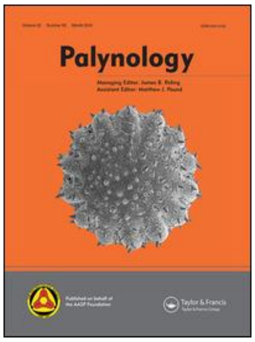

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Comment on '*Wetzeliella* and its allies – the 'hole' story: a taxonomic revision of the Paleogene dinoflagellate subfamily Wetzelielloideae' by Williams et al. (2015)

Peter K. Bijl[a], Henk Brinkhuis[a,b], Lisa M. Egger[c], James S. Eldrett[d], Joost Frieling[a], Arjen Grothe[a], Alexander J. P. Houben[e], Jörg Pross[c], Kasia K. Śliwińska[f] and Appy Sluijs[a]

[a]Marine Palynology and Paleoceanography, Laboratory of Palaeobotany and Palynology, Faculty of Geosciences, Utrecht University, Heidelberglaan 2, 3584 CS Utrecht, The Netherlands; [b]NIOZ Royal Netherlands Institute for Sea Research, Landsdiep 4, 1797 SZ 't Horntje, Texel, The Netherlands; [c]Paleoenvironmental Dynamics Group, Institute of Earth Sciences, Heidelberg University, Im Neuenheimer Feld 234, 69120 Heidelberg, Germany; [d]Shell International Exploration & Production B.V, Kesslerpark 1, 2288 GS Rijswijk, Netherlands; [e]Netherlands Organisation for Applied Scientific Research (TNO), Princetonlaan 6, 3584 CB, Utrecht, The Netherlands; [f]Geological Survey of Denmark and Greenland (GEUS), Øster Voldgade 10, DK-1350 Copenhagen K, Denmark

ABSTRACT

The taxonomic revision of the dinoflagellate cyst subfamily Wetzelielloideae by Williams et al. (2015) places primary emphasis on the type of archaeopyle, and secondarily on wall ornamentation. Williams et al. (2015) argues that this provides more clarity for taxonomic differentiation within the subfamily of Wetzelielloideae, and adds to the stratigraphical significance of species within. We find, however, that their proposed revision (1) introduces taxonomic criteria that divert drastically from these in other dinoflagellate cyst subfamilies, (2) unnecessarily erects and emends many new genera and species, and (3) poses serious practical limitations, which together (4) lead to profound reduction of the stratigraphical applicability of many marker species. In this contribution, we substantiate our concerns regarding the approach and criteria used by Williams et al. (2015). We propose to retain the generic definitions of Wetzelielloideae that existed prior to the revisions by Williams et al. (2015), until a revision supported by the community is available.

KEYWORDS
Comment; taxonomic revision; dinoflagellate cyst; Wetzelielloideae; stratigraphy

1. Introduction

Williams et al. (2015) have proposed a taxonomic revision of the dinoflagellate cyst subfamily Wetzelielloideae. In their view the 'generic definitions within the subfamily of Wetzelielloideae have been blurred, and too much focused on wall ornament and horn development' (Williams et al. 2015, p. 290). These authors further argue that the blurred generic definitions have 'limited the utility of Wetzelielloideae as biostratigraphic marker'. As an example the authors refer to *Wetzeliella articulata*, a species that has a remarkably long stratigraphical range of 32 million years, from the Paleocene to the Oligocene. In fact, they assume that the criteria used in this species concept are not satisfactorily distinctive to cover (apparent) morphological variability. Therefore, they have introduced novel concepts for the taxonomy at the generic level for the Wetzeliellioideae, placing primary emphasis on the type of archaeopyle, and secondarily on wall ornamentation. Williams et al. (2015) argued that the emphasis placed on the archaeopyle type provides much more clarity for taxonomic differentiation within the subfamily Wetzelielloideae.

Williams et al. (2015) defined five different types of the 2a intercalary archaeopyle (equiepeliform, hyperepeliform, latiepeliform, soleiform and hypersoleiform). Further, these authors defined five different types of wall ornamentation, which they applied as a secondary criterion at the generic level. The authors reviewed all species in the subfamily in terms of archaeopyle type and wall ornamentation, resulting in a matrix. Their review requires the formal description of no less than 13 new genera, emendation of the diagnosis of three existing genera, and the formal description of three new species. They concluded that the soleiform archaeopyle is a consistent feature in the younger stratigraphical range (i.e. Bartonian and younger) of the Wetzelielloideae, while the epeliform archaeopyles in this subfamily occur in the older stratigraphical record (Selandian–Bartonian).

