

Microphytoplankton from the Jena Formation (Lower Muschelkalk Subgroup, Anisian) in the forestry quarry at Herberhausen near Göttingen (Germany)

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Göttingen
Contributions to
Geosciences
www.gzg.uni-goettingen.de

77: 63-76, 6 figs. 2014

In a pilot project microphytoplankton has been studied from a 13 m thick section of carbonates from the upper part of the Anisian Jena Formation (Middle Triassic). The section is exposed in a small quarry near Göttingen, northern Germany, and located near the center of the Germanic Basin. The isolated phytoplankton assemblages consist exclusively of polygonomorph (*Verybachium*) and acanthomorph (mainly *Micrhystridium*) acritarchs and prasinophytes, while dinoflagellates are still missing. The diversity of acritarchs and prasinophytes is high and particularly remarkable since the Anisian stage is just prior to the turnover from the “Phytoplankton Blackout” to the appearance of modern phytoplankton. New for the Middle Triassic is the diversity and abundance of very small acanthomorphs and prasinophytes (<15 µm) as revealed by SEM, which requires more detailed systematic study.

Considering acritarchs as the more stenohaline and the prasinophytes as a rather euryhaline segment of the phytoplankton their relative proportion can be interpreted as indicating changes in salinity. Thus, quantitative phytoplankton analysis of our section suggests alternations of normal marine conditions and conditions restricted by increased salinity, which can be related to changes in lithofacies. Problems of the biologic nature and mode of life of small acanthomorphs and prasinophytes are briefly discussed. The results of our study are promising to considerably refine environmental interpretations within the Muschelkalk Group of the Germanic Basin in general.

Received: 13 May 2013

Subject Areas: Palaeobotany

Accepted: 01 August 2013

Keywords: Acritarchs, prasinophytes, palynofacies, Triassic, Anisian, Muschelkalk, Germanic Basin

Introduction

The eukaryotic microphytoplankton is a crucial segment of aquatic primary production. It is not only an important basic driver of the marine food web, but, being dependent on dissolved nutrients, light and salinity, also provides deep insights into the physico-chemical environment of

the marine realm and its variations in space and time. Indeed, the striking synchronicity of plate tectonic events, major faunal turnovers and changes in phytoplankton diversity is a clear signal of the pivotal role of microphytoplankton as a mediator between the biogeochemical cycle

and the development of marine biota in general as pointed out by a number of authors (e.g., Katz et al. 2004; Riegel 2008; Servais et al. 2008; van de Schootbrugge et al. 2005; Vecoli 2008). On a similar note, it has repeatedly been demonstrated that phytoplankton shows sensitive responses to changes in sedimentary environments and facies especially in coastal and shelf areas (e.g., Heunisch 1990; Loh et al. 1986; Prauss & Riegel 1989; Pross & Brinkhuis 2005).

Between the great end-Devonian demise of acritarchs and the mid-Mesozoic appearance of modern phytoplankton, primary productivity of late Palaeozoic and early Mesozoic seas appears to have been sustained on a relatively low level of diversity and abundance mainly by prasinophytes and a few survivors among the acritarchs. Therefore, the low microphytoplankton profile between the Devonian–Carboniferous boundary and the mid-Triassic has been somewhat provokingly termed the “Late Palaeozoic Phytoplankton Blackout” (Riegel 2008). Early Palaeozoic acritarchs and mid-Mesozoic to Cenozoic dinoflagellates and coccolithophorids proved to serve as excellent stratigraphic indices, while prasinophytes, main phytoplankton constituents during the gap in between, seemed to be rather long-ranging, less diversified morphologically, more facies dependent and highly vacillating in their occurrence. They seem to respond favourably to reduced salinity and temperature in surface waters and thrive particularly well under conditions of a stratified water column (Guy-Ohlson 1996; Prauss & Riegel 1989; Tappan 1980). Thus, the terms opportunistic or disaster species (Tappan 1980) have been commonly applied.

In this context, phytoplankton studies of the Germanic Muschelkalk Group (Anisian–Lower Ladinian, Triassic) are of particular interest since, for one, the Anisian is the last stage of the “Phytoplankton Blackout” immediately prior to the dawn of the modern phytoplankton (i.e., dinoflagellates, coccolithophorids and diatoms), and secondly, the Germanic Basin is an intracontinental, partially closed basin marginal to the Tethys Ocean, in which salinities, water column stability and benthic population density were highly variable.

The first unequivocal dinoflagellate cyst *Sabulodinium* appears in the Ladinian of Australia (Balme 1990; Stover & Helby 1987) and, little later, species of *Suessia*, *Rhaetogonyaulax* and other dinoflagellate genera invaded the Germanic Basin during marine incursions of the Upper Triassic, reaching a notable diversity only by the middle Rhaetian (Heunisch 1996). The same factors which promoted the diversification of many fossil groups since the Middle Triassic and initiated the rise of dinoflagellates, may also have fueled the productivity and diversity of phytoplankton associations in the terminal stages of the “Phytoplankton Blackout” just prior to the dinoflagellate entry. Although related comparative studies are still lacking, it seems that acritarchs and prasinophytes have developed a remarkable increase in diversity during the middle Triassic.

A striking feature of Mesozoic phytoplankton assemblages appears to be the occurrence of what has previously been described as “small acritarchs” (Habib & Knapp 1982; Schrank 2003). Their occasional abundance in the Triassic of the Germanic Basin has been recorded before (Heunisch 1990; Reitz 1985), but their significance is largely neglected in routine studies, since their diagnostic morphology can only be resolved by scanning electron microscopy (SEM) and their stratigraphic utility has been considered rather limited.

Responses of phytoplankton assemblages to environmental changes have previously been observed in the Germanic Basin in particular at the boundary Muschelkalk to Keuper groups, where facies changes are most pronounced (Brocke & Riegel 1996; Düringer & Doubinger 1985; Heunisch 1986, 1990; Reitz 1985). For the Lower Muschelkalk, Götz (1996) and Götz & Feist-Burkhardt (1999) focused on the response of phytoplankton assemblages to sea level fluctuations and on palaeogeographic aspects (Götz & Feist-Burkhardt 2012).

Here, we present a cross section of the “old” phytoplankton just prior to the dawn of modern phytoplankton as a pilot study to trace phytoplankton responses to aquafacies changes as deduced from lithological and macrofaunal changes with a vertical lithologic column. We selected an interval within the Jena Formation (Anisian, Lower Muschelkalk Subgroup, Middle Triassic), which is favourably exposed at Joachim Reitner’s backyard, the abandoned Herberhausen forestry quarry near Göttingen.

Geological framework

Generalities and lithostratigraphic context

The abandoned Herberhausen quarry is located about 1.3 km east of Göttingen and exposes parts of the Jena Formation (Anisian), which was deposited in an intracontinental sea marginal to the Tethys (“Germanic Basin”, Fig. 1A). Traditionally, the Jena Formation is subdivided lithostratigraphically into a succession of platy, wavy and marly (often heavily bioturbated) limestones and marls (“Wellenkalk”), in which intervals of thick bioclastic/oolithic limestone beds are intercalated (Oolith Member, Terebratula Member, Schaumkalk Member; Fig. 1B). These serve basinwide as marker beds in lithostratigraphic correlation. Widespread yellow marls and limestones (“Gelbkalk”: dedolomitised limestones and marls) are intercalated in some intervals, indicating short-term establishment of restricted hypersaline (lagoonal) environments in wide parts of the Germanic Basin.

