TEM evidence for eukaryotic diversity in mid-Proterozoic oceans

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ABSTRACT

Biomarker molecular fossils in 2770 Ma shales suggest that the Eucar a diverged from other principal domains earl in Earth histor. Nonetheless, at present, the oldest fossils that can be assigned to an e tant eukar otic

 $P_{\rm c}$ and $P_{\rm c}$ and $P_{\rm c}$ and $P_{\rm c}$ microfossils date from the late f 1960s to early 1980s (e.g. Jux, 1968, 1971, 1977; Kjellström, $19 \t{m}$, $190 \t{m}$, 80 , $197 \t{m}$ 1977. Peat, 1991). More recent work by Talyzina \mathbb{R} $M_{\rm{max}}$ (2000) on Early Cambrian acritecture revealed rev four structurally distinct types of vesicle walls. *Tasmanites tenellus has a homogeneous electron-dense wall punctuated by the second punctuated* by the second punctuated by the secon pore canals, similar to the phycomata of some prasinophyte green algae. Acanthomorphic (process-bearing) microfossils displayers displayers displayers of \mathcal{A} an electron-tenuous fibrous (*Archaeodiscina umbonulata*) or electron-dense homogeneous wall (*Globosphaeridium cerinum*, *Comasphaeridium brachyspinosum*, *Skiagia compressa*). *Leiosphaeridia* sp. shows a multilayered wall with an outer laminated $\frac{1}{\sqrt{2}}$ and the trilaminar sheath structure (TLS) for the trial sheath structure (TLS) found that $\frac{1}{\sqrt{2}}$ in many chlorococcalean green algae, an intermediate tenuous homogeneous layer, and an internal dense homogeneous layer. $\mathbf{a} = (1, 999, 000)$ chemistry of Neoproterozoic acritarchs from Australia, suggesting a dinoflagellate affinity for acanthomorph (processbearing) species (*Alicesphaeridium*, *Tanarium* and species \mathcal{L} with a multiplayered, fibrillar wall and children chall and children relationships for other taxa (*Multifronsphaeridium pelorium* and species \mathcal{A} , whose walls preserve a laminated organization or \mathcal{A} s in the trilamellar structure (TLS) for the trial structure \mathcal{L}_max green algae. Specimens of *Chuaria* and *Leiosphaeridia* sp. display a uni-layered electron-dense wall ultrastructure; *Tasmanites* sp. preserve a similar ultrastructure but perforated by numerous canals, again suggesting a prasinophyte green algae affinity. Both the set of the $(0,5,1,1)$ and the third thing \mathbf{r} $(\ldots \mu^r)$ specimens assigned to ℓ proterozoic Visingsö Group, Sweden, have a single-layered, electron-dense homogeneous $(\Delta \mathbf{v}, 000)$. Other contractions from the late N of P and α arises α West Africa, show a multiplanellar ultrastructure with structure with st tures interpreted as port can as port can as port can as port can as $(1-\alpha_1, 1, 99)$. In the case of chuarids from the Liulaobei Fomation in China (Steiner, 1997) display a variable wall structure ranging from massive to striate, multilayered walls in thick specimens with no or only local central central central central cavity to single-layered amorphous wall in \mathcal{R} thinner-walled specimens with a large central cavity. Steiner (1997) interpreted these fossils as *Nostoc*-like prokaryotic colonies, although living nostocaleans do not tolerate fully although living nostocaleans do not to marine environments. The Liulaobei remains could be cyanobacterial envelopes, but their phylogenetic relationship to \mathbf{F} is type locality or any extension in the locality or any extension of \mathbf{F} $\alpha = \alpha$ remains uncertainty uncertainty uncertainty α cannot be established with confidence, these fossils cannot be

used to establish the range of ultrastructures exhibited by $\mathbf{u}_i = \mathbf{u}_i \mathbf{u}_i$ prokaryotic vs. eukaryotic microorganisms. P_r on unambiguously even unambiguously entropy entropy \mathbb{R}^n . The context \mathbb{R}^n

ultrastructure, thus, shows that both acanthomophic and both acanthomophic and both acanthomophic and \mathcal{C} sphaeromorphic species can have multilayered or unilayered walls, with only *Tasmanites* spp. characterized by transverse can a characteristic of the physical cysts) of some $\frac{1}{2}$

property p algebra p is green algebra p (1971) in the property p wall of Palaeozoic genera *Baltisphaeridum* and *Peteinosphaeridum* are irregular in both shape and distribution and likely $\lambda \star$ (2000). $\mathbf{0}$ complex wall ultrastructure can only be adduced can only be adduced $\mathbf{0}$