We agree with Williams et al. (2015) that a thorough review of the taxonomic concepts and definitions for Wetzelliellioideae would benefit the scientific community, and we greatly appreciate the efforts made in this direction. In theory, the approach taken by Williams et al. (2015) could result in a solid, consistent taxonomic framework, since it is based on clear generic criteria. We also agree that some variability in archaeopyle type and level of detachment exists within the subfamily of Wetzelielloideae. After careful consideration, however, we find that their proposed revision (1) introduces taxonomic criteria that divert drastically from well-established conventions, (2) unnecessarily erects and emends many new genera and species, and (3) poses serious analytical and practical limitations, which together (4) lead to a profound reduction of the stratigraphical applicability of marker species, while not introducing any new stratigraphical markers in replacement. In this contribution, we

CONTACT Peter K. Bijl p.k.bijl@uu.nl

substantiate our concerns regarding the approach and criteria used by Williams et al. (2015) and, based on these concerns, propose to retain the original generic definitions of Wetzelielloideae.

2. Problems resulting from the new classification

Although in theory the taxonomic revision proposed by Williams et al. (2015) provides a clear and consistent set of definitions, we have identified several critical issues in its application that can essentially be narrowed down to four main issues.

2.1. *Pragmatism versus hypothesised evolutionary lineages*

Extinct dinoflagellate cyst species cannot be directly linked to the affiliated biological species – even extant motile/cyst relationships are not established fully (e.g. Head 1996). Therefore, any taxonomic framework for extinct dinoflagellate cysts must rely on clearly visible, distinguishable morphological characteristics. For this reason, dinoflagellate cyst families are typically separated based on plate tabulation patterns following the system of Fensome et al. (1993). Taxonomic definitions at the generic level are made predominantly based on specific morphological and geometric features (such as cyst outline, cavation, number of wall layers, process outline and distribution, plate and/or sutural ornamentation, etc.), with the archaeopyle type being a consequence of geometry. Williams et al. (2015) broke with this convention because they specifically consider archaeopyle type to be an indicator of phylogeny. Specifically, Williams et al. (2015) applied the basic assumption that the archaeopyle type directly reflects the shape of the plate(s) involved in archaeopyle formation, which is not necessarily the case for all dinoflagellate cyst species (e.g. Harland 1982). Because sutures are not always discernible for Wetzelielloideae, this cannot be proven for many Wetzelielloideae specimens. Therefore, we are sceptical about the validity of this fundamental assumption underlying the taxonomic revisions of Wetzelielloideae. We have concerns that the drastic revisions of the primary criteria for taxonomic classification as proposed by Williams et al. (2015) do not reflect phylogenetic significance. Regardless of our concerns, the revision of taxonomic concepts to accommodate just one subfamily seems an illogical step if the taxonomic concepts applied towards the other dinoflagellate cyst groups remain the same.

2.2. *Morphological differences between species should be more prominent than morphological variability within species*

