A bloom of *Tympanicysta* Balme (green algae of zygnematalean affinities) at the Permian-Triassic boundary

Sergey A. AFONIN
Paleontological Institute, 123 Profsoyuznaya, Moscow 117997 (Russia)
vkras@paleo.ru

Sophia S. BARINOVA
Institute of Nature Conservation, Znamenskye Sadki, Moscow 113628 (Russia)

Valentin A. KRASSILOV
Paleontological Institute, 123 Profsoyuznaya, Moscow 117997 (Russia)
vkras@paleo.ru

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ABSTRACT
Filamentous microfossils *Tympanicysta* Balme, formerly interpreted as conidia of ascomycetes, are similar to zygnemataceous algae *Spirogyra* Link in the general morphology, folding of transverse septa, chloroplasts and akinetes. Their rise at about the Permian-Triassic boundary is, therefore, unrelated to the boundary "fungal event", but is rather a consequence of a Permian-Triassic widespread ponding and swamping of river systems at the initial stage of the end Permian transgression.

KEY WORDS
Zygnematales,
Tympanicysta,
Permian-Triassic boundary,
fossil algae.

RÉSUMÉ
Épanouissement des algues vertes Tympanicysta *Balme à la limite du Permien et du Trias.*
Le microfossile filamenteux *Tympanicysta* Balme, jadis interprété comme un champignon ascomycète, est plutôt à rapprocher de *Spirogyra* Link (algues vertes Zygnemataceae), dont il possède la morphologie, le plissement des septa transversaux, les chloroplastes et les akinètes. Son épanouissement à la limite du Permien et du Trias n'est donc pas lié à un « événement fungique » mais à une grande transgression marine.

MOTS CLÉS
Zygnematales,
Tympanicysta,
limite Permien/Trias,
algues fossiles.

INTRODUCTION

Tympanicysta Balme is a genus of filamentous microfossils widespread in the Late Permian and Early Triassic. At about the Permian-Triassic boundary, *Tympanicysta* increases to become a dominant component of palynological assemblages (Visscher *et al.* 1996; Foster *et al.* 1997). The rise of *Tympanicysta* has been related to a mass land plants extinction around the Permian-Triassic boundary (Visscher *et al.* 1996). However these fossils are known also from the mid-Permian (Kazanian) of European Russia (Foster & Jones 1994; Foster *et al.* 1997) and the Wordian of Oklahoma, USA (Visscher *et al.* 1996). In his original description of *Tympanicysta*, Balme (1980) has suggested that this microfossil represents an encystment stage in the life cycle of some algae or fungi or else an animal organism. *Tympanicysta* and the related, if not congeneric, *Reduviasporonites* Wilson and *Chordecystia* Foster, has been interpreted as fungal remains (Mangerud 1994) representing hyphae and conidia of ascomycetes (Visscher *et al.* 1996), fungal cysts (Utting 1994) or fungal spores (Yaroshenko & Gomankov 1998). *Tympanicysta* thus contributed to the Permian-Triassic "fungal event". However Ouyang & Utting (1990) have suggested an algal affinity of *Tympanicysta*, while Foster *et al.* (1997) have noted that its fungal interpretation remains as yet speculative. In his recent revision of *Tympanicysta* and allied fossils, Elsik (1999) synonymized them to *Reduviasporonites* Wilson, originally described as a marine fungus. However, *Reduviasporonites* is much less frequently used in palynological literature than *Tympanicysta*. Fossils, described under these names are certainly similar, but their generic identity is still to prove. Elsik has included in *Reduviasporonites* both branched and unbranched forms interpreted as conidiophores and conidia respectively. Discussing the systematic affinities, he stated that "*Reduviasporonites* could be a Palaeozoic analogue of modern *Rhizoctonia*. If this proves to be the case from studies in progress, *Reduviasporonites* are the conidiophores and conidia of either an ascomycete or basidiomycete" (Elsik 1999: 38). Since *Rhizoctonia* belongs to the basidiomycetes, the comparison should logically be restricted to this class, rather than involving the ascomycetes. Generally, conidia are rare in the basidiomycetes and the conidiophores of the form and dimensions of *Reduviasporonites* (*Tympanicysta*) are not known.