A first description of the quarry with data on faunal assemblages was given by Hagdorn & Simon (1983), who figured a 15.5 m thick section from the middle of the Upper *Terebratula* Bed on (comp. Fig. 2). Together with the section given in Arp et al. (2004), a total thickness of ab-

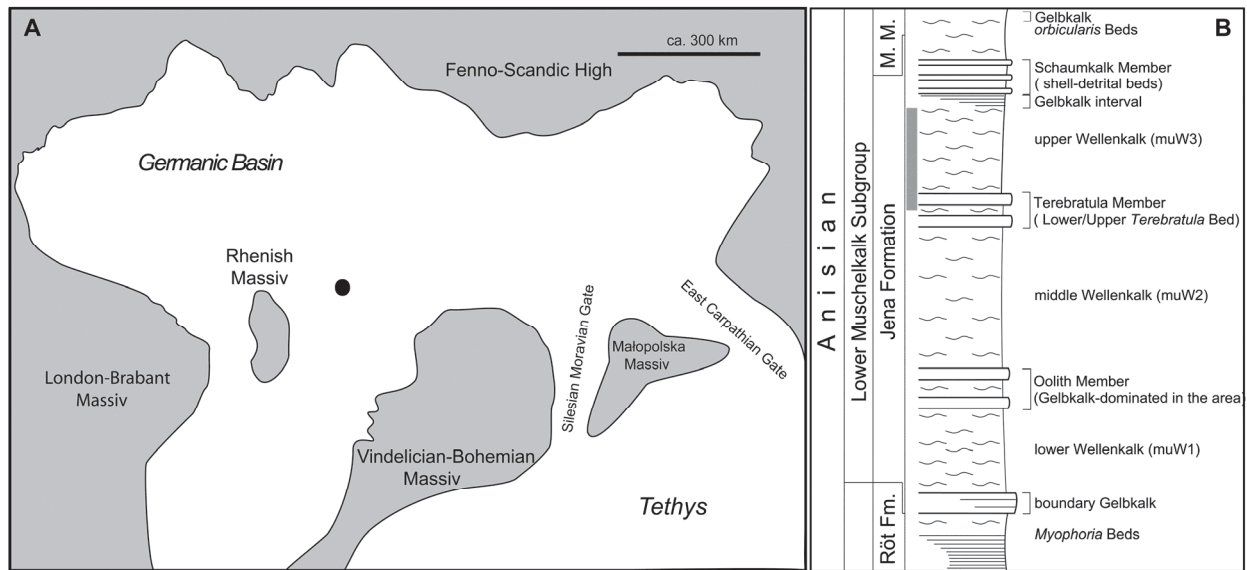


Fig. 1: (A) Anisian palaeogeography in Central Europe with location of studied section; (B) simplified lithostratigraphic subdivision of the Jena Formation (Lower Muschelkalk Subgroup, Anisian).

out 17 m (starting with wavy limestones separating the Lower and Upper *Terebratula* Beds: “Wellenkalkzwischenmittel”) was exposed with time. Crucial for correlation with other sections and for fitting the Herberhausen section into the well-established regional lithostratigraphic frameworks of the Jena Formation (see Kramm 1997; Stein 1968; Schulz 1972) is the occurrence of a 1.5 m thick Gelbkalk at the top of the section (Hagdorn & Simon 1983), which is not exposed today. The succeeding massive Gelbkalk above the Upper *Terebratula* Bed occurs at the top of the Upper Wellenkalk muW3, below the base of the Schaumkalk Member in the wider area (Kramm 1997; Schulz 1972; comp. Fig. 1B). Thus, the Herberhausen section covered almost the entire muW3, but the base of the Schaumkalk Member was not reached. The thickness of muW3 at Herberhausen from the top of the Upper *Terebratula* Bed to the top of the previously exposed Gelbkalk is about 13 m, which equates circa with the thickness as described from other sections in southern Lower Saxony and Northern Hesse (Schulz 1972).

Sedimentary cycles

Numerous authors divide the Jena Formation into a number of sedimentary cycles (Fiege 1938; Götz 1994; Kedzierski 2002; Klotz 1990; Lippmann et al. 2005; Schulz 1972). Although sea level is believed to be the main trigger of this cyclicity, the interpretation of sediment geometries and geochemical trends remains ambiguous, and no generally valid triggering mechanism has been presented yet (see summary in Lippmann et al. 2005). For the Lower Muschelkalk, Kramm (1997) presented a synthesis of observed cycles.

For the muW3, three small-scale cycles are inferred (muW3 IIIb, IIIc, IIId; numbering after Schulz 1972), which should be also recognisable in the Herberhausen section (Hagdorn & Simon 1983). However, the application of the cyclic framework to the Herberhausen section is difficult exclusively based on schematic representation of Arp et al. (2004) (used here as a basis for Fig. 2) and the section of Hagdorn & Simon (2003). Unfortunately, the quarry walls are deteriorated today, why the cycle boundaries are not unequivocally detectable. Cycle IIIb starts at the base of the Upper *Terebratula* Bed and, after a short period of flooding at the top of the Upper *Terebratula* Bed (beds 12–17), an overall shallowing trend towards shell-detrital beds and the hardground in bed 39 occurs, which might be a candidate for the base of IIIc. The base of IIId cannot be recognised but might be located around bed 78. In the working area in southern Lower Saxony, cycles IIIc and IIId are developed as fining-upwards cycles, which likewise represent shallowing-upwards cycles, in some sections associated with Gelbkalk occurrences (see also Schulz 1972). In the case of the Hildesheim area (~80 km N of Göttingen), Gelbkalk development occurs at the contact between cycles IIIc and IIId. Between Hildesheim and northern Hesse, Gelbkalk terminates cycle IIIc. The occurrence of Gelbkalk is not only an expression of shallowing, but sedimentary and biogenic structures (shrinkage cracks, microbial mat structures) witness increasing salinity in a progressively restricted depositional setting throughout wide parts of the Germanic Basin. The interpretation of the cyclicity to reflect salinity changes was, in agreement with Fiege (1938), Schüller (1967) and Schulz (1972) in the context of a discussion of the Gelbkalk as a deposit of hypersaline settings.

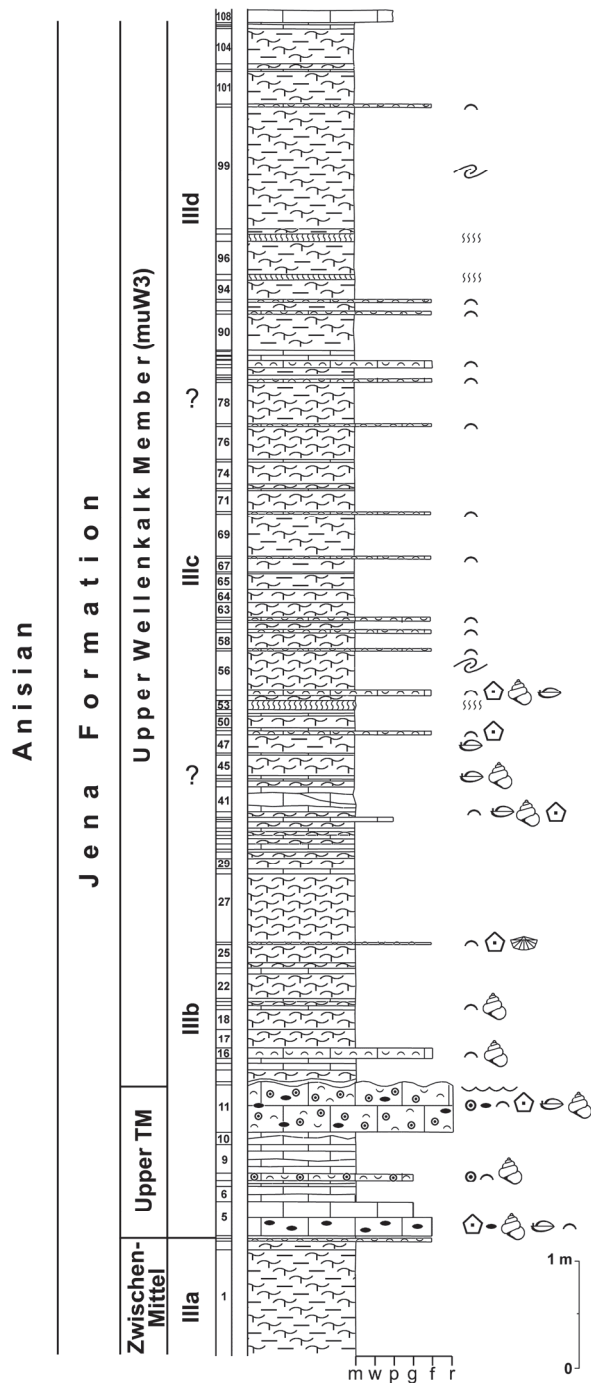


Fig. 2: Generalised overview of the lithology of the abandoned Herberhausen forestry quarry based on Arp et al. (2004). Numbering of cycles after Schulz (1972).