The validity of the proposed taxonomic definitions in the subdivision of Wetzelielloideae does not allow for plasticity in archaeopyle type within otherwise morphologically similar dinoflagellate cysts. This leads to taxonomic separation of – apart from the type of archaeopyle – morphologically indistinguishable species (Plate 1). However, many other dinoflagellate cyst taxa are characterised by variability in archaeopyle type, and the level of detachment of the operculum is permitted within a genus, and even within species definitions. For instance, *Dissiliodinium* and *Durotrigia* (Bailey 1987; Feist-Burkhardt et al. 2001) have a variable archaeopyle consisting of one to five precingular plates; *Lingulodinium machaerophorum* (Wall 1967) and *Diphyes* (Goodman & Witmer 1985) have either a 3′ precingular or a tA apical archaeopyle; *Florentinia* (e.g. Sluijs & Brinkhuis 2009) varies its archaeopyle involving from tA to tA3P; *Schematophora* (Bijl et al. 2013b) has various levels of detachment of the apical series; species of *Spinidinium* and *Vozzhennikovia* (Sluijs et al. 2009) involve either one (2A) or all three anterior intercalary plates in the archaeopyle; and *Phthanoperidinium* (Islam 1982) varies its archaeopyle by occasionally including the 4″ plate to the otherwise 2A archaeopyle. Notably, many *Protoperidinium* species (e.g. Harland 1982) vary in outline and type of the 2A archaeopyle. For these genera, taxonomic concepts at genus and species levels are not primarily set on archaeopyle type but, rather, on wall morphology, ornamentation and process distribution. We indeed observe variability in the type of archaeopyle in many Wetzelielloideae, even within the same samples, for example in specimens of *Apectodinium* in the original description (see examples in Plate 1). Scanning electron microscope images of a specimen of *Apectodinium hyperacanthum* (Bijl et al., 2013b, plate VII, figure n) show a clear angular, rectangular archaeopyle but with an adnate anterior end. These two characteristics together are not compatible with the proposed taxonomic concept of Williams et al. (2015) for *Apectodinium hyperacanthum*, which should have a detached operculum. If we followed the taxonomic concepts proposed, we should erect a new genus and new species for the specimen illustrated by Bijl et al. (2013). However, based on wall ornament, this specimen is clearly a species of *Apectodinium* in its original taxonomic concept. The proposed taxonomic revision of Williams et al. (2015) would place the specimens exhibiting adnate soleiform archaeopyles within *Wetzeliella*, while based on all the other morphological features, they have close affinities to *Apectodinium*, which it restricts to equiepeliform archaeopyles. In our view, the adnate soleiform versus free epeliform archaeopyles both occur within a complex of Wetzelielloidae that are similar in many more morphological characteristics than they differ, which is why in the original concept all of these were grouped into *Apectodinium*.

The original taxonomic concept of Wetzelielloideae is very practical for most of the species. Applying the new taxonomic concept to the latter leads to many discussions, confusion, and unnecessary and unwanted taxonomic splitting. Taxonomic uncertainty in the original concepts of Wetzelielloideae occurs predominantly at the species level and only very rarely at the generic level. For instance, in many cases (sub-optimal preservation, overload of amorphous organic matter, clumping, overoxidation), the – in our view – subtle differences in outline and ornament between *Charlesdowniea columna* and *Charlesdowniea coleothrypta* make it difficult to separate them from one another in the original taxonomic framework. However, Williams et al. (2015) considered these two species to be within two different genera, as they have noted slight differences in archaeopyle type. This proposed taxonomic revision does not at all alleviate the difficulty in deciding to which of the two species a specimen belongs. In fact it complicates the situation