Our material from the transitional latest Permian to basal Triassic deposits of the Vologda region, European Russia, definitely indicates an alliance of *Tympanicysta* with green algae, in particular with the Zygnematales. Our arguments in favour of the algal affinities are:

– in shape and dimensions *Tympanicysta* corresponds to filamentous green algae, such as *Spirogyra*;

– the lens-shaped joints are typical for this group of algae, with both septae invaginated in the cell lumen (such septae are not recorded in fungi);

– the thickened cells morphologically correspond to acinetes of zygnemataleans;

– branching occasionally occurs in the Zygnematales (in particular, in terrestrial forms [Rundina 1998]) and normally occurs in the allied orders, such as Cladophorales;

– the cells contain chloroplasts that are comparable with those of various green algae. The best preserved chloroplasts (Fig. 1) are the cylindrical membranal structures lining the cell walls and occasionally divided into two or more blocks. They show a microreticulate-perforate structure that is typical of chloroplasts in the Cladophorales (Vasser *et al.* 1989). Granular mass resembling a degraded chloroplast has been recorded also in the Carboniferous *Tetraporina* Naumova (Van Geel & Grenfell 1996);

– the absence of zygospores does not contradict our interpretation, because even in our samples of living zygnemataleans, zygospores rarely occur in association with filaments. Moreover, a palynological assemblage from an adjacent locality Sholga contains *Maculatasporites* Tiwari, a supposed zygnematalean zygospore (Grenfell 1995);

– the facial occurrences of *Tympanicysta* suggests an abundant fresh-water or brackish source, as in the present day green algae, but scarcely conceivable in saprophytic fungi.