Lithology

Although monotonous at first sight, the Jena Formation represents a variable succession of lithoclastic, bioclastic and oolitic limestones, wavy limestones and marly limestones or marls with interbedded limestone layers. The base of the section (beds 5 to 10) consists of slightly bioturbated wavy mudstone and dense mudstones with some intercalated bioclastic event beds (mollusc floatstone,

cross-bedded oolitic mollusc-bearing grainstones). The top of the bioclastic Upper *Terebratula* Bed (bed 11) is characterised by a well-exposed bedding plane with large current ripples which are sealed by a micritic drape (bed 12). It likewise marks the base of the Upper Wellenkalk Member (muW3) which is characterised by an alternation of wavy, marly or platy limestones and dark grey marl intercalations. In distinct intervals shell-detrital beds occur (tempestites, lumachelles). Echinoderm macrofossils such as crinoids, echinoids, ophiuroids and asteroids are specifically concentrated in an obrution deposit (bed 38) above a hardground. Bivalves, favourably enriched in tempestites, occur scattered throughout the section (for further details on fauna see Hagdorn & Simon 1983 and Arp et al. 2004).

Materials and methods

For our pilot study, we concentrated on mapping palynofacies changes within cycle IIIb covered by 10 samples from beds 1 to 27, equivalent to the basal 5 m of the section and including the interval which has been proposed as maximum flooding surface in the sequence stratigraphic model of Götz (1994). Three additional approximately equidistant samples irrespective of possible cycle boundaries were processed to test whether any changes can be recognised approaching the Gelbkalk (lagoonal setting) at the top of cycle IIIId.

50 to 100 g of solid pieces of carbonate rocks were cleaned from weathered clay and lichen growth on exposed surfaces by treating them with 15 % HCl for 5 to 10 minutes and carefully washing them. The cleaned pieces of rock were dissolved in 15 % HCl and concentrated HCl was added successively until all carbonate was dissolved. After removal of excessive HCl some HF was added to dissolve quartz and clay minerals and to separate organic particles from adhering minerals. The residue was finally sieved through a 10 µm mesh screen and the fraction >10 µm stored in glycerine. Mineral imprints on palynomorphs suggested that the original pyrite content (microcrystals and framboids) was already dissolved by surface weathering except for sample Her 18T, which contained abundant framboidal pyrite.

Preservation, assemblage composition and palynomorph diversity varies considerably within the section. Thus, pending further systematic scrutiny the observed palynomorph taxa have been grouped into broad systematic categories which were used as a basis for determining quantitative changes in assemblage composition throughout the section. 300 palynomorph specimens per sample have been counted for percentage calculations in the diagram (Fig. 3). Phytoclasts (black organic matter, e.g., charcoal particles) were also counted and calculated to 100 % of palynomorphs as additional percentages.

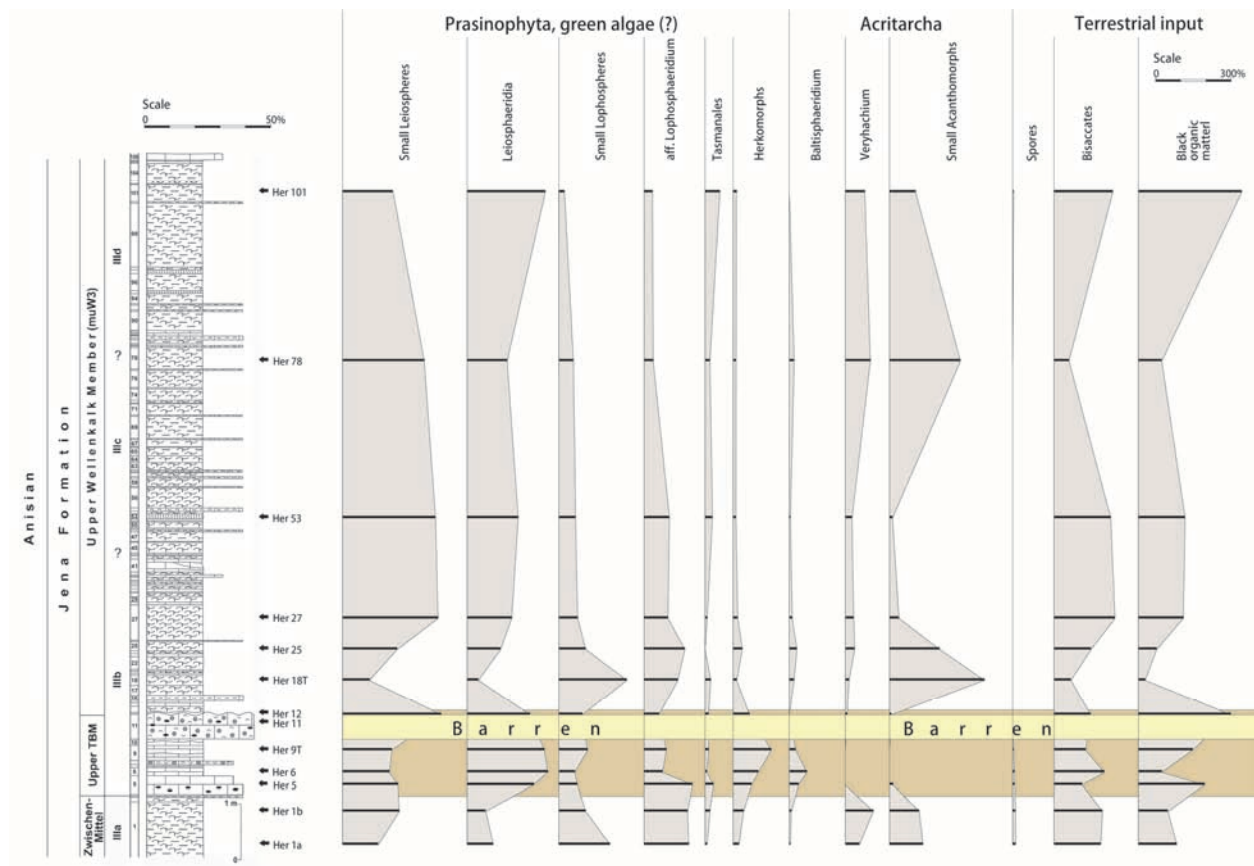


Fig. 3: Lithology, sample location and palynomorph spectrum of selected taxa or groups of taxa, respectively. Shaded area designates the Upper *Terebratula* Bed (TBM), the barren interval corresponds to the porous coquina at the top of the Upper *Terebratula* Bed. Sample Her 12 is from a thin, finely laminated micritic drape, which covers a ripple field, representing the top of the Upper *Terebratula* Bed. [Please note: 10 times reduced scale for black organic matter!]

Light microscope (LM) photographs of representative palynomorph taxa were taken in part from single grain mounts with a LEICA DFC 490 digital camera attached to a LEICA Metallux 3 microscope, SEM micrographs were made from strew mounts of samples Her 18T and Her 25 on a JEOL FM-6490LV, both at the Senckenberg Forschungsinstitut und Naturmuseum, Frankfurt.

The material described herein is deposited in the collections of the Geoscience Centre (GZG.PB), Georg-August University Göttingen (publication no. #1614).