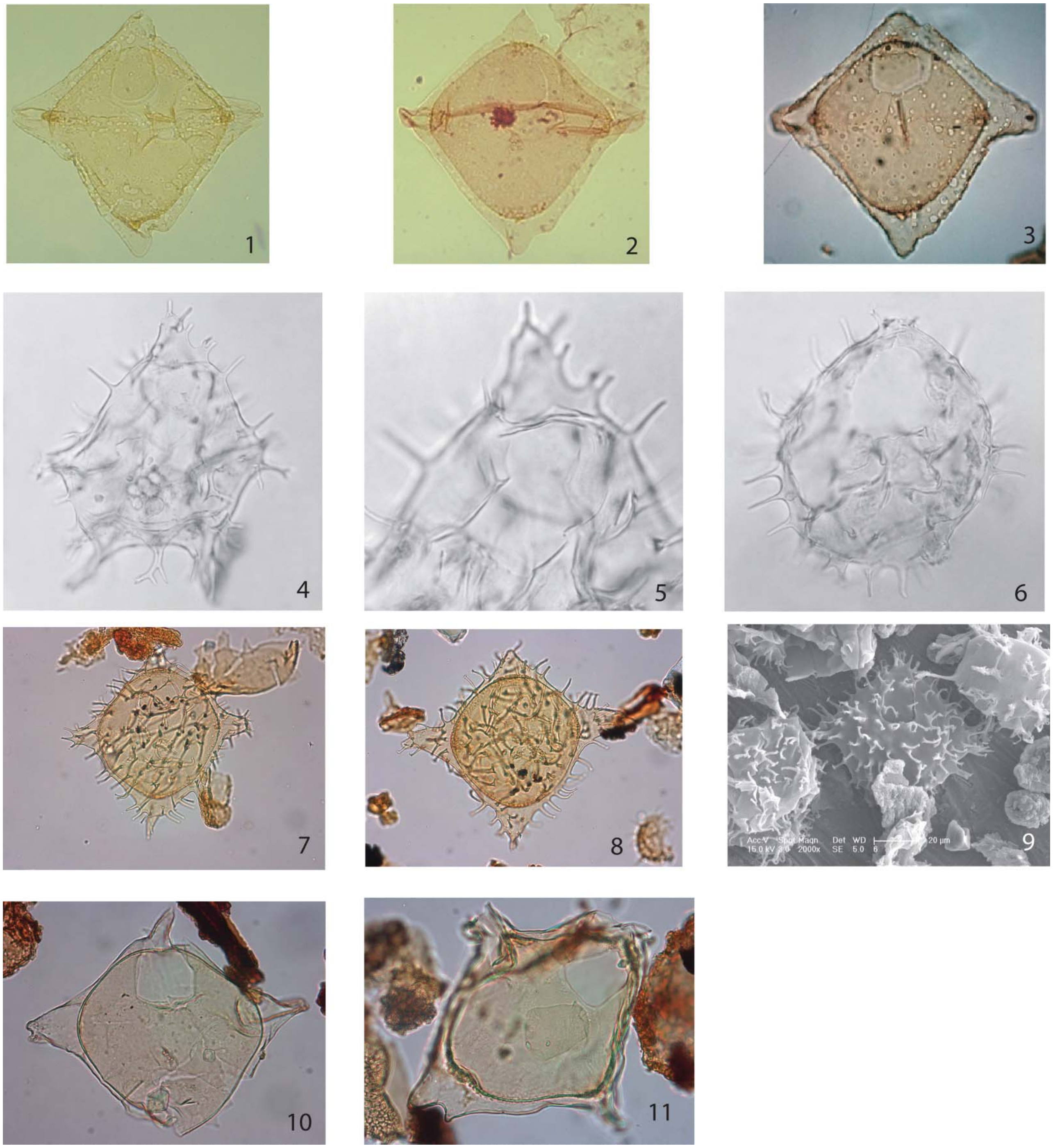

Plate 1. Examples of Wetzelielloideae specimens that show similar morphology but slight variability in archaeopyle type. Specimens herein are classified based on the taxonomic concepts prior to the contribution by Williams et al. (2015). 1–3. *Rhombodinium porosum* specimens published previously in Williams et al. (2004) showing variability in archaeopyle type from hypersoleiform to ?epeliform. In our view, the strikingly similar morphological features of these specimens indicate these species should be placed within one genus. According to the taxonomic concepts of Williams et al. (2015), the specimens should be placed in at least two different genera. 4–6. *Apectodinium* specimens showing an archaeopyle, which involves also the 4″ precingular plate (previously published in Crouch et al. 2003). If involvement of the 4″ plate in the archaeopyle formation is not allowed within *Apectodinium*, a new genus must be erected for these specimens. 7, 8. *Wetzeliella symmetrica* specimens from the Oligocene of the North Sea showing a soleiform archaeopyle (7) and a (slightly?) hypersoleiform archaeopyle (8). To us, the morphological features indicate these species should be placed in one species, and not in different genera which would be the case if the taxonomic concepts of Williams et al. (2015) were to be followed strictly. 9. Scanning electron microscope image of a specimen of *Apectodinium* with an angular archaeopyle with clear posterior attached archaeopyle. The specimen is from Paleocene–Eocene boundary sediments from Ocean Drilling Program Site 1172, and has previously been illustrated in Bijl et al. (2013). 10, 11. *Rhombodinium draco* from the mid-Oligocene of the North Sea Basin. 10. At first sight this specimen has a hyperepeliform archeopyle; hence, it should be considered a (new?) species of *Rhadinodinium* according to Williams et al. (2015). However, the anterior margin of the archaeopyle shows clear signs of rupture of the (likely) once-soleiform archaeopyle. When it becomes questionable whether an operculum is secondarily ruptured or primarily attached/detached, identification at the genus level becomes impossible if too much emphasis is given to the archaeopyle type for classification. However, this specimen clearly belongs to *Rhombodinium draco* if we allow for some plasticity in archaeopyle type.

because, in the new taxonomic concept, the generic classification is compromised if the archaeopyle type is not clearly discernible. We argue that because the two species share so many morphological features, it is most practical to at least retain these species in the same genus. Williams et al. (2015) broke with this basic principle of hierarchy in morphological variation for the Wetzelielloideae, which is a profound concern for the field of dinoflagellate cyst palaeontology.

