

Figure 5 The properties of a continuous sequence of 36 annual cycles within 6-m-thick cross-strata of set A. Strata deformed by rain-induced slumping (red) are typically at the base or top of annual cycles, suggesting strong seasonality of major rainfall events (that is, monsoonal circulation). Thin deformed zones in mid-cycle positions (5, 7, 11 and 33) are interpreted as products of winter storms. Measured thicknesses of deformed zones were decreased by 50% to offset structural thickening. Location by Global Positioning System: 36°55' 49.4"N, 112°0' 43.5"W.

strata are clearly clustered at this surface. Of the 24 deformed zones in set A, 20 are bounded (above or below) by this surface. All 5 of the deformed zones in set B are in this position (see Supplementary Information). Both sets A and B are exposed in dip-parallel section. Only if all slumping were laterally continuous along the entire dune lee face would such a section intersect all slumps. Therefore, for this 36-year interval, we interpret slumping to have been an annual process.

We consider the dominant dune-driving winds to have been the northwesterly winter flow around the high-pressure zone at the western margin of Pangaea. The opposing winds that moved sand obliquely up the slip faces were the northeasterly trade winds of spring and autumn. Northeasterly flow at the southern edge of the dune field was followed by the arrival of heavy rains at the northern margin of the intertropical convergence zone (ITCZ). Slumps generated during these rains would have been truncated and buried by wind-ripple deposits when northeasterly flow resumed as the ITCZ migrated southwards again. The dunes would have resumed their southeastward migration in winter as the anticyclone off the west coast of Pangaea migrated southwards (Fig. 1).

The thicknesses of the deformed zones in Navajo Sandstone strata record rainfall magnitudes of individual storms. The thickest deformed zone (cycle 26, set A) measures 84 cm. Assuming a doubling of thickness during thrusting, and that the slope failure was caused by positive porewater pressure, a slab of sand about 42 cm thick would need to become saturated by water. For our calculation, we assume a porosity of 50%, residual moisture (before rainfall) of another 10%, and that failure and saturation were coincident. A minimum of 170 mm of rain would be required to saturate and destabilize such a slab.

Our observations and interpretations coincide closely with results from the only quantitative Early Jurassic climate model that is currently available³. In particular, this model shows that for the Navajo sand sea, winter winds were stronger than summer winds. It also shows that, during the summer, monsoonal flow of moist air entered the study area from the west and delivered an average of 2 mm rainfall per day. If the precipitation fell as heavy downpours from cumulonimbus clouds, such a quantity would be sufficient to generate the slumps that we have observed in the Navajo Sandstone. □

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Supplementary information is available on Nature's World-Wide Web site (<http://www.nature.com>) or as paper copy from the London editorial office of Nature.

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Morphological and ecological complexity in early eukaryotic ecosystems

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Molecular phylogeny and biogeochemistry indicate that eukaryotes differentiated early in Earth history. Sequence comparisons of small-subunit ribosomal RNA genes suggest a deep evolutionary divergence of Eukarya and Archaea; C₂₇–C₂₉ steranes (derived from sterols synthesized by eukaryotes) and strong depletion of ¹³C (a biogeochemical signature of methanogenic Archaea) in 2,700 Myr old kerogens independently place a minimum age on this split^{2,3}. Steranes, large spheroidal microfossils, and rare macrofossils of possible eukaryotic origin occur in Palaeoproterozoic rocks^{4–6}. Until now, however, evidence for morphological and taxonomic diversification within the domain has generally been restricted to very late Mesoproterozoic and Neoproterozoic successions⁷. Here we show that the cytoskeletal and ecological prerequisites for eukaryotic diversification were already established in eukaryotic microorganisms fossilized nearly 1,500 Myr ago in shales of the early Mesoproterozoic Roper Group in northern Australia.

The most distinctive Roper fossils are acritarchs attributable to *Tappania plana*. *Tappania* populations consist of irregularly spheroidal organic vesicles up to 160 μm in diameter⁸ distinguished by bulbous protrusions and from zero to twenty hollow, cylindrical processes (Fig. 1a–c). The processes have closed, slightly expanded terminations and may branch dichotomously (Fig. 1b). Moreover, and in contrast to most younger acritarchs, processes are distributed irregularly and asymmetrically on the vesicle surface (Fig. 1a and c).

Acritarchs are conventionally interpreted as metabolically inert resting stages of algae, their symmetric ornamentation reflecting morphological self-organization during cyst-wall synthesis. In contrast, the irregular number and length, asymmetric distribution, and branching of processes in *Tappania* suggest an actively growing cell or germinating cyst⁹. The bulbous protrusions in some specimens further suggest vegetative reproduction through budding.