Results

Twelve samples have yielded phytoplankton, pollen and spores in various degrees of abundance and preservation sufficient for quantitative analysis. A sample of bed 11, a highly porous coquina with iron oxide drapes, proved to be barren. Diversity and abundance is highest and preservation best in samples Her 18T and Her 25.

Since very few rigorous systematic studies of Triassic phytoplankton are available thus far, and preservation is rather variable, taxonomic assignment has been kept to a minimum at this stage. Thus, palynomorphs have been divided into broad morphologic groups as listed below.

Phytoplankton

***Leiosphaeridia* group:** All spherical to lenticular laevigate forms regardless of size, wall thickness and preservation are included here. Small vesicles clearly less than 20 µm in diameter and often with a median split or lateral rupture are quite abundant in some samples and may be distinguished as a separate subgroup. Larger forms, with a diameter above 20 µm are also common and may actually be assigned to the genus *Leiosphaeridia* (e.g., Fig. 4.15). There is considerable variation in wall thickness. At this stage, however, it would be premature to distinguish different species on this basis. Some forms with a very irregular wall thickness are rather distinctive components in some samples. They may be considered as preservational variants of *Leiosphaeridia* and are included in this group with some reservation.

***Lophosphaeridium* group:** Forms assigned to this group are mostly small, thin-walled and spherical and commonly show a median split or lateral rupture. They can be divided into two size classes above and below about 15 µm. The small forms generally appear ornamented with minute grains or very short spines under the light microscope and can not always be distinguished with certainty from small

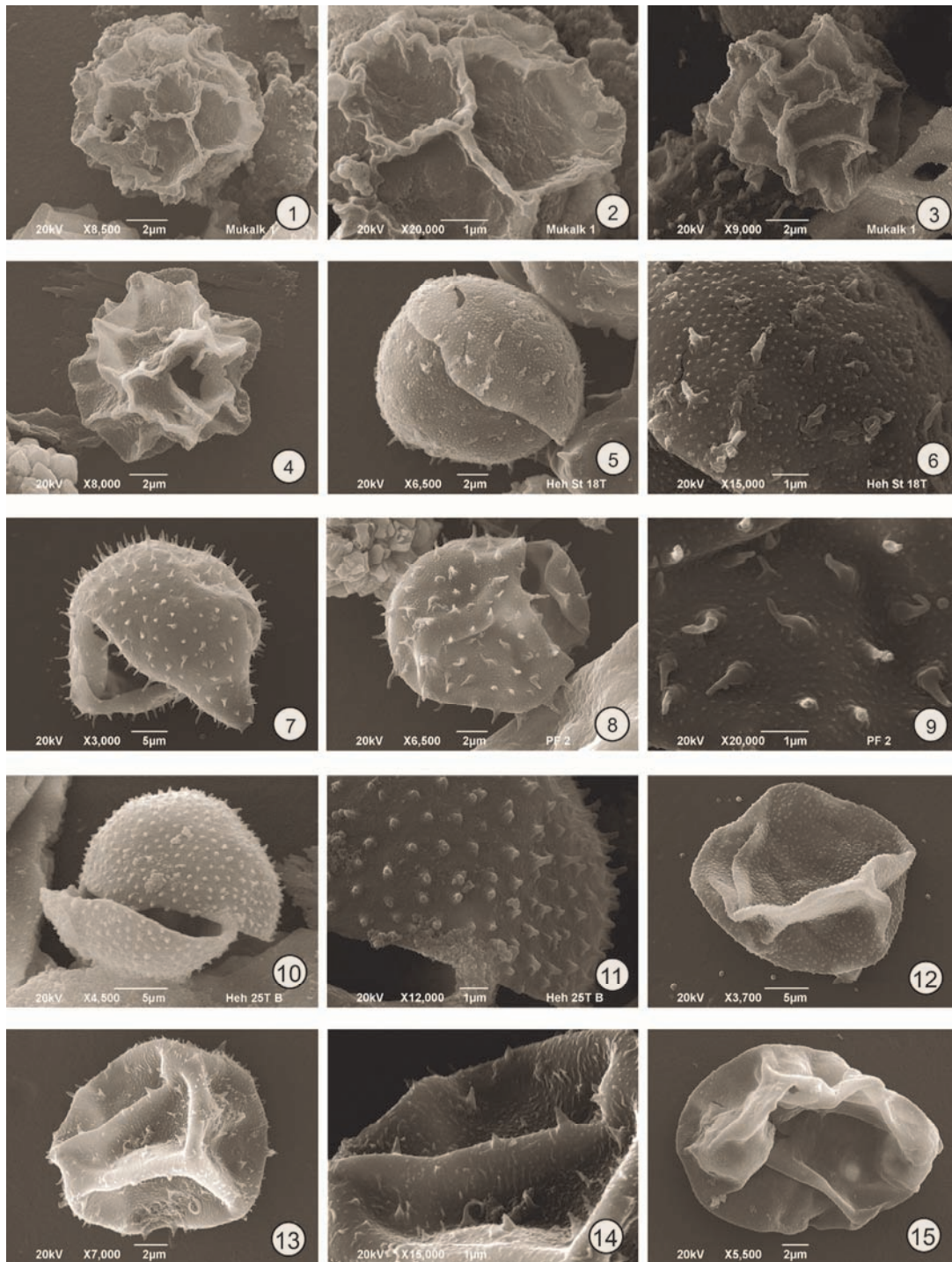


Fig. 4: SEM images of selected herkomorph and sphaeromorph acritarchs. **(1)** *Cymatiosphaera* sp. A, Her 18T, with crenulated crests of ridges, surrounding polygonal fields. \varnothing 9 μ m, ridges about 1 μ m high; **(2)** Detail of (1) showing fine perforation of fields and a central pore which is not elevated; therefore, the species is not assigned to Pterosphaeridia; **(3)** *Cymatiosphaera* sp. B, Her 18T, with more or less straight ridges surrounding non-perforated fields; Opening (pylome or "archoeopyle"?) at top of specimen. \varnothing 10 μ m, ridges low, <1 μ m; **(4)** *Cymatiosphaera* sp. C, Her 18T, with opening in one field similar to C. sp. B but with higher ridges. \varnothing 10 μ m including ridges; **(5)** *Lophosphaeridium* sp. A, Her 18T, with rigid vesicle wall and median split, surface ornamentation of very regular fine granulation and loosely spaced coni with basal ringlike structure. \varnothing 14 μ m, length of coni up to 1 μ m; **(6)** Detail of (5) illustrating surface ornamentation; **(7)** *Lophosphaeridium* sp. B, relatively thick-walled vesicle with lateral rupture and dense surface ornamentation of thin short spines about 2 μ m in length; **(8)** *Lophosphaeridium* sp. C, Her 18T, similar to *L.* sp. A, but with lateral rupture and flexible vesicle wall. \varnothing 15 μ m; **(9)** Detail of (8) illustrating surface ornamentation consisting of very fine granulation and loosely spaced flexible spines 1 μ m or slightly more in length; **(10)** *Lophosphaeridium* sp. D, Her 25, with relatively rigid vesicle wall and median split. \varnothing 20 μ m; **(11)** Detail of (10) illustrating surface ornamentation of regularly spaced small coni (<1 μ m) and very fine subordinate granulation; **(12)** *Lophosphaeridium* sp.?, Her 18T, strongly folded compressed specimen, originally nearly spherical, with thin wall and very finely granular surface ornamentation which would not be recognisable in transmitted light; the specimen would therefore be identified as *Leiosphaeridia*; **(13)** *Lophosphaeridium* sp. E, Her 18T, folded specimen with thin wall and complex surface ornamentation consisting of fine granulation and irregularly spaced, in part flexible spines of varying size up to 0.5 μ m. \varnothing 14 μ m; **(14)** Detail of (13) illustrating the type of surface ornamentation; **(15)** *Leiosphaeridia* sp., Her 18T, strongly folded compressed specimen, originally spherical, with thin nearly smooth wall. \varnothing 18 μ m.