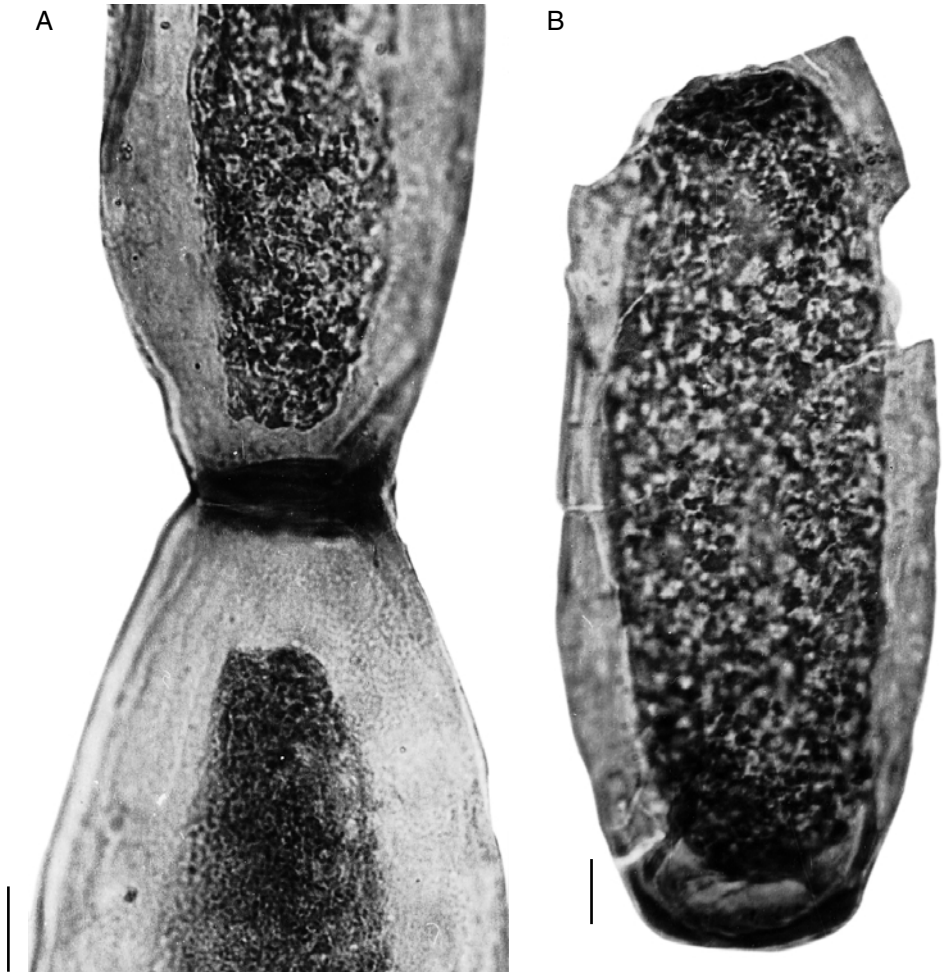

FIG. 1. — *Tympanicysta stoschiana* Balme from the basal Vetlugian of Nedubrovo, Vologda region; **A**, two vegetative cells with chloroplasts; **B**, vegetative cell with well-preserved chloroplast. Scale bars: 10 µm.

MATERIAL AND METHODS

Our material came from the Vetlugian Series traditionally assigned to the lowermost Early Triassic (Lozovsky & Esaulova 1998). Recently we found a rich plant macro- and microfossil assemblage in the outcrops of lowermost Vetlugian about 10 m above the regional Permian-Triassic boundary on the left bank of the Kichmenga River near Nedubrovo Village, Vologda region, European Russia (Krassilov *et al.* 1999). The boundary is marked by cross-bedded sandstones with gravel brown clays that are interpreted as the channel-oxbow deposits. The plant-bearing bed immediately above is a thin alternation of gray siltstones and sandy clay with abundant organic debris locally forming thin coal lenses. It is overlain by variegated siltstones and red clays. Most plant remains are leaf cuticles, peltasperm ovulate disks and dispersed seeds. There are also a few ostracod and conchostracan shells, as well as terrestrial insect impressions.

The fossil flora contains abundant peltasperms *Tatarina* S. Meyen and conifers *Quadrocladus*

Mädler and *Ullmannia* Eichwald, the typical Late Permian genera, whereas the palynological assemblage is dominated by *Klausipollenites schaubergeri* (Potonié & Klaus) Jansonius, *Striatoabieites richteri* (Klaus) Hart and *Lunatisporites* spp. in association with abundant *Cycadopites* (Wodehouse) ex. Wilson & Webster and a megaspore morphotype *Otynisporites eotriassicus* Fugl. characteristic of the basal Buntsandstein (Fuglewicz 1977). A few planktonic unicells are represented by *Inaperturopollenites* Thomson & Phlug. and *Pilasporites* Balme & Hennelly. *Tympanicysta* is common in this assemblage as well as in the redbed horizon upsection.

The microfossils described later in the paper came from the palynological liquid samples # 35-7-12 Nedubrovo locality and # 36-7-8 from the Ryabian deposits on the left bank of Yug River, 1 km South of Sholga Village, Vologda region. The filaments and dispersed cells were mounted in Canada balsam and glycerin gelly on glass slides. Light micrographs were taken with a Zeiss (Axioplan 2) microscope in immersion oil.

SYSTEMATICS

Genus *Tympanicysta* Balme

Tympanicysta stoschiana Balme
(Figs 1; 2A-C, E, F)

EMENDED DIAGNOSIS. — Unbranched, rarely branched filaments of cylindrical to barrel-shaped cells with elliptical to ovate terminal cell. Cell walls smooth. Septa smooth or folded, forming lens-shaped joints. Chloroplasts cylindrical, microreticulate-perforate, lining cell walls. Akinetes thick with constricted chloroplast.

DESCRIPTION

Fragments of filaments from four to five cells long are preserved alongside with dispersed cells. The cell shapes vary from cylindrical thin-walled in vegetative filaments to swollen barrel-shaped and thick-walled, supposedly representing an initial dormant stage, or akinete, 70-130 µm long, 43-97 µm wide, lacking median constrictions or segmentation of cell walls. The cell walls are unilayered, smooth, lacking pores. The transverse septa are smooth or, in the thick-walled filaments, folded forming lenticular joints. The terminal cells, when preserved, are swollen, elliptical or ovate, bluntly pointed, about 120 µm long, 56 µm wide. Chloroplasts are preserved as a granular dark matter in the central part of the cells. The better preserved chloroplasts appear as cylindrical membranes with microreticulate-perforate structure lining the cell walls (Fig. 1A). A few cells representing the fully formed akinetes are cylindrical to slightly bell-shaped owing to a median constriction, fitting the initial cell, with thick walls, 178 µm long, 65 µm wide.

