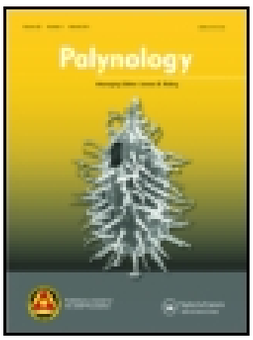

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From hystrichospheres to dinoflagellate cysts: Scandinavian contributions to Evitt's pivotal recognition of fossil dinoflagellate cysts

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ABSTRACT

As one of the remaining living links with two early Scandinavian researchers, the author examines their contribution to Bill Evitt's breakthrough that launched the development of fossil dinoflagellate cysts into palynology. Evitt, in the early 1960s, revealed that many fossil hystrichospheres were in fact dinoflagellate cysts. Trygve Braarud, a Norwegian phytoplankton biologist, and Gunnar Erdtman, a Swedish palynologist, collaborated in 1954 to identify the first examples of living hystrichospheres as dinoflagellate cysts. This and a related study by the Norwegian Erling Nordli provided important evidence for Evitt's breakthrough in 1961, but the wider palynological literature does not yet reflect the full significance of the Scandinavian work. Copies of correspondence between Braarud and Erdtman reproduced here together with the author's personal observations help to clarify the extent to which this earlier work influenced the breakthrough. The Scandinavians were not aware at the time of the wider significance of their work for palynology, realized only later through Evitt's perception. Reexamining this Scandinavian connection now therefore in no way detracts from Evitt's pivotal role in launching 'dinos' into palynology. This example from palynology shows details of how exciting breakthroughs in science often happen, as work in separate but related fields is coalesced into a larger, more significant concept.

KEYWORDS

hystrichospheres; dinoflagellate cysts; Evitt; Braarud; Erdtman; Nordli

1. Introduction

Scientific breakthroughs often arise from the collective ideas of earlier workers in related fields. This was certainly the case with the breakthrough in palynology in the 1960s that led to the recognition of dinoflagellate cysts as a critical group of microfossils for biostratigraphic and paleoenvironmental research. The breakthrough built on earlier ideas, some of which had been around for many years, scattered in the then widely separated literature of biology and micropaleontology. William R. (Bill) Evitt's pivotal role deservedly received credit (e.g. Sarjeant 2002; Riding and Lucas-Clark 2016). He showed that many fossil palynomorphs of unknown affinities, previously referred to as hystrichospheres, were in fact dinoflagellate cysts. David Wall's subsequent role leading research that helped to prove Evitt's ideas also deservedly shares some of the credit for this breakthrough. Using incubation experiments, Wall and co-workers showed that many fossil cysts had modern living representatives, formed as resting cysts in dinoflagellate life cycles. The literature covering this early work is easily accessible today (Evitt 1961, 1963; Evitt and Davidson 1964; Wall 1965; Wall and Dale 1966, 1968).

What is not so accessible, however, is much of the earlier work in the 1940s and 1950s by several Scandinavian scientists who contributed significantly to Evitt's breakthrough. Three are of particular interest here: Trygve Braarud (Figure 1A) and Erling Nordli, both Norwegian, and the Swede Gunnar Erdtman (Figure 1B). Their work was sparsely reported, often in local journals with limited circulation, and sometimes in a Scandinavian language. Evitt (1961) gratefully acknowledged the Scandinavian workers' contributions to his ideas, and the Scandinavian work has been referenced by others since, but the palynological literature does not fully reflect its far-reaching influence. For example, it was not mentioned in the detailed histories of palynology by Sarjeant (1970, 1973, 2002). The limited thanks it is possible to express in the restricted space allowed for acknowledgements in a publication can never adequately communicate the extent of such help. However, when it plays such an important part in a breakthrough such as linking fossil and modern dinoflagellates, it is always worth examining the complete historical perspective. In the present paper, I hope to reveal a more complete historical perspective for the years preceding Evitt's work.