The kind of dynamic cell remodelling documented by *Tappania* morphologies does not occur in prokaryotic organisms. In eukaryotes, it is made possible by the cytoskeleton, an internal scaffolding of actin and other proteins regulated by a sophisticated network of molecular signalling pathways^{10,11}. The systematic relationships of *Tappania* are uncertain, but its distinctive morphology indicates that by 1,500 Myr ago protists already possessed the cytoskeletal

architecture and regulatory networks that characterize living protists. Thus, the cytological prerequisites for morphological radiation in eukaryotes were in place long before the taxonomic diversification documented by Neoproterozoic fossils.

Tappania was first discovered in carbonaceous shales of the Ruyang Group, northern China⁸, but beyond being demonstrably

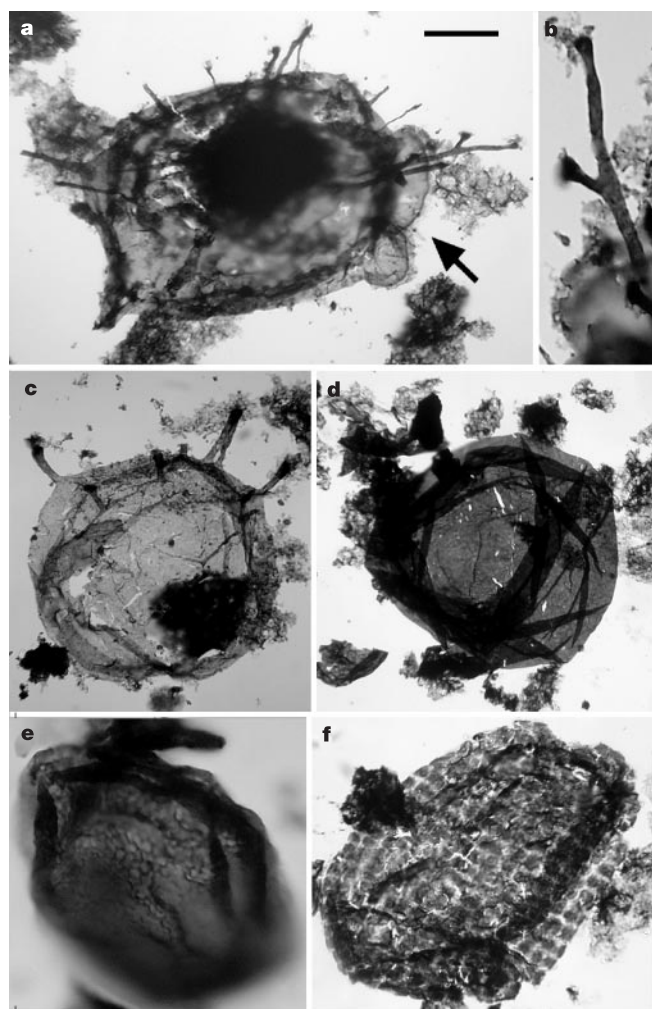


Figure 1 Protistan microfossils from the Roper Group. **a, c**, *Tappania plana*, showing asymmetrically distributed processes and bulbous protrusions (arrow in **a**). **b**, detail of **a**, showing dichotomously branching process. **d**, *Valeria lophostriata*. **e**, *Dictyosphaera* sp. **f**, *Satka favosa*. The scale bar in **a** is 35 μm for **a** and **c**; 10 μm for **b**; 100 μm for **d**; 15 μm for **e**; and 40 μm for **f**.