COMPARISON

In the character of cell joints, these microfossils resemble zygnematalean green algae (Zygnematophyceae). Classification of extant zygnemataleans is based primarily on the conjugation and zygotic characters that are often lacking even in living material, while their vegetative characters are widely convergent in different genera. In the general morphology, *Tympanicysta* is most similar to the extant zygnemataceous green algal genera *Spirogyra* Link and *Mougeotia* Ag. which have typically unbranched filaments of cylindrical cells that can be swollen at forming thick-walled dormant cells, or akinetes. In the same way, *Tympanicysta* is represented by two kinds of filaments-slender with cylindrical cells and relatively robust with barrel-shaped thick-walled cells, the latter perhaps overrepresented in microfossil assemblages. Moreover, a typical akinete is found in our material.

Other morphological features of *Tympanicysta* also match the typical zygnematalean characters. In *Tympanicysta*, the transverse cell walls, or septa are either smooth or, in the thick-walled forms, folded by invagination of the cell wall. In the extant *Mougeotia*, the septa are typically smooth, forming a lenticular joint, whereas folded septa more commonly occur in *Spirogyra*. A granular dark matter in the central part of the cells corresponds to chloroplasts of zygnematalean algae in which it can be either axial or parietal, laminar or

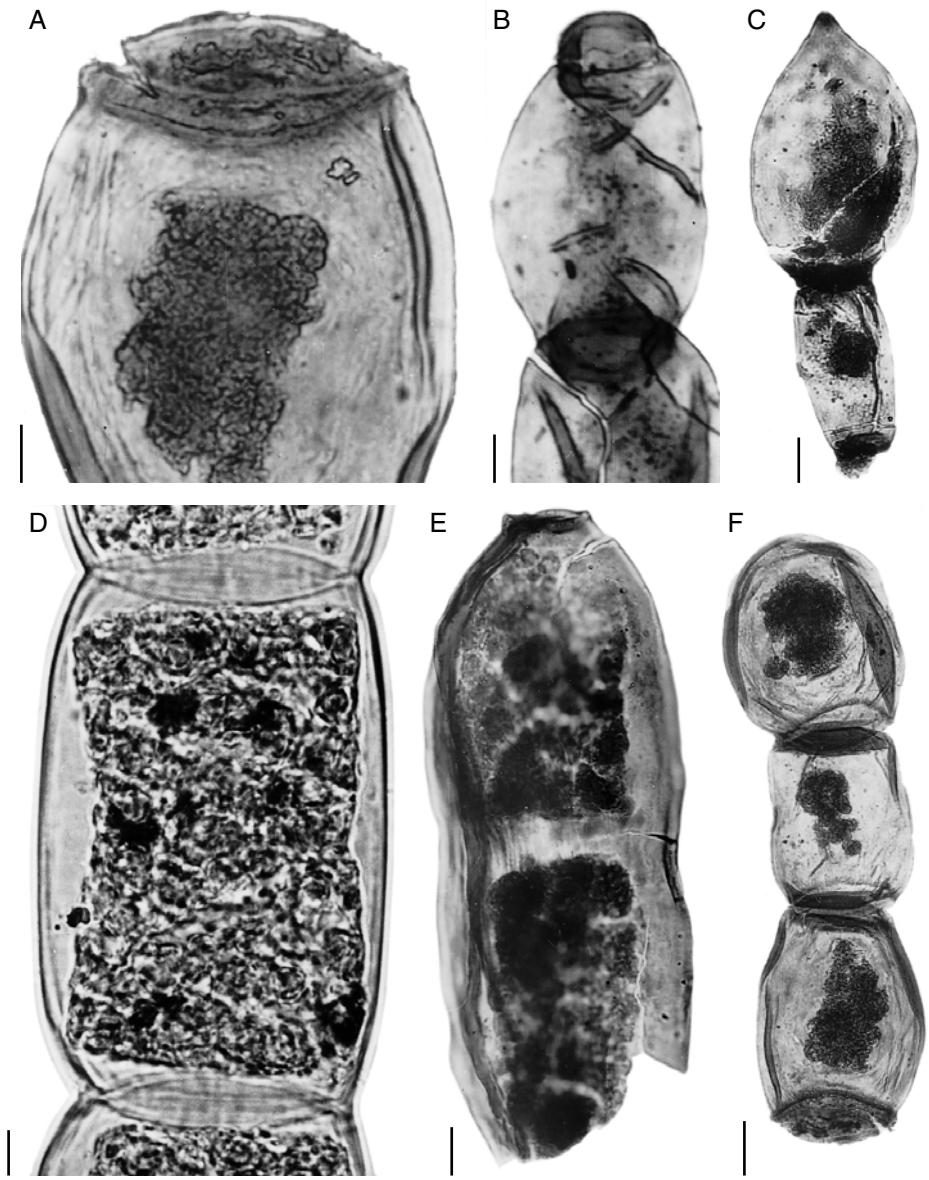

FIG. 2. — **A**-**C**, **E**, **F**, *Tympanicysta stoschiana* Balme from the basal Vetlugian of Nedubrovo and Sholga, Vologda region; **A**, vegetative cell showing chloroplast and infolded septa at the top; **B**, vegetative cells with infolded septae; **C**, swollen terminal cell; **E**, akinete-like cell; **F**, vegetative filament; **D**, *Spirogyra* sp., extant, from a floating mat of a floodplain pond, Bitsa River, the Moscow River Basin, collected in June 1999, vegetative filament at transition to akinete. Scale bars: A, B, D, E, 10 µm; C, 20 µm; F, 30 µm.

star-shaped, but in compressed cells appearing exactly as in the fossil. The better preserved chloroplasts resemble those of the Cladophorales (Vasser *et al.* 1989).