Examination of correspondence between two of these Scandinavians in 1952 has provided new insight into their contributions to ideas expressed by Evitt (1961). Copies of two letters with English translations are included here as appendices. Also included (Figure 2) are copies of illustrations from publications by the Scandinavians. Figure references to the present paper are designated in the upper case (Fig.), those to the original figures are designated in the lower case (fig.).

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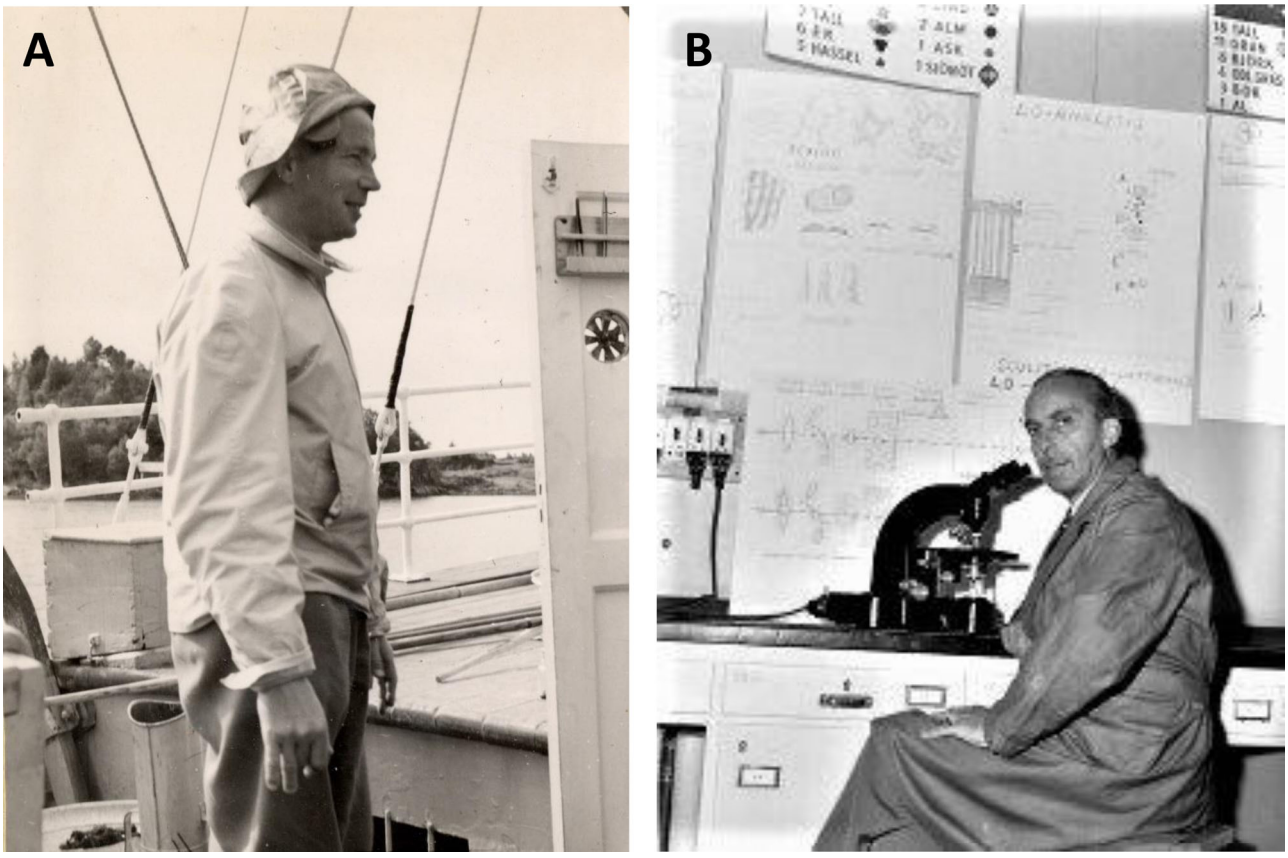

