2017). Two new species of Vexillarius (Prymnesiophyceae) from the eastern Indian Ocean. Phycologia 56: 510-516. Jordan RW, Knappertsbusch M, Simpson WR & Chamberlain AHL (1991). Turrilithus latericioides gen. et sp. nov., a new coccolithophorid from the deep photic zone. Br. phyc. J. 26: 175-183. ordan RW & Winter A (2000). Assemblages of coccolithophorids and other living microplankton off the coast of Puerto Rico during January-May 1995. Marine Micropaleontology 39: 113-130.

(Young *et al.,* 2018).



Young JR, Bown PR, Cros L, Hagino K & Jordan RW (2018). Syracosphaera azureaplaneta sp. nov. and revision of Syracosphaera corolla Lecal, 1966. J. Nanno. Res. 38: online, open access.





Abe K, Pellegrino L, Lozar F, Tsutsui H & Jordan RW (2022). Hyalolithus didymus sp. nov. (Haptophyta): a late Miocene siliceous microfoss from Sicily, Italy. *Phycologia* **61**: 504-513. Abe K, Tsutsui H & Jordan RW (2016). Hyalolithus tumescens sp. nov., a siliceous scale-bearing haptophyte from the middle Eocene. Journal of Micropaleontology 35: 143-149. Jordan RW, Abe K et al. (2016). Observations on the morphological diversity and distribution of two siliceous nannoplankton genera

Hyalolithus and Petasaria. Micropaleontology **61**: 439-455.

#### DIATOMS

My undergraduate thesis (1984) was on polysaccharides and freshwater diatoms, but my studies on marine diatom taxonomy didn't start until I worked for the British Antarctic Survey in Cambridge, UK (1988-1991). This connection to polar research still continues today, although in Yamagata my studies have branched out into tropical regions, and older fossil records. Here I introduce my studies of two old lineages, Proboscia and *Corethron,* which I began working on 35 years ago (Jordan & Priddle, 1991; Jordan et al., 1991).

#### 35 years of *Proboscia* research

Initially, my studies focused on transferring some of the living Rhizosolenia species to Proboscia (Jordan et al., 1991) and describing some new ones. However, I soon began to describe new fossil taxa; from the late Miocene (Japan), Late Cretaceous (Southern Ocean; Jordan & Ito, 2002), and more recently, the early Eocene (Jutland; Abe & Jordan, 2023).



### The enigmatic genus, *Corethron*

Among living diatoms, *Corethron* has unique features – articulated spines in sockets, and hooked spines. But where did it come from? Until recently, there were no known ancestors. Our research has now revealed three older genera; *Praecorethron* and *Micrampulla* from the Late Cretaceous (Abe et al., 2021; 2022), and Davidharwoodia from the early Eocene (Abe & Jordan, 2023).



# **Coral reefs and farmer-fish territories**

Tropical environments are poorly investigated, because they are in remote areas or located in countries which lack good research facilities. Over the last 20 years we have sampled various habitats, describing new taxa from farmer-fish territories in Guam (Lobban et al., 2011), marine lakes in Palau (Konno & Jordan, 2008), and atolls in the South Pacific and Indian Ocean (e.g., Riaux-Gobin *et al.,* 2015).







ordan RW & Priddle J (1991). Fossil members of the diatom genus *Proboscia*. Diatom Research 6: 55-61. ordan RW, Priddle J, Pudsey CJ, Barker PF & Whitehouse MJ (1991). Unusual diatom layers in Upper Pleistocene sediments from the northern Weddell Sea. Deep-Sea Research 38: 829-843.

Abe K & Jordan RW (2023). On the enigmatic diatom Rhizosolenia dubia, its relationship to Pseudopyxilla and Proboscia. and description of a new species, *Proboscia pinocchioi* sp. nov. *Diatom Research* **38**: 1-12. Jordan RW & Ito R (2002). Observations on Proboscia species from Late Cretaceous sediments, and their possible evolution from Kreagra. In: 15<sup>th</sup> IDS, Koeltz Scientific Publishers: 313-329.