Occasional cells in the fossil material are similar to the typical akinetes of zygnematalean algae that are thick-walled dormant cells formed of vegetative cells in adverse environments

(Transeau 1951). A terminal cell shown in (Fig. 2C) corresponds in shape to that of filamentous colonies developing from zygospores (De Bary 1858).

Although the fossil form is close to the Zygnematales in a number of characters, it might also show characters typical of other groups of green algae. Thus a frequent branching, as well as the parietal chloroplasts, occur in Cladophorales rather than Zygnematales. Such unusual combinations of characters are to be expected in Palaeozoic forms.

DISCUSSION

The Zygnematophyceae include widespread extant forms of which *Spirogyra* is the largest and the most common genus including about 350 species. They typically inhabit relatively clear still or running, sometimes swamped fresh waters forming dense mats but occur also in brackish waters and mineral springs. Conjugation takes place in warm season preferably in warm shoals. Fossil zygnemataleans are represented primarily by their zygospores that appear in the Carboniferous and are common later on (Van Geel & Grenfell 1996).

If the ecology of extinct zygnemataleans has been comparable to their living representatives, then an increase of these algae in the terminal Permian to early Triassic might have been owing to the rise of ground water level and a widespread ponding of rivers at the early stage of global transgression that started in the late Changhsingian (latest Permian) time (Yang Zunyi *et al.* 1995). Incidentally, the fossil plant bed of Nedubrovo locality is an anoxic estuarine deposit with well-preserved terrestrial plant compression material and planktonic unicells. This kind of aquatic environment might have been favourable for zygnemataleans. At the same time, a rapid change of lithofacies indicates an unstable sedimentary environments, with lithologies fluctuating from coaly graystones to redbeds within a few meters of the stratigraphic sequence. Such fluctuations, apparently characteristic of transboundary sequences, might impose environmental hazards on zygnematalean populations enhancing the encystment and formation of thick-walled cells owing to which these algae became conspicuous as fossils.