Figure 1. Photographs of Trygve Braarud (1903–1985) and Gunnar Erdtman (1897–1973). 1A Professor Trygve Braarud on the deck of the research vessel 'Herman Friele' on a field excursion to the Biological Station Espegrend, near Bergen, August 1952. Unknown photographer, from the Museum for University History, University of Oslo. 1B Dr. Gunnar Erdtman at his Palynological Laboratory near Stockholm, July 1950. Photographer John Kjellstrom, Svenska Dagbladet 5 July 1950. From the Collection Pollen, Swedish Museum of Natural History.

2. What were hystrichospheres?

Wetzel (1933) gave rise to the informal name 'hystrichosphere' (spiny sphere, from the Latin *hystrix* for porcupine) that was generally used for many years afterwards for a group of spiny organic-walled fossil microplankton that was then beginning to interest micropaleontologists. In the following few decades, hystrichospheres were reported from sediments ranging in age from Cambrian to Quaternary (Sarjeant 2002). Quaternary palynologists working with pollen also recorded hystrichospheres, but as no living representatives were recognized they generally considered the group extinct. They assumed that hystrichospheres in Quaternary sediments had been re-sedimented from older sources, and at least one prominent palynologist (Eisenack 1963) persisted in this belief even after Evitt's breakthrough. However, not all Quaternary palynologists accepted this explanation; Mohrén (1942) and Erdtman (1950) both suggested they were not extinct, and West (1961), considered hystrichospheres he recovered from borehole samples to be in place rather than reworked.

3. The Scandinavian contributions

3.1. Biologists Braarud and Nordli discovered living dinoflagellate cysts in laboratory cultures and plankton samples from a Norwegian fjord

In the 1940s and 1950s, two Scandinavian researchers were the first to discover that some hystrichospheres were in fact dinoflagellate cysts. Trygve Braarud, a leading Norwegian phytoplankton worker, observed and described resting-stages (cysts) in several dinoflagellate cultures from Oslofjord plankton, grown in his laboratory at the University of Oslo, Norway (Braarud 1945). One of these cysts, a spherical body with numerous spines, produced by *Protoceratium reticulatum*, was in fact a living hystrichosphere, but Braarud did not make this connection at that time. His well-illustrated description of the living cyst would permit its identification today (Figure 2A–D). A further living hystrichosphere, the cyst of *Gonyaulax polyedra* (= *Lingulodinium polyedrum*) was reported by Braarud's Norwegian co-worker Erling Nordli (Nordli 1951) from plankton samples from a large bloom in the Oslofjord in September 1950, again without noting the link to hystrichospheres. Nordli (1951, fig.1a-f) provided an excellent illustrated description of the living cysts and documented their sinking in the water column after formation in the plankton. He also documented cysts with part of the motile-stage wall (epitheca) attached, confirming details of encystment in natural populations (Nordli 1951, fig.1d).

3.2. A palynologist, Erdtman, discovered living hystrichospheres in sediment trap samples from a Swedish fjord

At around this time, Gunnar Erdtman, a leading Swedish Quaternary palynologist, found the remains of