as evidence for eukaryotic cell biology only if prokaryotic organisms do not form similar acetolysis-resistant walls (see review in Javaux *et al*., 2003). Few bacteria make spores with and size, surface or namentation, and preservation, and preservation potential po observed in Protection in Protection and the second in \mathbb{R}^n the Myxobacteria (which are mostly terrestrial), have sports \mathcal{M} \tilde{g}_i (sports in diameter) up to \tilde{g}_i in diameter, in di but these are smooth walled structures of unknown chemical composition that are not known to survive in sediments. Although vegetative cells of Actinobacteria can be relatively large (a few microsoft colonies, and form complex branching colonies, \mathbf{q}_1 the sports are $0.5-2$ points. The sports are μ in diameter and form chains. These sports can be ornamented but their rodlets, spines, spin warts, cristae, or hair-like tufts are named to hair-like tufts are named to hair-like tufts are named to hairstructures unlikely to survive in geological environments. Cyanobacterial sheaths are more likely candidates for comparison with Proterozoic fossils. Spheroidal envelopes of coc c_0 coidal coidal colonies can exceed 100 microns in size, c_0 and the second these polysical structures are commonly fossilized structures are commonly fossilized are commonly fossilized as \mathcal{A} $(\cdot,\overline{q}$ \mathbb{R} \math envelopes do not display surface ornamentation, so only simple spheroidal fossils (leiosphaerids) bear comparison. These \mathcal{C}_c and \mathcal{C}_c is the proton protistant from proton proto cellular eukaryotes) walls at the ultrastructural level, consisting $\mathbf{y}_{\mathbf{q}} = \mathbf{x}_{\mathbf{q}} \left(\mathbf{y}_{\mathbf{q}} \right)$, $\mathbf{y}_{\mathbf{q}} \in \mathbb{R}$, $\mathbf{y}_{\mathbf{q}} \in \mathbb{R}$; $\mathbf{y}_{\mathbf{q}} = \mathbf{y}_{\mathbf{q}}$; $\mathbf{y}_{\mathbf{q}} = \mathbf{y}_{\mathbf{q}}$ distinct from any of the ultrastructures described in this paper (J. Waterbury, pers. comm., 2003).

Thus, existing data indicate that the structural complexity of eukaryotic cell walls can be preserved in ancient microfossils and distinguished from acetolysis-resistant structures formed β , β , β , β , β , γ , α ultrastructural features can provide evidence for eukaryotic affinities, even in \mathbf{R}_i and i rocks, where m_i and m_i may be ambiguous.

MATERIALS AND METHODS

Most of the fossils treated here were recovered from carbonaceous shales of the early Mesoproterozoic Ropers of the early Mesoproterozoic Ropers and \mathcal{M} $\mathbf{G}_\mathbf{F} = \left(\begin{array}{c c c c} \mathbf{F}_\mathbf{F} \cdot \mathbf{F}_\mathbf{F} & \mathbf{F}_\mathbf{F} \cdot \mathbf{F}_\mathbf{F} \cdot \mathbf{F}_\mathbf{F} & \mathbf{F}_\mathbf{F} \cdot \mathbf{F}_\mathbf{F} \cdot$ characterized in terms of sedimentary architecture (Abbott & Sweet, $(1, 000)$ and is abundantly for $(1, 0, 1)$ e_r , 00). e_r we of decreasing abundance, decreasing abundance, decreasing \mathbf{v} and changing dominance (Java α , 2001). UP SHRIMP analyses of \mathcal{F}_{eff} and as in the Mainorus Formation and Mainorus Formation fix and agent $\frac{1}{2}$ and $\frac{1}{2}$ Max for early Roper deposition (Page deposition $\frac{1}{2}$ φ ., 000). $\qquad \theta \pm \qquad \qquad -\epsilon$ ₁ age for illite in \mathbf{r} siltstones near the top of the succession is consistent with the

O 2004 Blackwell Publishing Ltd, $\frac{\partial f}{\partial x^2}$, 121–132², 121–1322, 121–1322, 121–1322, 121–1322, 121–1322, 121–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1221–1322, 1

top of the Roper Group, also contain low abundances of steranes abundances of steranes of steranes abundances of steranes abundanc $\mathbf{s}_1 = \mathbf{s}_2 = \mathbf{s}_1$, $\mathbf{s}_2 = \mathbf{s}_3 = \mathbf{s}_4$, $\mathbf{s}_3 = \mathbf{s}_4 = \mathbf{s}_5 = \mathbf{s}_6 = \mathbf{s}_7$, $\mathbf{s}_8 = \mathbf{s}_8 = \mathbf{s}_7$, $\mathbf{s}_9 = \mathbf{s}_8 = \mathbf{s}_7 = \mathbf{s}_7$, $\mathbf{s}_9 = \mathbf{s}_8 = \mathbf{s}_7 = \math$ One highly ornamented fossil also treated here, *Shuiyous* $p \nmid_{\mathcal{F}} p$ Group, northern China. Ruyang deposition is not well con- $\mathbf{S}_\mathbf{B}$ strained by radiometric dates, but appears to be at least broadly broad coeval with Roper sedimentation. A *c*. 1000 Ma granite (U-Pb zircon date) intrudes the Ruyang succession, providing a minimum age for the group; moreover, abundant microdigitate precipitates and C-isotopic profiles that vary little from 0‰ in t_{max} thick, overlying carbonates suggests that Ruyang shales are older are older are older are older as than *c*. 1250 Ma (Xiao *et al*., 1997). Ruyang shales share several distinctive taxa (species of *Tappania*, *aleria*, and *Dictyosphaera*) with the Roper Group. Similar microfossil assemblages occurred assemblages occurred assemblages occurred assemblages occurred assemblages of the α in the c.1.3 Ga \sim Ga \sim Total Formation, Siberia (Sergeev, pers. comm., comm 2002), and the poorly dated but broadly correlations of the poorly dated but broadly correlations of the poor
1990), and the poorly dated but broadly correlations of the poorly dated but broadly correlations of the poor \blacksquare , \blacksquare). Microfossils were extracted from shales using a modified palynological method involving slow hydrofluoric acid diges-