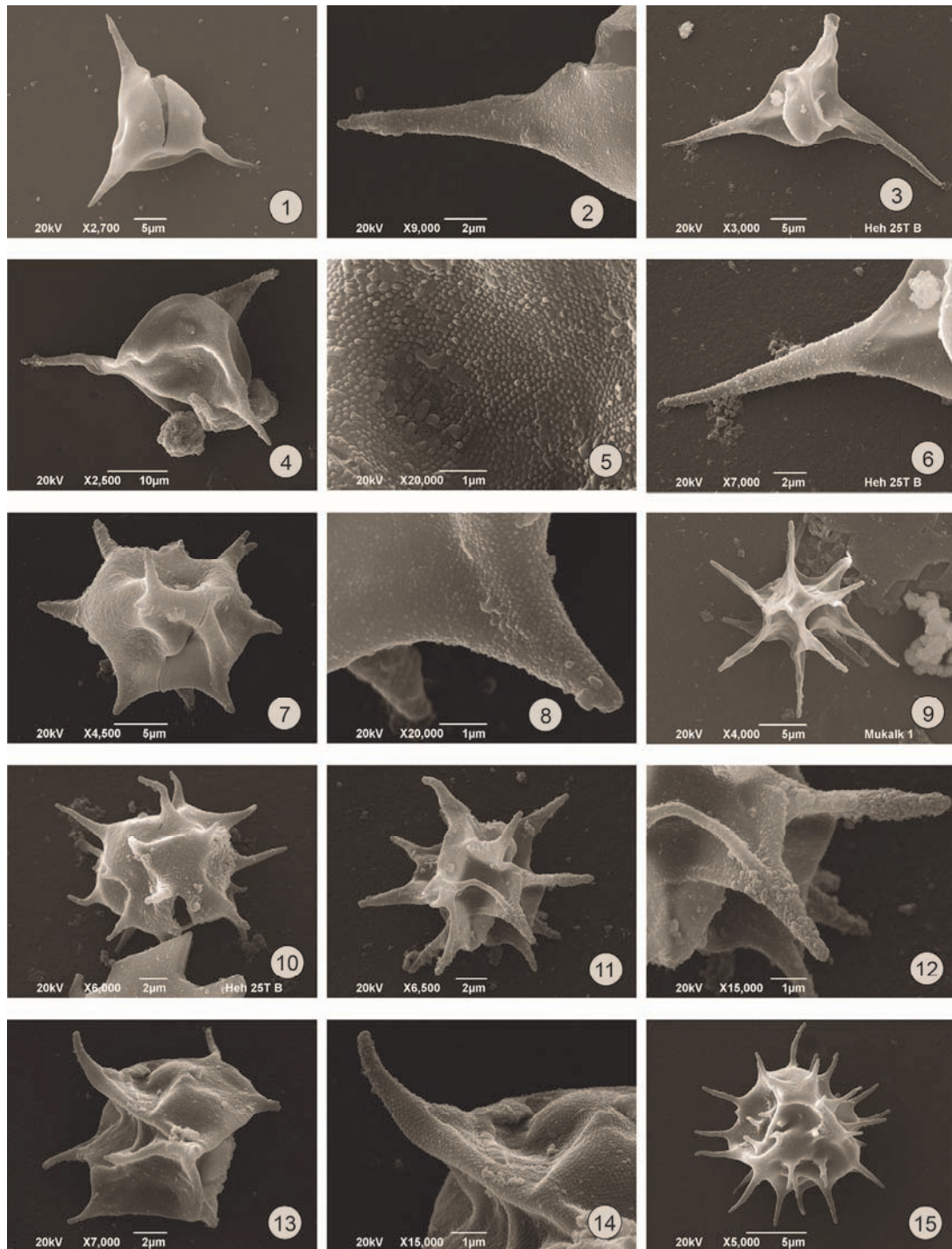


Fig. 5: SEM images of selected polygonomorph and acanthomorph acritarchs. (1) *Veryhachium reductum*, Her 18T, with short horns, triangular vesicle 15 µm in \emptyset with accidental split; (2) Detail of (1) showing very fine granulation increasing in density on horn; (3) *Veryhachium trispinosum*, Her 25, with long horns, length of horns and vesicle \emptyset equal (about 15 µm), horns hollow as shown by broken off tip of upper horn; (4) *Veryhachium* sp., Her 18T, large form, vesicle with strongly convex sides, \emptyset ~25 µm; (5) Detail of (4) showing very regular dense and fine granulation on central body, granules <0.1 µm in \emptyset ; (6) Detail of (3) showing increasing density of granulation on horn; (7) *Michystridium* sp. A, Her 18T, central body about 15 µm in \emptyset , with stout short horns about 3 to 4 µm long; (8) Detail of (7) showing very fine granulation on horn; (9) *Michystridium* sp. B, Her 18T, with very long horns, central body about 9 µm, horns 7 to 8 µm, surface of wall more or less smooth; (10) *Michystridium* sp. C, Her 25, subrounded central body about 12 µm in \emptyset , with relatively slender horns up to 5 µm long. Opening by damage, not preformed; (11) *Michystridium* sp. D, Her 18T, with collapsed polygonal central body and conical horns, central body 8 µm in \emptyset , horns about 5 µm long and up to 2 µm wide at base; (12) Detail of (11) showing fine irregular granulation on horns; (13) *Michystridium* sp. E, Her 18T, with polygonal central body and broad-based horns of variable size, central body about 11 µm in \emptyset ; (14) Detail of (13) showing very regular fine granulation extending over both, central body and horns; (15) aff. *Baltisphaeridium* sp. with spherical central body and slender flexible spines, central body 10 µm in \emptyset , horns up to 4 µm long.

leiospheres at 400 times magnification in quantitative counts. In SEM (Figs. 4.5–9, 4.13) they clearly show a loosely spinose ornamentation superimposed on very fine granulation. Some of the larger forms (20–25 µm) are distinctive by their rigid wall facilitating three-dimensional preservation and a rather regular arrangement of grana (Figs. 4.10–11).

Tasmanites group: Relatively thick-walled tests often with recognisable pore canals can be assigned to the genus *Tasmanites*, however, pore canals may be obscured by poor preservation. Some forms assignable to *Pleurozonaria* may be preservational states of *Tasmanites* (Guy-Ohlson 1996) and are therefore included here. Also added to this group may be relatively large specimens with an irregularly thick wall vaguely suggesting a coarse rugulate sculpture thus far not assignable to any previously described taxon.

Herkomorph group: Most of the discoidal forms with a distinct reticulate ornamentation are assignable to the genus *Dictyotidium* which is represented in our section by several species differing in size and type of reticulation. The genus *Cymatiosphaera* is characterised by wider lumina separated by high walls and mainly represented by very small specimens of less than 20 µm in diameter. Two types can be distinguished: one with crenulated wall tops and perforated lumina with central pore (Figs. 4.1–2) and another with more or less straight walls and smooth lumina (Figs. 4.3–4). *Pterosphaeridia* is recorded in rare cases (Fig. 6.12) but often not distinguishable from *Cymatiosphaera* and *Dictyotidium* due to marginal preservation and limited optical resolution in routine studies. Further SEM studies have to confirm, whether taxa with perforated lumina and central pore (Figs. 4.1–2) should be assigned to *Pterosphaeridia*.

Polygonomorph acritarchs: *Verybichium* is present to common in all samples above and below the Terebratula horizon but absent from within (samples Her 5, Her 6, Her 9T and Her 11). All specimens are triangular in outline with either short horns (Figs. 5.1–2; *V. reductum*) or long horns (Figs. 5.3, 5.6; *V. trispinosum*) at their corners. In either case, the vesicle surface is rather smooth and the horns are finely ornamented. A third somewhat larger type can be recognised on the basis of high resolution SEM images by the dense granulation which is evenly distributed over vesicle and horns (Figs. 5.4–5).