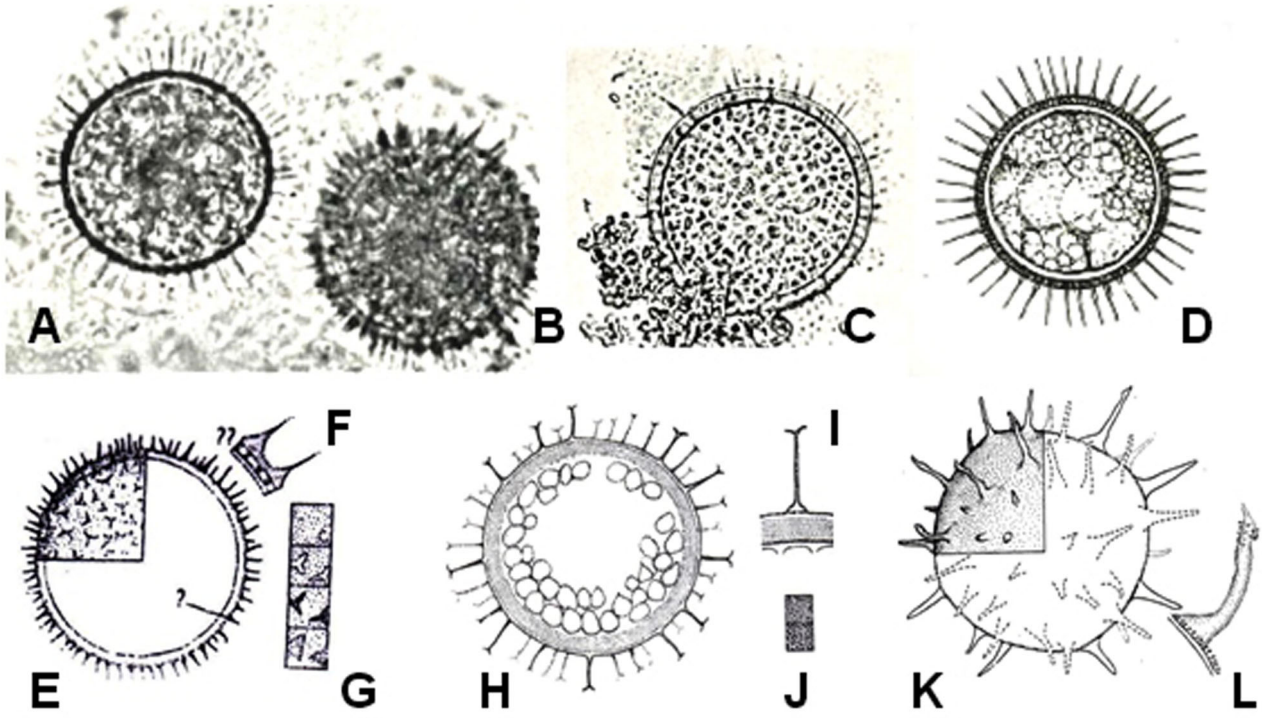

Figure 2. Copied figures from Braarud (1945) and Erdtman (1954). The original figure reference and text is shown first, in brackets and in italics, followed by text pertaining to this presentation where appropriate. A-D Cysts of *Protoceratium reticulatum* from laboratory cultures, in Braarud (1945). A-B *(Pl. IV, d. Two cysts focused at medium and high level, x 500.).* C. *(Pl. IV, e. Cyst with cell contents partly squeezed out, showing the thickness of the wall, x 500.).* The originals for A-C here were photomicrographs. D. (*Fig. 6. Cyst of Protoceratium reticulatum from Allen culture. Diameter without spines 40* μ*).* Drawing of a cyst with mature cell contents. E-L Drawings of cysts that Braarud identified in Erdtman (1954) – N.B. Braarud identified specimens in palynological preparations on slides, while these are drawings from Erdtman for his paper (an important point explained in the text). E-G *(Fig. 1, A. Protoceratium reticulatum (BRAARUD det.); June, 1952; fixed in formaline; smaller and provided with shorter spines than the cysts described by* BRAARUD (1945; N.B.: the line from the lower query should end at the inner contour line of the cyst wall.). This would fall within the known size range established since Erdtman (1954). H–J *(Fig. 4. a, c, d. 'Probably a dinoflagellate cyst' (BRAARUD); July 1952; fixed in formaline; a, b, x 1000; c, x 2000.).* This superficially resembles *Protoceratium reticulatum*, but process tips appear bifurcated, therefore not compatible with Braarud's original observations of the species shown in A–D in this Figure. K-L *(Fig. 3 A, Goniaulax polyedra (BRAARUD det.); Sept. 1-Oct. 7, 1948; cf. Fig. 1, p. 191, in EISENACK 1951!).* This specimen was from an acid-treated sample proving the link between fossil hystrichospheres and dinoflagellate cysts. Noting the basic morphological similarity between this cyst and what are now considered acritarchs in Eisenack's work on the Paleozoic shows that Erdtman considered his own work as relevant for the hystrichosphere-problem.