Jordan RW, Ligowski R, Nöthig E-M & Priddle J (1991). The diatom genus Proboscia in Antarctic waters. Diatom Research 6: 63-78.

Abe K, Harwood DM & Jordan RW (2022). Observations on Late Cretaceous Micrampulla (Corethrales, Bacillariophyceae) from the Campbell Plateau (Zealandia), southwest Pacific Ocean. Diatom Research 38: 1-12.

Abe K & Jordan RW (2023). Davidharwoodia megaspina gen. et sp. nov. (Corethrales), a new fossil marine diatom genus from Mors, Jutland (early Eocene). Diatom Research 38: 13-20.

Abe K, Lam DW, Ashworth MP, Harwood DM & Jordan RW (2021). Observations on Praecorethron crawfordii gen. et sp. nov. (Corethrales, Bacillariophyceae) from the Upper Cretaceous marine sediments, southwest Pacific. Nova Hedwigia, Beiheft 151: 273-314.

Konno S & Jordan RW (2008). Paralia longispina sp. nov., an extant species from Palau and Haha-jima, western North Pacific. Proceedings of the Nineteenth International Diatom Symposium 2006 Listvyanka, Russia. Biopress Ltd.: 55-69. Lobban CS, Ashworth MP, Arai Y & Jordan RW (2011). Marine necklace-chain Fragilariaceae (Bacillariophyceae) from Guam, including descriptions of Koernerella

and Perideraion, genera nova. Phycological Research 59: 175-193.

Riaux-Gobin C, Compère P & Jordan RW (2015). Cocconeis Ehrenberg assemblage (Bacillariophyceae) from Napuka Atoll (Tuamotu Archipelago, South Pacific) with description of two new taxa. Diatom Research 30: 175-196.

#### PARMALES

During Dec. 1996-Feb. 1997 and summer 1999, I participated in two R/V Hakuho-mar cruises. On these cruises I collected underway surface seawater samples, as well as vertical water samples (0-300m) at designated stations, and core sediments. The water samples were filtered through membrane filters and investigated for phytoplankton assemblages using an SEM. The data from the vertical samples at Station KNOT, in western North Pacific, gave us the first picture of Parmales seasonality (dark shade in figure below) and their abundance revealed their importance to primary production (Komuro *et al.,* 2005).



Komuro C, Narita H, Imai K, Nojiri Y & Jordan RW (2005). Microplankton assemblages at Station KNOT, subarctic western Pacific, in 1999-2000. Deep-Sea Research II 52: 2206-2217.

New taxa and plate configurations

After studying the polar taxa it was realised that the published plate configurations of the Parmales genera were wrong, so we revised them (Konno & Jordan, 2007). The filters from the two R/V *Hakuho-maru* cruises allowed us to describe many new taxa and to further understand their ecology (Konno et al., 2007; Fujita & Jordan, 2017). Subarctic



Fujita R & Jordan RW (2017). Tropical Parmales (Bolidophyceae) assemblages from the Sulu Sea and South China Sea, including the description of five new taxa. Phycologia 56: 499-509. Konno S & Jordan RW (2007). An emended terminology for the Parmales (Chrysophyceae). Phycologia 46: 612-616. Konno S, Ohira R, Komuro C, Harada N & Jordan RW (2007). Six new taxa of subarctic Parmales (Chrysophyceae). J. Nanno. Res. 29: 108-128.

The 'Big Mac Project'

Marine phytoplankton samples on membrane filters were collected from all over the world by US scientists (notably A. McIntyre) from the 1960s. This huge filter collection therefore represents a great resource for studying phytoplankton before the current rise in CO<sub>2</sub> levels. We used the filters to look at Parmales distribution, and described numerous new taxa (Hoshina et al., 2021a-c).



Hoshina K, Narita H, Harada N & Jordan RW (2021b). Triparma laevis f. marchantii f. nov. (Bolidophyceae) from the Southern Ocean, and comparison with other infraspecific taxa of T. laevis. Phycologia 60: 180-187.