2.3. *Applicability of archaeopyle type as a primary generic criterion*

Central to the taxonomic definitions proposed by Williams et al. (2015) is the type of archaeopyle. In practice, however, this particular morphological feature is not easily assessed using transmissed light microscopy, particularly in Wetzelliellioideae. This is because the archaeopyle can be poorly visible in many specimens for numerous factors including poor contrast between the archaeopyle and the translucent wall; specimens are often sub-ideally oriented on the microscope slide, lack parasutural/penitabular ornamentation, and in some instances bear numerous processes that may obscure the visibility of the archaeopyle (e.g. Sluijs & Brinkhuis 2009 plate 1, figures I, J; Bijl et al. 2013, plate I, figures e, j). Finally, some specimens (may) have partially adnate opercula (see examples in Plate 2), to say nothing of specimens that have not hatched.

The orientation of the cyst relative to the plane of view poses a serious limitation on the practicality of the proposed taxonomic criteria underlying the revision. In the paper by Williams et al. (2015), this problem was illustrated in figures 15 and 16 of plate 1, and figures 15 and 16 of plate 2. Two seemingly similar specimens with identical cyst outline and wall ornament were illustrated. However, Williams et al. (2015) placed these two specimens into two different genera because they deduced a difference in archaeopyle type. According to Williams et al. (2015) the specimen illustrated in plate 1 has an equiepeliform archaeopyle, and, according to their scheme, is to be placed in *Sophismatia*, while the specimen illustrated in plate 2 exhibits a hyperepeliform archaeopyle and is therefore to be assigned to another genus, i.e. *Sagenodinium*. However, the specimen in plate 1 is oriented in oblique polar view, while the specimen in plate 2 is photographed in equatorial view. The oblique polar view results in an underestimation of the height of the archaeopyle relative to its width, giving the impression of an equiepeliform archaeopyle. This example also supports the inference that two cysts that are as similar as these two specimens should be assigned to the same species, or at least the same genus, based on outline and ornamentation, even if the archaeopyles differ slightly (see Section 2.2).

The practical application of taxonomic concepts should be reconsidered when generic assignment is easily influenced by analytical issues, such as the angle of view. Even more crucially, taxa with identical cyst outline and wall ornamentation, such as the above examples, cannot be classified to the genus level if the archaeopyle type cannot be determined, which is often the case in Wetzelielloideae. Our example given here clearly points to the ambiguity induced by the taxonomic concepts proposed.

We therefore find that the proposed revision leads to unnecessary speciation of dinoflagellate cyst taxa that are highly similar (if not identical) in cyst outline and wall ornamentation, but only vary slightly, if at all (see examples above), in archaeopyle type. We now observe very chaotic, inconsistent genus and species concepts, in which cysts with the same wall features are placed in different genera just because of a slight, often non-diagnostic difference in archaeopyle type.

2.4. *Applicability of the proposed taxonomic framework to existing stratigraphically important species*