Acanthomorph acritarchs: Most of the acanthomorph acritarchs are represented by exceptionally small forms in considerable diversity. They are even abundant in samples Her 18T and Her 25 but, together with *Verybichium*, they are absent from within the Upper Terebratula Bed.

The majority is broadly assignable to the genus *Michystridium* sensu Sarjeant (1967), but in contrast to other authors (e.g., Courtinat 1983), we excluded taxa with very small spines, coni or grana and included them with the lophospheres. At this stage, no attempt has been made to assign the observed taxa to established species. The selection shown in Figs. 5.7–14 illustrates the observed variation involving size, length, number and distribution of horns, ratio of vesicle size to length of horns and type and distribution of surface ornamentation. Detailed SEM studies are required for closer taxonomic resolution. By their small size the acanthomorph acritarchs in our section and of the Triassic in general represent a unique population differing from their generally larger Palaeozoic counterparts.

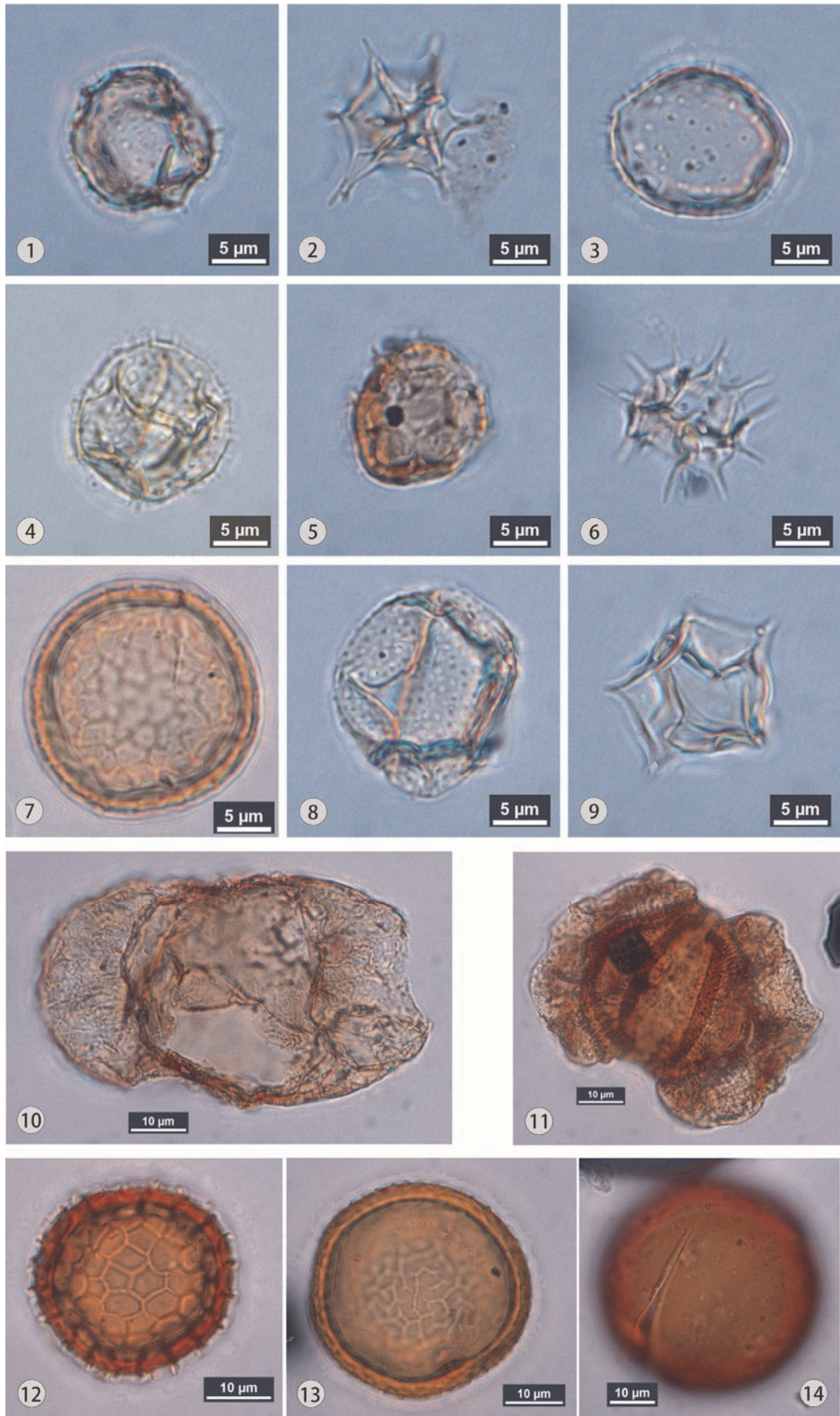
Baltisphaeridium group: Small thin-walled spherical vesicles in the order of 10 to 20 µm in diameter with slender flexible appendages exceeding 2 µm in length (Fig. 5.15) are common only within the Terebratula horizon and are tentatively classified with this group.

Pollen and spores

Trilete spores are exceptionally rare and generally without noteworthy diagnostic features, except for a few specimens of zonate forms resembling *Aequitriradites*. *Aratrisporites*, a monolete spore of lycopod affinity (Traverse 2007), has been occasionally recorded in samples Her 1b and Her 78. Very common are bisaccate pollen, the poor preservation of which, however, defies closer taxonomic assignment in most cases. The vast majority has sacci broadly attached to the central body similar to *Alisporites* (e.g., Fig. 6.10), but in some relatively well-preserved specimens the genera *Vitreisporites*, *Protodiploxypinus* and *Platysaccus* have been identified.

► **Fig. 6:** LM images of selected acritarchs and prasinophytes. (1, 3–4, 8) Various types of *Lophosphaeridium*. (1, 4) corresponding to *Lophosphaeridium* sp. B in Fig. 4.7; (3) corresponds to *Lophosphaeridium* sp. A or sp. C in Figs. 4.5–6 and Figs. 4.8–9; (8) corresponds to *Lophosphaeridium* sp. D in Figs. 4.10–11; (5) *Cymatiosphaera* sp., corresponding to *Cymatiosphaera* sp. C in Fig. 4.4; (2, 6, 9) Various types of *Michystridium*. (2) corresponds to *Michystridium* sp. A in Fig. 5.7; (6) corresponds to *Michystridium* sp. C in Fig. 5.10; (9) not comparable to any figured specimens in Fig. 5; (7) *Cymatiosphaera* sp. with incomplete reticulum; (10) *Alisporites* sp.; (11) Bisaccate pollen indet.; (12) *Pterosphaeridia* sp.; (13) Tasmanian prasinophyte with low rugulate surface ornamentation; (14) *Tasmanites* sp.

All correspondences between LM and SEM images are tentative. (7, 14) from Her 78, all others (1–6, 8–13) from Her 18T.



Black organic matter (BOM)

BOM occurs almost exclusively in small particles in the order of a few tens of microns as one of the major organic constituent in all samples except immediately above the Upper *Terebratula* Bed (sample Her 18T). More or less rectangular particles especially when showing traces of pitting are considered to be charcoal, irregularly shaped particles may be phytoclasts reworked from metamorphic rocks or aggregates of soot. In any case, they are terrestrially sourced and together with pollen and spores represent the terrestrial input.

Quantitative analysis

In order to detect any changes in assemblage composition in relation to lithofacies especially with respect to the Upper *Terebratula* Bed, a quantitative analysis based on a count of 300 specimens of total palynomorphs has been carried out on all productive samples. The dominant elements in most samples are very small spherical cysts most of them less than 15 µm in diameter. The majority of them appears entirely smooth and is listed in Fig. 3 as small leiospheres, but commonly a surface ornamentation by minute granules can be recognised in LM and demonstrated by SEM (Figs. 4.5–11, 4.13–14). The latter are then included within the *Lophosphaeridium* group as small lophospheres (Fig. 3). In routine quantitative analysis, however, the distinction between the smooth and granular forms remains rather arbitrary. At present, there seems to be an inverse relationship between the two groups, possibly an artefact due to differences in preservation and identification.