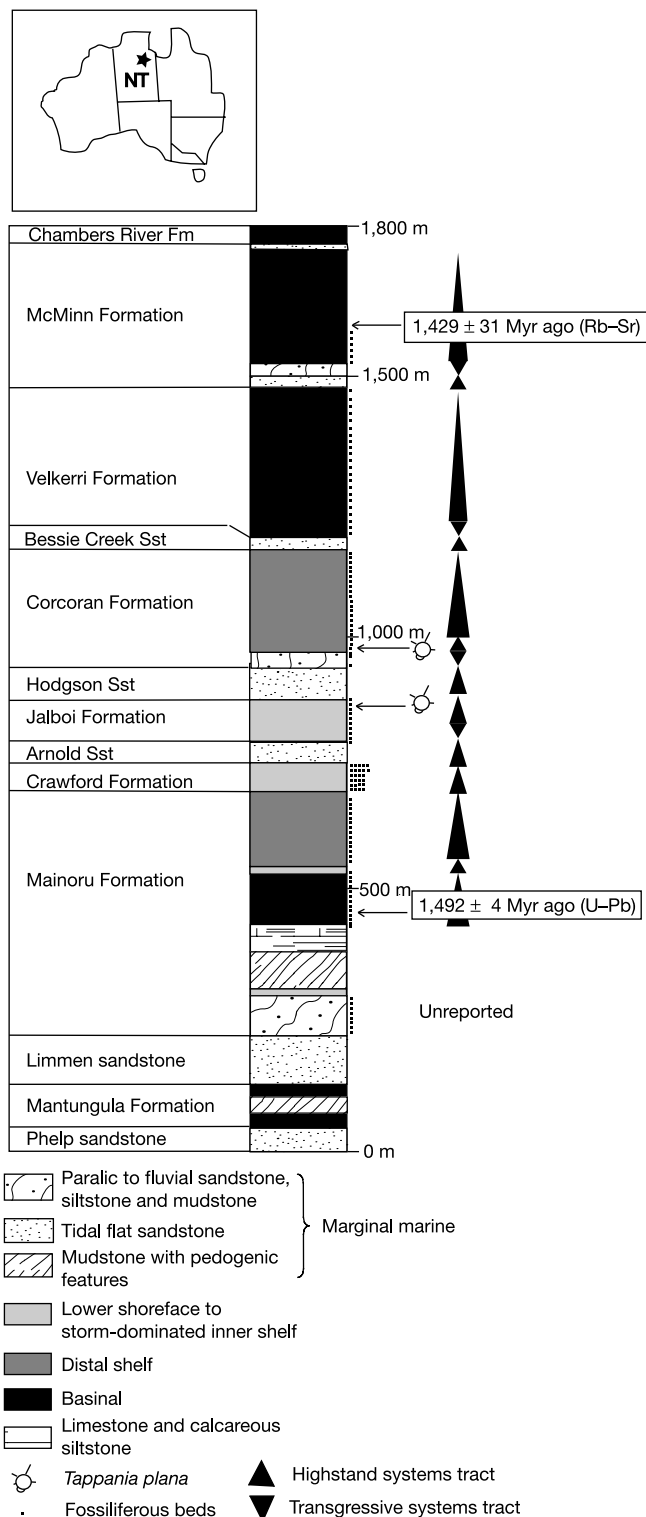


Figure 2 Location and generalized stratigraphy of the Roper Group, northern Australia. The stratigraphic distribution of facies, systems tracts and microfossils is shown, including the distinctive process-bearing protist *Tappania*. Modified from ref. 15; radiometric data from refs 13 and 14. NT, Northern Territory; Sst, Sandstone; Fm, Formation.

Mesoproterozoic, the age of the Chinese fossils is poorly constrained¹². In contrast, the new Australia populations occur in a basin that is well dated, exceptionally well characterized in terms of sedimentary architecture, and abundantly fossiliferous (Fig. 2). Thus, we are able to constrain the age, environment and ecological associations of Australian *Tappania*.

U–Pb SHRIMP analyses of zircons from an ash bed in the Mainoru Formation fix an age of $1,492 \pm 3$ Myr for early Roper deposition¹³. A $1,429 \pm 31$ Myr Rb–Sr age for illite in dolomitic siltstones near the top of the succession¹⁴ is consistent with the zircon age, albeit less reliable. Abbott and Sweet¹⁵ interpreted the stratigraphic architecture of Roper rocks in terms of six principal depositional sequences bounded by conformable surfaces in the basin interior. Sequences are highly asymmetric, consisting mostly of highstand systems tracts dominated by deep basinal to distal shelf mudstones that become more shallow upward to coastal sandstones and intercalated shales. Marine deposition is indicated by facies development and associations, which closely parallel those of younger marine successions. This is supported by distinctive sedimentary structures such as hummocky cross-stratification; evidence of reversing tidal events; and C–S ratios generally characteristic of marine basins^{15,16}.

Fossils were first discovered in Roper rocks by Peat *et al.*¹⁷, who reported leiosphaerid acritarchs, clusters of small spheroidal unicells and filamentous microfossils in shales of the McMinn Formation, near the top of the Roper succession. Our study of 126 samples from five drill cores (Urapunga 4, 5, 6; Amoco 82/3; Golden Grove 1) shows that microfossils are both abundant and unusually well preserved throughout the 2,000-m-thick group (Fig. 2).

The most abundant and species-rich Roper assemblages come from estuarine or deltaic to tide-dominated shoreline facies (Fig. 3). Coastal shales contain large (>200 µm) spheroidal microfossils, including *Leiosphaeridia* spp., the distinctively striated *Valeria lophostriata* (Fig. 1d), and thick-walled vesicles more than a millimetre in diameter. Conventional (50–100 µm) leiosphaerids are also abundant, as is *Satka favosa*, a spheroidal acritarch with walls of interlocking rectangular panels (Fig. 1f). Although species richness is highest in coastal samples, these assemblages also exhibit strong concentration of dominance in one or two species (Fig. 3); most of the diversity is contributed by rare taxa.