hystrichospheres in palynological preparations of particles collected in a simple sediment trap and from recent sediments from a Swedish fjord. He argued that this strongly suggested that hystrichospheres were not extinct (Erdtman 1950), as was also suggested previously by another Swedish Quaternary palynologist, Erik Mohrén (1942, p. 23). Erdtman eventually sent 12 of his pollen slides (then often called 'preparations') containing hystrichospheres from sediment traps to Braarud in Oslo, to see if Braarud could identify possible dinoflagellate cysts.

3.3. Braarud and Erdtman together make the first identification of hystrichospheres as dinoflagellate cysts

The first of the two letters reproduced in the appendices is a cover letter dated 08/12/52 that was sent by Erdtman to Braarud, at the same time as the microscope slides (Supplementary Data Appendix 1A, with an English translation in Supplementary Data Appendix 1B). It is clear from the opening sentence that Braarud had previously sent Erdtman two reprints which the latter had read with interest (almost certainly Braarud (1945) and Nordli (1951), describing living dinoflagellate cysts from the Oslofjord). In the letter, Erdtman clarifies that some of the slides contain residues resulting from strong palynological treatment (acetolysis and HF) confirming that the cysts and hystrichospheres present must be acid-resistant palynomorphs comparable to fossilizable pollen and spores. Erdtman says that in the past few years he had become interested in the hystrichosphere literature, and that the German micropaleontologist Otto Wetzel had already identified one of his forms as a hystrichosphere, *Hystrichosphaera* cf. *furcata* Ehrenb. He invited Braarud to identify any of the forms he had marked on the slides, obviously based on Braarud's experience with living dinoflagellate cysts.

The second letter is Braarud's reply, dated 12/13/52 (Supplementary Data Appendix 2A with an English translation in Supplementary Data Appendix 2B). Of particular interest here is the interest he, too, expressed in the identity of the hystrichospheres since many of the living forms that he had seen in the plankton were identical to those described from fossil assemblages. He noted that he had been trying for a long time to find time to collect resting spores (i.e. cysts) from bottom sediments and incubate them. He pointed out that he had a collection of photomicrographs of hystrichospheres from plankton samples that he hoped to use to build a type collection for identifying forms from their quantitative plankton samples.

Attached to the second letter (Supplementary Data Appendix 2B) is a list of identifications by Braarud, aided by a Norwegian colleague, Karen Gaarder (Supplementary Data Appendices 3A-B). The first group of identified dinoflagellate cysts includes *Protoceratium reticulatum* (in formalin-preserved material in slides 8 and 9), first reported by Braarud (1945), and *Gonyaulax polyedra* (in both preserved and acid-treated material in slides 3 and 5), first reported by Nordli (1951). This represents the first known example of hystrichospheres subsequently identified as dinoflagellate cysts. Both Braarud and Erdtman had suspected that some hystrichospheres and motile dinoflagellates were from the same biological species, and their cooperation through these two letters and exchanged reprints confirmed it.