Williams et al. (2015) argued that some species within *Wetzeliella* (notably *W. articulata*) have a generic species definition and as such have a long stratigraphical range. The proposed revision aims to add more stratigraphical importance to such long-ranging species. Interestingly, even after the proposed taxonomic revision, *Wetzeliella articulata* remains a species with a rather broad taxonomic description and a long stratigraphical range. There are, however, numerous examples where species within the Wetzelielloideae, well defined within the original taxonomic framework, represent clear, unambiguous stratigraphical markers, such as; *Apectodinium augustum* at the Paleocene–Eocene Thermal Maximum (e.g. Sluijs et al. 2007); *Charlesdowniea edwardsii*, *Dracodinium waipawaense* and *Wetzeliella samlandica* in the early Eocene (Hollis et al. 2009; Hollis et al. 2012; Bijl et al. 2013a, b; Dallanave et al. 2016); *Dracodinium rhomboideum*, *Dracodinium pachydermum* and *Charlesdowniea columna* in the middle Eocene (Eldrett et al. 2004; Eldrett & Harding 2009; Firth et al. 2013); and *Wetzeliella gochtii* and *Rhombodinium perforatum* in the Oligocene (e.g. Pross 2001; Fensome et al. 2008; Pross et al. 2010; Sliwinska et al. 2012; Egger et al. in press). Williams et al. (2004) published a cornerstone stratigraphical article in which many wetzelielloid dinoflagellate cyst species are listed as good biostratigraphical markers including *Charlesdowniea columna*, *C. crassiramosa*, *C. edwardsii*, *Dracodinium condylos*, *D. politum*, *D. varielongitudum*, *D. waipawaense*, *Rhombodinium draco*, *R. perforatum*, *R. porosum*, *Wetzeliella gochtii*, *W. meckelfeldensis* and *Wilsonidium echinosuturatum.* If we accept the proposed taxonomic revisions, the stratigraphical ranges of many of these species may need to be seriously reconsidered and, in the worst case, may become practically useless if we do not allow for some plasticity in archaeopyle type. The stratigraphical ranges of species with a stable archaeopyle type and morphology will in theory remain unaffected by the taxonomic revision. However, we cannot be certain that these species really have stable archaeopyle types, as this has never been the primary criterion to distinguish genera or species. Therefore, it would require a thorough revisiting of the stratigraphical records where species were initially stratigraphically calibrated to verify whether, according to the taxonomic concepts of Williams et al. (2015), the stratigraphical calibration of the species is still correct, or whether the species which were initially grouped together now need to be separated based on a different archaeopyle type. Contrary to Williams et al. (2015), we thus see no improvement in the stratigraphical applicability of Wetzelielloideae in the revised taxonomic concepts.