Hoshina K, Narita H, Harada N & Jordan RW (2021c). Diversity within the Triparma strigata-Triparma verrucosa group (Bolidophyceae) including five new taxa from polar-subpolar regions. Phycologia 60: 215-224.

Hoshina K, Uezato Y & Jordan RW (2021a). Parmales (Bolidophyceae) assemblages in the subarctic Pacific Ocean during the mid-1960s. Phycologia 60: 35-47.

### The oldest fossil Parmales

The diatoms are thought to have evolved from a siliceous scaly ancestor. However, until recently, there were only a few studies on fossil Parmales, and these were from either surface sediments or the Quaternary. The general feeling was that the Parmales plates were too fragile to survive deep-time preservation. However, during our study of Late Cretaceous diatoms we noticed wellpreserved Parmales with fused plates, apart from the shield plates (Abe & Jordan, 2022). Now the search is on for more fossil species.



Abe K & Jordan RW (2022). Re-examination of Archaeomonas mirabilis from the Late Cretaceous reveals its true identity as the oldest known fossil Parmales (Bolidophyceae). Phycologia 60: 362-367.

#### SILICOFLAGELLATES

Although I'd published images of silicoflagellates before, everything changed when I met Kevin McCartney in 2013. He gave a talk on the rarity of silicoflagellate double skeletons and asked if anyone had seen one. I knew my students had seen over 30. Kevin initially doubted my claim, but the rest is history. What came next is a series of papers on the taxonomy and evolution of silicoflagellates ... and lots of double skeletons (McCartney *et al.,* 2022).



Dictyocha octangulata

McCartney K, Witkowski J, Jordan RW, Abe K et al. (2022). Silicoflagellate evolution through the Cenozoic. Marine Micropaleontology 172: 102108.

Abe K, McCartney K, Fukunaga Y, Narita H & Jordan RW (2015). Silicoflagellates and ebridians from the Seto Inland Sea and Kuroshio, including the description of Octactis pulchra var. takahashii var. nov. J. Nanno. Res. 35: 111-128.

# **Ecological varieties**

A new and thinner variety of Octactis pulchra was found in the oligotrophic Kuroshio, while the thicker variety lived in the eutrophic Seto Inland Sea (Abe et al., 2015).



**Double skeletons** 

Double skeletons are formed when cells divide, so do not remain attached for very long. Hence, they are rare. Modern species only make corner-tocorner configurations, whereas some fossil species can make Star-of-David configurations (McCartney *et al.*, 2014; 2015).

Double skeletons



McCartney K, Witkowski J, Jordan RW et al. (2014). Fine structure of silicoflagellate double skeletons. Marine Micropaleontology 113: 10-19. McCartney K, Abe K, Harrison MA et al. (2015). Silicoflagellate double skeletons in the geologic record. Marine Micropaleontology 117: 65-79.

#### **Skeletal variation Double skeleton models**

Usually, silicoflagellates are observed as single skeletons. So, how can we determine what kind of double skeletons they can make? In one paper, we produced physical models (wire models, 3D-printer plastic models) and 3D rotating computer models (McCartney *et al.*, 2015).



to help process hundreds of photos for morphometric data (Tsutsui & Jordan, 2016; Tsutsui et al., 2018).

We also developed computer programmes



utsui H & Jordan RW (2016). A semi-automatic two-dimensional image system for studying the skeletal design of the silicoflagellate genus Corbisema (Dictyochales, Dictyochophyceae). J. Nanno. Res. 36: 139-147. utsui H, Jordan RW, Nishiwaki N & Nishida S (2018). Morphometric analysis of early Eocene Corbisema skeletons (Silicoflagellata) in Mors, Denmark. J. micropal. **37**: 283-293.

# Silicoflagellate evolution

After a decade of collaborative research, we now have a much better idea of silicoflagellate evolution and of the timing of key events (McCartney et al., 2022). However, we still need to understand how pike-bearing and pike-less forms and double skeleton configurations fit into the evolution.