The most striking change in phytoplankton assemblages is shown by four samples from the Upper *Terebratula* Bed (Her 5, Her 6, Her 9T). *Verybichium* is fairly abundant below the Upper *Terebratula* Bed (“Wellenkalk-Zwischenmittel”, see Figs. 2–3), while *Verybichium* and *Micrhystridium* – the most typically marine Triassic acritarch genera – are completely absent within the Upper *Terebratula* Bed (samples Her 5, Her 6, Her 9T, Her 12). The loss of *Verybichium* and small acanthomorphs within the Upper *Terebratula* Bed is compensated by a marked increase in the abundance of larger leiospheres (*Leiosphaeridia*), a moderate increase of the *Baltisphaeridium* group and a notable rise in diversity and abundance of herkomorphs, especially *Dictyotidium* and *Cymatiosphaera*.

Members of the *Tasmanites* group are conspicuous by their size and thick deep orange coloured wall, but appear quantitatively insignificant. They are somewhat more frequent in samples Her 5, Her 53 and Her 78 and quite common in sample Her 101, thus showing an increasing trend towards the top of the section.

Among terrestrial palynomorphs, bisaccate pollen are by far the most common element, but no clear vertical trend can be recognised in their distribution. BOM, i.e., charcoal

and others, has been counted separately and calculated to 100 % of total palynomorphs. In Fig. 3 it is represented together with pollen and spores as terrestrial input but at a scale reduced by 10 times. As would be expected from terrestrially sourced components, bisaccate pollen and BOM show a remarkably parallel trend.

Discussion

Acritarchs and prasinophytes as indicators of salinity

Since the early Palaeozoic, the *Verybichium-Micrhystridium* complex plays a unique role among acritarchs in its response to environmental changes such as bursting into abundance around the late Ordovician (Hirnantian) glaciation (Vecoli 2008) and at the base of the Carboniferous in widely spaced localities, e.g., Poland (Filipiak 2005) and Ohio, USA (Winslow 1962) subsequent to the extinction of most acritarch genera. The *Verybichium-Micrhystridium* complex reaches up to 50 % of total palynomorph assemblages just above the Permian–Triassic boundary in several sections of Israel and is considered to signal the beginning recovery after the deep end-Permian ecological crisis (Eshet et al. 1995). Thus, *Verybichium* and *Micrhystridium* display a similar opportunistic behaviour and broad ecologic tolerance as many of the prasinophytes. Nevertheless, for want of any more sensitive indices they are generally regarded and used here as the most typical marine phytoplankton in the Triassic (Visscher et al. 1993). Thus, their common presence respectively abundance below and especially above the Upper *Terebratula* Bed can be considered to indicate normal marine conditions, while their absence in an interval within the Upper *Terebratula* Bed suggests restricted conditions during this interval.

Among the acritarch taxa listed above, the genus *Baltisphaeridium* is considered as a fully marine acritarch on the basis of its Palaeozoic record, but assignments to this genus are still very tentative in our analysis and its ecologic signal remains rather doubtful. In fact, it shows a slight peak in abundance within the Upper *Terebratula* Bed and, thus, shows a reverse trend to *Verybichium* and the small acanthomorphs.

Leiospheres are a broad, morphologically indistinct and therefore probably rather heterogeneous group which has been variously attributed to acritarchs or prasinophytes and may even include other unicellular organisms. A prasinophyte affinity is preferred here at least for the larger forms (clearly above 20 µm), which we assign to the genus *Leiosphaeridia*, but the biological source of the abundant small forms (mostly 15 µm or less) is rather doubtful. The same uncertainty exists for the abundant small granular forms included here in the *Lophosphaeridium* group. Since the emended diagnosis of *Lophosphaeridium* (Timofeyev) Lister 1970 is still rather broad and non-descript, we have loosely grouped all tuberculate spherical forms

and attributed them tentatively to the prasinophytes regardless of size. It is generally agreed that most of the larger sphaeromorphs such as *Tasmanites* and *Pleurozonaria* are fossilised phycomata of prasinophytes, originally containing numerous motile cells. Guy-Ohlson (1996), however, shows SEM images of small sphaeromorphs, leiospheres as well as lophospheres, and suggests that they may represent phycomata (respectively cysts?) of individual cells from an earlier still smaller stage in the life cycle of prasinophytes, an argument, which we accept here in view of the many open questions regarding the various stages in the life cycle of prasinophytes. Somewhat larger lophospheres have been previously recorded from the Jena Formation (Lower Muschelkalk) of northern Hesse (Reitz 1985), but erroneously assigned to the genus *Tyrtodiscus*, which is considered to be a prasinophyte. Thus, in our study, we tentatively consider all sphaeromorph taxa as prasinophytes and, therefore, as potentially euryhaline.

Most members of the herkomorph group such as *Dictyotidium*, *Cymatiosphaera* and *Pterosphaeridia*, are generally considered to be prasinophyte phycomata. *Dictyotidium* and *Cymatiosphaera* are quite common throughout the section and even dominant within the Upper *Terebratula* Bed, in which *Verybichium* and the small acanthomorphs are missing. Very small specimens of *Cymatiosphaera* (<15 µm) are infrequent but occur regularly throughout the section. They are listed as small acritarchs by Habib & Knapp (1982) and Schrank (2003), but from a morphological point of view it seems taxonomically and biologically inappropriate to separate them from the prasinophytes. They should, therefore, be also considered as part of the euryhaline phytoplankton.

Interpreting the proportion of the mainly prasinophycean euryhaline phytoplankton and the *Verybichium*–*Micrhystridium* complex as essentially salinity controlled, the changes in salinity within the Herberhausen section can be summarised as follows: (1) Normal marine conditions existed at the base of the section (“Wellenkalk-Zwischenmittel”, bed 1), where *Verybichium* and small acanthomorphs are frequent and prasinophytes moderately present; (2) A marked change occurs in the slightly bioturbated calcareous mudstones above (Her 6, Her 5, Her 9), which are sandwiched between the two bioclastic limestone beds, bounding the Upper *Terebratula* Bed. Most striking there is the lack of both, *Verybichium* and small acanthomorphs, which, together with a distinct increase of *Leiosphaeridia* and herkomorph prasinophytes (*Cymatiosphaera* and *Dictyotidium*), clearly indicates restricted conditions for this interval. A decrease of marine phytoplankton is also recorded by Rameil et al. (2000) from the base of the Upper *Terebratula* Bed of the Steudnitz quarry, Thuringia. These observations are in accordance with Lukas (1991, 1993), who demonstrated the strong lateral facies variability within the *Terebratula* Member, shifting between carbonate shoals and more lagoonal settings. Normal marine conditions were restored above the top of the Upper *Terebratula* Bed

as indicated by the peak abundance of small acanthomorphs in sample Her 18T. This interval corresponds to the position of a maximum flooding in the sense of the cycle model of Götzt (1994), and corresponds to the data provided by Rameil et al. (2000). Our results, however, are in conflict with Götzt & Feist-Burkhardt (2012), who show peak abundance of marine phytoplankton within the *Terebratula* Member and a decrease above.

Small acanthomorphs gradually decline as leiospheres become more abundant up to a point in the section, which may be identified as the top of cycle IIIb. The large sampling gaps in the upper part of the section limit identification of further trends, but the intermittent frequency of small acritarchs in sample Her 78 suggests that additional salinity fluctuations may eventually be revealed by higher resolution. Important to note is the numerically small but significant increase of *Tasmanites* and a distinct increase of *Leiosphaeridia* together with a concurrent decrease of small acanthomorphs in sample Her 101. This suggests a renewed trend towards restricted conditions as the previously exposed Gelbkalk is approached. Since Gelbkalk deposited under hypersaline conditions, it seems appropriate to generally interpret shifts towards euryhaline elements in phytoplankton assemblages of the Jena Formation as a response to increased salinities.