Erdtman (1954, fig.1A, fig.3A) included and acknowledged Braarud's identifications. Copies of the figures in that paper pertinent to the present discussion are reproduced here together with relevant figures from Braarud (1954) to allow comparisons (Figure 2A–D herein from Braarud (1945); 2E-L herein from Erdtman (1954)). Based on Braarud's (1945) clear illustration of the cyst of *Protoceratium reticulatum* (Figure 2D), and my own personal observations of living cysts from Scandinavian waters, it appears possible that Erdtman (Figure 2E) made a mistake in reporting Braarud's identifications. Erdtman noted that this cyst was smaller and had shorter spines than previously shown by Braarud (1945). On first consideration, another cyst illustrated in Erdtman 1954 (Figure 2H herein), appears more likely to be that which Braarud would have identified as *Protoceratium reticulatum,* but the publication states that Braarud only identified this specimen as 'likely to be a dinoflagellate cyst'. However, Braarud had observed many cysts of this species previously and was not likely to make such a mistake. In assessing this possible disparity in hindsight, it is important to realize that Braarud made his identifications from specimens on slides, not drawings probably made later by Erdtman for his publication. We now know that *Protoceratium reticulatum* cysts show a broad size range, and that process lengths vary greatly (Mertens et al. 2012): none of Erdtman's drawings (Figure 2E–J) show processes that are typical for *Protoceratium reticulatum* cysts. In any case, this probable confusion does not detract from the basic point that Braarud identified two hystrichospheres as cysts related to two living dinoflagellates, *Protoceratium reticulatum* and *Gonyaulax polyedra*. Erdtman had provided microscope slides of palynological preparations containing hystrichospheres, from which Braarud identified dinoflagellate cysts, for the first time proving that some fossil hystrichospheres are dinoflagellate cysts.

4. The significance of the Scandinavian work for Evitt's pivotal recognition of fossil dinoflagellate cysts

4.1. Evitt discussed his ideas with Braarud before publishing his pivotal 1961 paper

It is worth noting that Evitt discussed his ideas with Braarud, before he presented his now famous observations on the morphology of fossil dinoflagellates (Evitt 1961), most likely prompted by him having read at least some of the earlier Scandinavian work. Braarud probably was able to share with him much unpublished experience of living cysts and plankton gained since 1945, including Nordli's work. Evitt included Braarud's help in his acknowledgments in the paper, as one of an impressive list of most of the pioneers of fossil dinoflagellate workers of that time. Braarud is the only one mentioned who had personal knowledge of living dinoflagellate cysts. He almost certainly contributed through his discussions with Evitt to those parts of the 1961 paper dealing with living cysts. However, the greatest contribution from the Scandinavian workers is cited in the first of Evitt's (1961) conclusions, where he states that he believed that many fossil hystrichospheres in fact represent dinoflagellate cysts. This pivotal statement launched fossil dinoflagellate cysts as one of the prominent groups of microfossils applied in geology today. It is significant that Evitt went on to say that this idea was not new, and he cited Nordli (1951) and Braarud (in Erdtman 1954) as examples of earlier revelations of this idea (Evitt 1961, p. 403). He also cited McKee et al. (1959), but since they in turn had cited Braarud (1945) and Erdtman (1954), they can hardly be credited for the original idea. Nordli (1951) had not noted the link between his cysts and hystrichospheres, leaving only Braarud (in Erdtman 1954) as the actual reference for this 'new idea' supporting Evitt's conclusions.

4.2. Braarud and co-workers' contribution to *Evitt and Davidson's 1964* paper

Braarud also contributed ideas and crucial samples to a further paper often cited as pivotal to the 1960s breakthrough: Evitt and Davidson (1964). This paper included a photograph of a specimen of *Hystrichosphaera* (= *Spiniferites*) with cell contents, and with fragments of the outer wall (theca) of a motile dinoflagellate attached. The 'hystrichosphere' shown has a basic morphology that Evitt had previously identified in fossil dinoflagellate cysts. The authors reported seeing other examples with thecae completely surrounding the cyst, confirming encystment by a dinoflagellate and supporting Evitt's now published ideas concerning the fossils. Braarud had supplied the plankton sample from the Oslofjord used for this observation, from the same bloom studied earlier by Nordli (1951) where he had also in the same way documented encystment of *Gonyaulax polyedra*. Braarud and Gaarder also helped to identify the dinoflagellates that Evitt and Davidson (1964) used to illustrate the connection between the 'living hystrichospheres' and fossil dinoflagellate cysts. The plankton samples from Braarud were chosen from periods when he and his co-workers had observed encystment in the field. Again, their help was gratefully acknowledged by the authors.