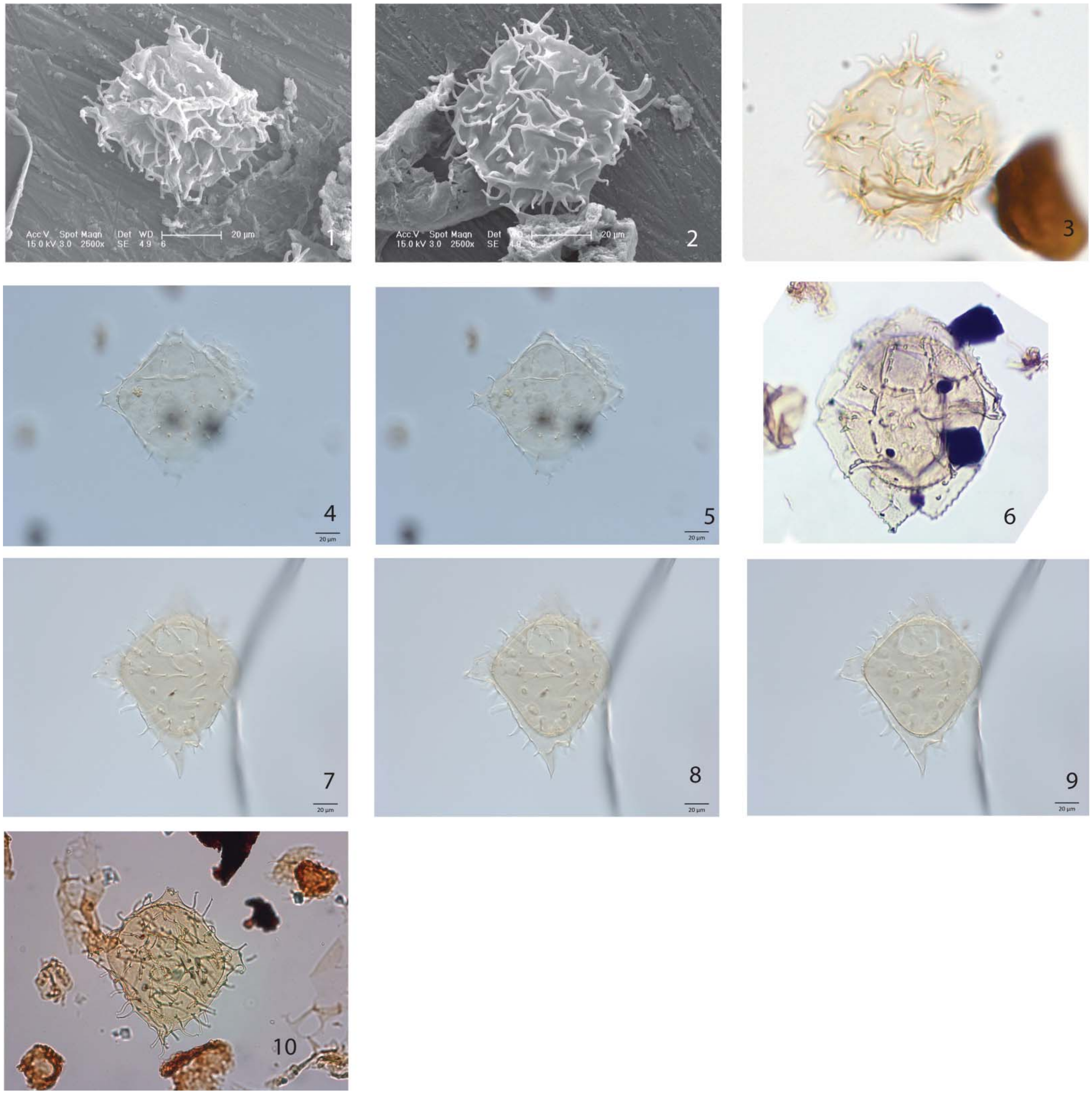

Plate 2. Examples of specimens that do not clearly show an archaeopyle type, and, therefore, are impossible to classify at the genus level using the proposed taxonomic concepts of Williams et al. (2015). The dominance of such specimens that are folded or in which the archaeopyle is otherwise poorly visible over those with a clear archaeopyle outline illustrates the problems of practicality of the proposed taxonomic division. 1, 2. Scanning electron microscope images of specimens of *Apectodinium* from the Palaeocene–Eocene boundary sediments from Ocean Drilling Program Site 1172, which were previously published in Bijl et al. (2013). Ambiguity about archaeopyle outline and whether the operculum is posteriorly attached makes it impossible to classify these specimens at the genus level. With light microscopy such subtle archaeopyle outlines are even more difficult to discern. Based on morphological features of the wall and pericoels, these specimens are easily recognised as *Apectodinium homomorphum*, but with the primary focus on archaeopyle type, they can only be classified on a subfamily level. 3. Specimen of *Apectodinium homomorphum* from the Palaeocene–Eocene boundary sediments from Ocean Drilling Program Site 1172, which was previously published in Bijl et al. (2013). This specimen seems to show a hyperepeliform archaeopyle, but it might also be the result of folding. 4, 5. *Wetzeliella symmetrica* specimen from the Oligocene of the western North Atlantic [Integrated Ocean Discovery Program (IODP) Leg 342, Site U1411]. The operculum is still in place, yet it is difficult to discern whether it is still posteriorly attached. 6. *Wilsonidium echinosuturatum* with an operculum in place, which seems to be attached at the posterior left corner. This specimen illustrates the possibility that any archaeopyle type can be attached to some degree. 7–9. *Wetzeliella symmetrica* specimen from the Oligocene of the western North Atlantic (IODP Leg 342, Site U1411). Operculum seems to be in place, but it is difficult to discern whether the operculum is still attached or not. The Williams et al. (2015) concepts would impose a serious limitation on classifying this specimen at the genus level, while using previous classifications this specimen clearly belongs to *Wetzeliella symmetrica*. Also note the apparent variability in archaeopyle outline between this specimen and that shown in figures 4 and 5. 10. *Wetzeliella symmetrica* from the North Sea Basin. The archaeopyle is difficult to discern, making classification at the genus level impossible according to the classifications of Williams et al. (2015).

3. Concluding remarks

We recognise that dinoflagellate cyst taxonomy is imperfect for all groups, including the Wetzeliellioideae, and that there is a constant need for improvement. Williams and colleagues are profound experts in this field and their countless high-quality contributions are invaluable. However, based on the material we have observed, we find the variability and plasticity of cyst-wall and archaeopyle morphology within the Wetzelielloideae equally large, but render the cyst-wall morphology in practice a much more practical criterion for taxonomic differentiation than archaeopyle type, and more in line with that within other families. The above considerations on the taxonomic revisions proposed by Williams et al. (2015) lead us to propose to retain the taxonomic concepts within Wetzeliellioideae that existed prior to their contribution.