On a broader regional scale, Götzt & Feist-Burkhardt (2012) suggest that marine phytoplankton selected for palaeogeographic realms during the Anisian. They show that acritarchs dominate over prasinophytes in the open Tethyan shelf and gateways to the Germanic Basin, while prasinophytes dominate in the Germanic Basin under conditions of varying salinity gradients including water column stratification and oxygen depleted bottom conditions. Furthermore, within the acritarch group *Micrhystridium* is characteristic of the shelf and gate areas, *Verybichium* of the central basin. However, Götzt & Feist-Burkhardt (2012) apparently did not take the abundance of small acanthomorph acritarchs into account, to which the micrhystridians in our section belong. Thus, the question of the preference of small acanthomorphs for more open marine environments requires additional comments.

Several authors interpreted palynological changes in the Muschelkalk Group in terms of sequence stratigraphy (“sequence palynology”) at various levels of resolution (Götzt 1996; Götzt & Feist-Burkhardt 1999; Rameil et al. 2000; Visscher et al. 1993). Maximum abundance of acritarchs, mainly *Micrhystridium* with accessory *Verybichium*, has previously been used to identify the maximum flooding surface of third order sequences of Aigner & Bachmann (1992) in the upper part of the Lower Muschelkalk Subgroup (Visscher et al. 1993), at a level presumably corresponding to the *Terebratula* Member, where Götzt & Feist-Burkhardt (1999) placed their maximum flooding surface on the basis of peak abundance of marine phytoplankton, i.e., acritarchs plus prasinophytes. The succeed-

ing highstand systems tract within the muW3 is characterised by a general decrease of phytoplankton. Small cycles in the range of about 10 m are superimposed showing phytoplankton responses similar to those of the higher order systems tracts (Götz & Feist-Burkhardt 1999), however, this similarity appears rather vague.

Palynological results from the Herberhausen section (Fig. 3) rather suggest that changes in phytoplankton associations are primarily controlled by salinity changes, which in turn can be influenced by sea level fluctuations but other factors may be involved in salinity changes. An alternative view has, for instance, been presented by Brocke & Riegel (1996), interrelating repeated successions in the dominance of terrestrial input, prasinophytes and acritarchs as responses to pulses of delta advance at the top of the Muschelkalk Group.

Ecological role of "small acritarchs"

Small acritarchs form a unique segment of many microphytoplankton assemblages and appear to be abundant in special environments and at certain stratigraphic levels of the Mesozoic. Their ecological role and biological affinity, however, remain rather enigmatic. A possible biological link to prasinophytes has been discussed above. Taking up ideas expressed previously (Courtinat 1983; Dale 1977), Schrank (2003) argues in favour of a biologic affinity of small acritarchs to dinoflagellates for at least two of his genera (*Mecsekia* and *Recticystis*), which bear considerable similarity in size and morphology to the tiny lophospheres in our preparations. An affinity to dinoflagellates has even been suggested for some spiny acritarchs (Fensome et al. 1999). However, accepting that the adaptive radiation of dinoflagellates started in the Upper Triassic and Lower Jurassic (Fensome et al. 1996), a dinoflagellate affinity of the small lophospheres in our section seems highly unlikely and can be excluded for the spiny acritarchs on a morphological basis. Extending the idea of dinoflagellate affinity, Schrank (2003) points out that living dinoflagellates are concentrated in the upper centimetres of marine sands (Sarjeant & Taylor 1999), and he suggests an adaptation to a similar interstitial mode of life for the "small acritarchs" from the phosphoritic sands of the Upper Cretaceous of Egypt. This interpretation appears rather intriguing since a number of authors have observed that small acritarchs occur preferentially in relatively coarse-grained littoral sediments (Courtinat 2000; Fechner 1996; Sarjeant & Taylor 1999; Schrank 1984; Wall 1965). This can not, however, be applied to the small acritarchs of Habib & Knapp (1982) from the Lower Cretaceous oceanic clays and marls nor to the small acanthomorph acritarchs and small cymatiospheres in the mainly micritic limestones of the Jena Formation in our section, which might have been originally aragonite mud (Lippmann et al. 2005). Apparently, the phenomenon of "small acritarchs" can neither be explained by a single biological affinity or mode of life.

Habib & Knapp (1982) demonstrated that small acritarchs changed at relatively short intervals in Lower Creta-

ceous successions of the western North Atlantic (Continental slope, Bermuda Rise, Blake-Bahama Basin) and suggested that they provide a useful yet untapped biostratigraphic tool. But these changes may be facies controlled rather than the result of rapid evolutionary development, since at least some forms appear to be long-lived. For instance, forms shown in Figs. 5.7, 5.10 appear to be identical with *Micrhystridium karamurzae* from the late Permian of Australia (McMinn 1982), and others (e.g., Fig. 4.10) seems to correspond to cf. *Micrhystridium deflandrei* from the Upper Jurassic of France (Courtinat 1983). Very similar small acritarchs have also been reported from the Oxfordian (Upper Jurassic) of Lower Saxony, Germany (Kunz 1990).

Conclusions

In our pilot study on organic-walled microphytoplankton from a short section of the Jena Formation (Lower Muschelkalk Subgroup), we are able to show that changes in assemblage composition correspond well with changes in lithology and provide important additional evidence for environment interpretations. Assemblages are exclusively composed of prasinophytes and a relatively narrow segment of acritarchs, i.e., *Verybichium* and small acanthomorphs. Despite limited quality of preservation and mostly low abundance, an unexpected high diversity has been observed, especially when SEM has been applied to the so-called small acritarchs, which demands further research.

Using the generally accepted euryhaline nature of prasinophytes and the stenohaline preference of *Verybichium*, *Micrhystridium* and small acanthomorphs, respectively, we suggest that salinity changes were the main trigger for changes in phytoplankton assemblages. Increased salinities are indicated within the Upper *Terebratula* Bed and in the uppermost part of the succession (top of cycle IIIId) below the Gelbkalk (comp. Figs. 1B, 2). Fully marine conditions may be interpreted for beds 1 and 18 to 27. The total lack of *Verybichium* and small acanthomorphs within the Upper *Terebratula* Bed shows that these salinity trends are not necessarily straight forward, but may be interrupted by short-term events recognisable only at high resolution. Our results suggest that changes in composition of microphytoplankton assemblages are controlled directly by salinity and reflect evaporation cycles in the first place. However, sea level may be instrumental in as much as salinity is influenced by changes in sea level. Obviously, the sensitive response of microphytoplankton to facies changes observed at Herberhausen opens a promising new approach to the improvement of environment interpretations of the Muschelkalk Group in general.

Several problems surround the so-called small acritarchs, which are diverse and abundant in our section. Their taxonomy requires critical analysis by SEM, which has hitherto applied only to few occurrences in relatively

narrow stratigraphic intervals (Jurassic, France: Courtinat 1983; Lower Cretaceous, North Atlantic: Habib & Knapp 1982; Upper Cretaceous, Egypt: Schrank 2003) and never attempted for the Muschelkalk Group of the Germanic Basin. Much additional work is needed and intended to assess their stratigraphic ranges and possible evolutionary patterns. Various ideas have been proposed regarding their biological affinity and mode of life. But neither an affinity to dinoflagellates nor an interstitial mode of life can thus far be confirmed by our pilot study.

Acknowledgements

The authors are grateful for useful comments and corrections of an anonymous reviewer which improved the original manuscript.

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Cite this article: Riegel, W.; Wiese, F.; Arp, G. & Wilde, V. (2014): Microphytoplankton from the Jena Formation (Lower Muschelkalk Subgroup, Anisian) in the forestry quarry at Herberhausen near Göttingen, Germany. In: Wiese, F.; Reich, M. & Arp, G. (eds.): "Spongy, slimy, cosy & more...". Commemorative volume in celebration of the 60th birthday of Joachim Reitner. *Göttingen Contributions to Geosciences* **77**: 63–76.

<http://dx.doi.org/10.3249/webdoc-3918>