 $z_{\rm in}$ age, if an extension $\mathcal{R}_{\rm in}$ (Kralik, 1982). Highly carbonaceous shales in basinal deposits of the Velkerri Formation, near the were mounted with european and the microscopy. The light microscopy is a light microscopy. The light microscopy. For SEM, individual microfossils were picked from unmounted macerates and placed on glass coverslips glued onto aluminium stubs. Stubs were then coated with a 22 nm layer of goldpalladium. Scanning electron microscopy was carried out using $9 - \epsilon$ For TEM, various preparation methods were tried and adapted, especially with regard to infinite and polymeriza-

tion times, microfossil manipulations and type of resin used. Microfossils were embedded in agar, dehydrated in a series of ethanol solutions, and then infiltrated with a mixture of pro-

Eukar otic diversit in mid-Protero oic oceans **123**

tion with minimal minimal ages ($\epsilon_{\rm eq}$, 1999). Equ

Fig. 2 Eukar otic microfossils from the Roper Group, Australia. a–e: *Tappania plana*, a–c: light microscop, a: specimen Lith heteromorphic processes (including a branched process-long arro Δ) distributed as mmetricall about the vesicle and budding (short arro Δ), b: specimen Δ th possible e c stment structure (arro Δ), c: specimen Lith as mmetricall distributed processes Lith closed, slightl e panded terminations, d: SEM sho Ling structural continuit bet en vesicle Lall and process bases, e: TEM sho Ling unila ered homogeneous electron-dense Lall Lith variable thickness due to taphonomic processes; f-i: Valeria lophostriata, f: partiall enrolled half vesicle, likel resulting from medial split (light microscop), g: SEM sho ing ridges spaced 1 µm apart on the internal surface of the vesicle, h, i: TEM sho Ling t Lo Lalls of compressed vesicle Lith ridges (h) and unila ered homogeneous electron-dense Lall (i). Scale bar in a = 35 µm for a, 20 µm for b, 25 µm for c, 33.5 µm for d, 1.4 µm for e, 32 µm for f, 2.5 µm for g, 2 µm for h, 0.25 µm for i.

Large striated tubes occur abundantly in inner shelf shales of the Roper Group. The carbonaceous tubes are up to $\ln \theta$ μ in diameter and more than a millimeter long (Fig. 3g). Light microscopy shows longitudinal, micron-scale striations along the tubes (arrows in \mathbf{a}_i are vecales layers of densely packed packed by \mathbf{a}_i granules but does not show structures that could account for show $\mathbf{f} = \mathbf{f} + \mathbf$ however, transverse sections of the wall show a clear alternations of the wall show a clear alternation of the of electron-dense and electron-tenuous bands that corresponds that co

in size and distribution to the striations observed by light microscopy (Figs 3). The strip \mathbf{r}_k is strip str positional heterogeneities in the tube wall, indicating complex physiological controls on wall formation. The wall is about one $\mathfrak{\mu}$

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Fig. 4 Leiosphaerids from the Roper Group, Australia. a-d, m: *Leiosphaeridia jacutica*. a: specimen sho Ling thick folds (light microscop), b: SEM sho Ling a smooth

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130 EMMANUELLE J. JAVAUX

from the North China Platform. **Precambing** P 9° 0 . \mathbf{x} , \mathbf{x} , \mathbf{x} , \mathbf{x} , \mathbf{x} , \mathbf{x} carbonaceous compressions in a terminal Proterozoic shales: a systematic reassessment of the Miaohe biota, South China. $J_{\mathbf{r}}$ \longrightarrow $J_{\mathbf{r}}$ \longrightarrow $J_{\mathbf{r}}$ \longrightarrow $J_{\mathbf{r}}$ in $(\begin{array}{c} 99 \end{array})$ according to $\begin{array}{cc} \bullet & \bullet & \bullet & \bullet & \bullet \end{array}$ for $\begin{array}{cc} \bullet & \bullet & \bullet & \bullet \end{array}$ shales of the Ruyang Group, Shanxi, China. *Review of Palaeobotany and Palynology* **98**, 15–25.

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