It is worth pointing out that Nordli (1951, fig.1d) unknowingly made an astute observation concerning the encystment process that had been overlooked until Dale (1983). Nordli noted that the cysts of *Gonyaulax polyedra* showing thecal attachment that he observed, only ever had part of the theca (e.g. epitheca) attached. Furthermore, such cysts usually had

markedly shorter processes than many cysts completely released from their attachments (later support for this was provided by Kokinos and Anderson 1995). He interpreted this as indicating that the completion of full process growth occurred after the cyst was released from the theca in which it was produced. From a sample of the same bloom, Evitt and Davidson (1964, figs.1 and 10) showed a similar example of a *Gonyaulax digitale* cyst with several attached thecal plates, which they interpreted differently. They had seen another cyst completely enclosed by its theca, and reported that process growth was completed *before* cyst release. Their diagram illustrating this was generally accepted as confirmation of 'the contractional growth hypothesis' of cyst development (e.g. Evitt, 1969; Sarjeant 1974) still espoused by many today. Dale (1983, p. 102–103, figs.1 and 10) offered a detailed discussion of this controversy that supports Nordli's original observations (which were not realized at the time) and argues against the 'contractional growth' hypothesis. Interestingly, Braarud's illustrations of *Protoceratium. reticulatum* cysts also suggest progressive growth after release from the theca, from an early stage with shorter processes and immature cell contents (Figure 2C) to a later stage with longer processes and mature cell contents (Figure 2D).

4.3. The Scandinavian work influenced early developments in marine palynology at Sheffield University

Evitt had also visited and discussed his ideas with Charles Downie in 1959, prior to the 1961 paper (Riding and Lucas-Clark 2016), as he acknowledged (Evitt, 1961). Downie was a staff member in a dynamically expanding research group of palynologists at Sheffield University, England (Sarjeant 2002). Downie's interests focused on fossil microplankton, and before his discussions with Evitt he was already aware of the extensive literature on the hystrichosphere identity problem. I have not been able to ascertain if, prior to these discussions, Downie was also aware of the earlier Scandinavian work and Braarud's unfinished plan to study living cysts. Nevertheless, shortly afterwards, he and his first graduated doctoral student, Bill Sarjeant, cooperated on a joint publication with Evitt that included acknowledgements for discussions with Braarud and cited Erdtman (1954) (Downie et al. 1963). It would be reasonable to infer that Downie's familiarity with the Scandinavian work at that time influenced the destiny of another of Downie's students, David Wall. Sarjeant (1961) acknowledges discussions with Wall in a paper considering the possibility that hystrichospheres included dinoflagellate cysts. Wall later embarked on a post-doctoral fellowship in 1963 to initiate the studies of living cysts which I later joined at the Woods Hole Oceanographic Institution (WHOI), USA (Wall 1965; Wall and Dale 1966).

5. A personal note

I moved from my work with David Wall at WHOI in 1974, to join the phytoplankton group at the University of Oslo as a Visiting Scientist (Dale 2004). Professor Braarud and Karen Gaarder were both still working there, well past retirement age, and it was a privilege to meet them and begin learning more about living plankton from such legendary pioneers. They had followed our work at WHOI in the literature, and it was particularly moving to share with Braarud my excitement years before upon 'hatching' the first cyst to produce a motile dinoflagellate (Wall 1965, figs. 24–29). I did not realize at the time that I was following research that he had hoped to pursue many years before, as shown by his letter, reproduced in Supplementary Data Appendix 2A here.