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Author biographies

PETER BIJL finished his PhD in 2011 in the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands with Henk Brinkhuis, Stefan Schouten and Appy Sluijs. His research focuses on the environmental and climatological evolution of the Cretaceous-Cenozoic of the Southern Ocean, by applying palynological and organic geochemical proxies and comparing with numerical models. Peter is currently assistant professor of applied biostratigraphy in Utrecht, and director of the LPP Foundation.

HENK BRINKHUIS is general director of the Royal Netherlands Institute for Sea Research (NIOZ) and part-time professor in marine palynology and palaeoecology at Utrecht University. He received his doctorate in Eocene-Oligocene marine palynology, palaeoecology and palaeoceanography from Utrecht University. Henk has a strong taste for Phanerozoic extreme climate change, (palaeo)oceanography and (palaeo)ecology. He has (co-)authored over 125 peer-reviewed scientific publications and (co-)supervised over 25 PhD students. As a Dutch national representative, Henk is strongly involved in the International Ocean Discovery Program (IODP).

LISA M. EGGER is currently a PhD student at the Institute of Earth Sciences, Heidelberg University, Germany. Supervised by Oliver Friedrich and Jörg Pross, she studies Oligocene dinoflagellate cysts based on material from IODP Expedition 342 (Paleogene Newfoundland sediment drifts), with the aim of deciphering changes in surface-water characteristics across the Eocene-Oligocene transition, the 'mid'-Oligocene and the Oligocene-Miocene transition. She is also strongly interested in late Eocene to early Miocene dinoflagellate cyst biostratigraphy.

JAMES. S. ELDRETT joined Shell Exploration and Production in 2006 as a biostratigrapher. Since 2011, James has been working in the Integrated Geoscience Research Team based in Houston, USA and Rijswijk, the Netherlands. His research covers all aspects of global geology, specialising in stratigraphy and geochemistry of the Phanerozoic in support of regional exploration activities.

JOOST FRIELING finished his PhD in 2016 in the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands with Appy Sluijs and Gert-Jan Reichart. His research focuses on the climate, carbon cycle and ecological response during the Paleocene-Eocene Thermal Maximum using palynology, and organic and inorganic geochemical proxies.

ARJEN GROTHE finished his PhD in 2016 at the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands with Henk Brinkhuis and Wout Krijgsman. His research focuses on the palaeoenvironmental evolution of the Paratethys Sea and its connectivity with the Mediterranean Sea from the Eocene to the Pliocene, by applying palynological and inorganic geochemical proxies. Arjen is currently a post-doctoral researcher in Utrecht.

ALEXANDER J. P. (SANDER) HOUBEN obtained his PhD in 2012 from Utrecht University, where he studied the climatic and environmental boundary conditions for glacial expansion across the Eocene-Oligocene Transition, mainly using palynology. Sander is currently an exploration geologist and biostratigrapher in the Basin Analysis Team of TNO (the Netherlands Organisation for Applied Scientific Research), where he addresses palaeoenvironmental and biostratigraphical constraints in complex tectonostratigraphical studies.

JÖRG PROSS holds a professorship in palynology and palaeoenvironmental dynamics at the Institute of Earth Sciences, Heidelberg University, Germany. His research focuses on palaeoenvironmental and palaeoclimatic reconstructions based on palynomorphs from both the marine and terrestrial realms with emphasis on the Cenozoic.

KASIA K. ŚLIWIŃSKA received her PhD in 2011 from Århus University, Denmark. Currently she is working as a researcher at the Geological Survey of Denmark and Greenland (GEUS). Her research interests are palynology, biostratigraphy and palaeoclimatology of the North Sea Basin, North Atlantic and Arctic regions during the Early Cretaceous and the Paleogene.

APPY SLUIJS received his PhD in 2006 (*cum laude*) at the Laboratory of Palaeobotany and Palynology, Utrecht University, the Netherlands, working with André F. Lotter and Henk Brinkhuis, where he is currently a full professor of Palaeoceanography. His interests include the functioning of climate, oceans and ecosystems during past climates and particularly during events of massive change, currently mostly focused on the early Paleogene and Miocene. Recent studies also include culturing experiments to elucidate dinoflagellate carbon acquisition physiology and related isotopic fractionation to evaluate the potential for reconstructing palaeo-CO_2 concentrations based on dinoflagellate cyst biogeochemistry.

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