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REFERENCES

BALME B. E. 1980. — Palynology of Permian-Triassic boundary beds at Kap Stosch, East Greenland. *Meddelelser om Grønland, udgivne af Komissionen for Videnskabelige Underrsøgelser i Grønland* 200 (6): 1-37.

DE BARY A. 1858. — *Untersuchungen über die Familie der Conjugaten (Zygnemeen und Desmidieen)*. Leipzig, 91 p.

ELSIK W. C. 1999. — Reduviasporonites Wilson 1962: synonymy of the fungal organism involved in the late permian crisis. *Palynology* 23: 37-41.

FOSTER C. B. & JONES P. J. 1994. — Correlation between Australia and type Tatarian, Russian Platform, evidence from palynology and conchostraca: a discussion. *Permophiles* 24: 36-42.

FOSTER C. B., LOGAN G. A., SUMMONS R. E., GORTER J. D. & EDWARDS D. S. 1997. — Carbon isotopes, kerogen types and the Permian-Triasssic boundary in Australia: implications for exploration. *APPEA Journal*: 472-489.

FUGLEWICZ R. 1977. — New species of megaspores from the Trias of Poland. *Acta Palaeontologica Polonica* 22 (4): 405-431.

GRENFELL H. R. 1995. — Probable fossil zygnemataceae algal spore genera. *Review of Palaeobotany and Palynology* 84: 201-220.

KRASSILOV V. A., AFONIN S. A. & LOZOVSKY V. R. 1999. — Floristic evidence of transitional Permian-Triassic deposits of the Volga-Dvina region. *Permophiles* 34: 12-14.

LOZOVSKY V. R. & ESAULOVA N. K. 1998. — *Permian-Triassic Boundary in the Continental Series of East Europe (International Symposium "Upper Permian Stratotypes of the Volga Region").* GEOS, Moscow, 246 p. (in Russian).

MANGERUD G. 1994. — Palynostratigraphy of the Permian and Lowermost Triassic succession, Finnmark Platform, Barents Sea. *Review of Palaeobotany and Palynology* 82: 317-348.

OUYANG S. & UTTING J. 1990. — Palynology of Upper Permian and Lower Triassic rocks, Meishan, Changxing County, Zhejiang Province, China. *Review of Palaeobotany and Palynology* 66: 65-103.

RUNDINA L. A. 1998. — *Zygnematalean algae of Russia (Chlorophyta: Zygnematophyceae. Zygnematales).* Nauka, Saint-Petersburg, 351 p. (in Russian).

TRANSEAU E. N. 1951. — *The Zygnemataceae (Freshwater Conjugate Algae)*. Graduate School Monographs, Contribution in Botany 1, Columbus, 327 p.

UTTING J. 1994. — Palynostratigraphy of Permian and Lower Triassic rocks, Sverdrup Basin, Canadian Arctic Archipelago. *Geological Survey of Canada, Bulletin* 478, 107 p.

VAN GEEL B. & GRENFELL H. R. 1996. — Spores of Zygnemataceae, *in* JANSONIUS J. & MCGREGOR D. C. (eds), Palynology: principles and applications. *American Association of Stratigraphic Palynologist Foundation* 1: 173-179.

VASSER S. P., KONDRATYEVA N. V., MASUK H. P. *et al.* 1989. — *Algues*. Reference Book Naukova Dumka, Kiev, 608 p. (in Russian).

VISSCHER H., BRINKHUIS H., DILCHER D. L., ELSIK W. C., ESHET Y., LOOY C. V., RAMPINO M. R. & TRAVERSE A. 1996. — The terminal Paleozoic fungal event: evidence of terrestrial ecosystem destabilization and collapse. *Proceedings of the National Academy of Science* 93: 2155-2158.

YANG ZUNYI, SHENG JINZHANG & YIN HENGFU 1995. — The Permian-Triassic boundary: the global stratotype section and point (GSSP). *Episodes* 18 (1, 2): 49-53.

YAROSHENKO O. P. & GOMANKOV A. V. 1998. — Spores and Pollen, *in* ESAULOVA N. K. & LOZOVSKY V. R. (eds), *Permian-Triassic Boundary in the Continental Series of East Europe*. GEOS, Moscow: 113-130 (in Russian).

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