One main reason why the full importance of the Scandinavian contributions was overlooked in the history of palynology is that those involved at the time seemed not to have realized its full significance in the broader context of a newly evolving discipline. Erdtman (1954) himself did not emphasize Braarud's crucial contribution in a paper primarily concerned with sedimenting pollen, or the paper's potential importance for marine palynology: Braarud never followed up on this work in his subsequent publications. This probably explains why neither Erdtman (1954) nor Evitt (1961) heralded Braarud's pioneering first identification of hystrichospheres as dinoflagellate cysts.

There are limits to the extent of other workers' assistance that may be included in the inevitably short acknowledgements in a publication. Most publications suffice by citing previous publications or simple acknowledgements for samples or other help provided. It is much more difficult to acknowledge adequately the full extent of personal discussions, even with the most grateful thanks. I appreciated through my personal discussions with the Oslo plankton group, many years later, just how much more information Braarud had assembled concerning the identity of the hystrichospheres before his earlier discussions with Evitt than is commonly known; it was information that Braarud never published. I also witnessed the same appreciation from Evitt when he visited Braarud and myself in Oslo, in 1976. Evitt expressed his gratitude for Braarud's contributions to his earlier developing ideas, more fully than would ever have been possible in his publications. Braarud in turn expressed his gratitude for having seen his own work contribute to the much wider context of Evitt's breakthrough for palynology.

Erdtman (1954) was clearly not aware of the full significance of his and Braarud's findings. Braarud, also, was not aware of this prior to his discussions with Evitt. Shedding light on this Scandinavian connection therefore in no way detracts from Bill Evitt's pivotal role in launching 'dinos' into palynology, or David Wall's contribution in launching 'living cysts' into palynology and biology. It does serve as a good illustration, however, of the way in which major scientific breakthroughs often arise from the collective ideas of earlier workers, in this case working in the related fields of biology and paleontology.

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improved this presentation. I dedicate this work to the memory of Professor Trygve Braarud, a true gentleman and scholar, for his impressive, yet ever humble contribution to our science.

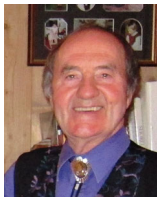
Addendum

Many years after the events described here, I realized why, in all likelihood, Braarud and Nordli had concentrated on the two species *Protoceratium reticulatum* and *Gonyaulax polyedra* in their work in the Oslofjord in the 1940s and 1950s. The fjord at that time was heavily polluted, and their work contributed to the first comprehensive scientific investigation of marine cultural eutrophication. When I and co-workers analyzed dated core sediments for dinoflagellate cysts in the 1990s, we were able to identify a signal tracing the past development of eutrophication in the fjord: comprising a marked increase in total cysts/g sediment, dominated by these same two species (e.g. the eutrophication signal in Dale 2009). The time when this signal peaked corresponded to the time when the two Norwegians first described dinoflagellate cysts.

Disclosure statement

No potential conflict of interest was reported by the authors.

Notes on contributor



BARRIE DALE is Professor emeritus, GeoSciences Department, University of Oslo. His career in palynology began 60 years ago as a Research Technician in the Geology Department, Sheffield University, UK. It included nearly 10 years as Research Assistant/Associate at the Woods Hole Oceanographic Institution, USA, prior to moving to Oslo in 1974. He has received awards in both main fields of his research with living and fossil dinoflagellate cysts: The AASP Medal for Scientific Excellence, 2004, and the 2010 Yasumoto Lifetime Achievement Award from The International Society for the Study of Harmful Algae. Memorable highlights of his career include: 1. Observing and recording the first dinoflagellate motile emerging from its cyst (referred to in this paper), 2. Making two of the first scientific deep-sea dives with the brand new Research Submersible Alvin while at WHOI, 3. Submersing in one of the 'hot springs' we were investigating while camping at sub-zero temperatures on permafrost in the High Arctic Svalbard, and 4. Wondering at cysts thriving in $>40\,^{\circ}C$ and >40 salinity waters of Abu Dhabi. Further bibliographic details may be found in Palynology 28:4–13.

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