Shales in lower-shoreface to storm-dominated inner-shelf facies preserve a lower abundance and diversity of sphaeromorphic

acritarchs, common *Satka squamifera* (distinguished by rounded wall textures imparted by included cell packets), and large (up to 150 µm in cross-sectional diameter) striated tubes of uncertain, but probably eukaryotic, affinities. (A few sulphur-oxidizing bacteria can produce comparably large sheaths, but none is known to produce thick, regularly striated walls comparable to the Roper fossils.) More distal shelf shales contain still fewer fossils. *Tappania* populations are restricted to this facies, where they occur with filamentous, probably cyanobacterial, sheaths and scattered spheroidal acritarchs. This may explain the apparent absence of *Tappania* in well studied Mesoproterozoic successions from the Urals and Siberia, which are dominated by inshore depositional facies^{18,19}. Chinese *Tappania* populations also occur in distal shelf shales²⁰.

Most basinal mudstones contain abundant organic debris but few well preserved microfossils. A few samples, however, contain monospecific assemblages of *Stictosphaeridium* sp., 40–70 µm spheroidal acritarchs with thin, chagrinat walls.

The onshore–offshore pattern (Fig. 3) of decreasing abundance, declining diversity, and changing dominance among fossils of probable eukaryotic origin is observed consistently throughout our large sample set. Younger successions commonly show maximum eukaryotic diversity in inner shelf settings, with decreasing diversity offshore^{21–24}. Rarely, however, do abundance and diversity peak in marginal marine facies, as observed in the Roper Group. An explanation for this unusual palaeoenvironmental pattern may lie in chemistry of Mesoproterozoic oceans, where biologically important trace elements (especially Mo, required for nitrate assimilation) were possibly scarce in offshore waters distant from continental runoff^{25–26}. Regardless of the explanation for fossil distributions in the Roper Group, the simple observation of strong facies associations among taxa shows that 1,500 Myr ago natural selection had long since begun to distribute protistan populations among physical habitats—contributing to the rise of biological diversity (and providing tools for palaeoenvironmental reconstruction).

The discovery of distinctive microfossils in the well dated Roper Group and its Chinese counterpart raises the prospect of a biostratigraphic characterization of early Mesoproterozoic sedimentary rocks. Process-bearing microfossils also occur in younger Mesoproterozoic successions, but they are distinct from those observed in Roper and Ruyang shales^{27–28}. We predict that the Mesoproterozoic era will prove to be divisible into at least two broad intervals based on microfossil assemblages and carbon isotope profiles, although

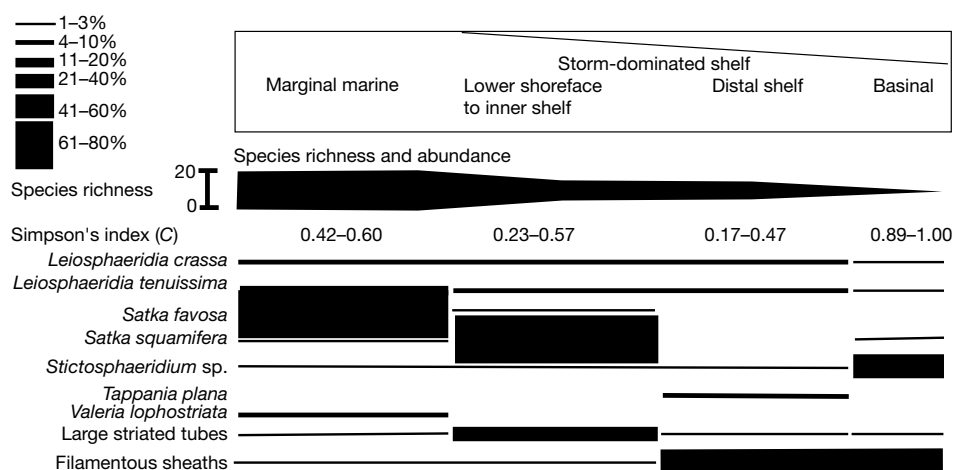


Figure 3 Palaeoenvironmental distribution of Roper fossils, showing relationships among physical environment, fossil abundance, and taxonomic diversity. Of the 126 samples used in this study, 13 come from marginal marine facies, 26 from lower-shoreface to storm-dominated inner-shelf facies, 30 from middle to distal shelf facies, and 57 from

basinal facies. Species richness and Simpson's index of dominance concentration (*C*) are based on size-standardized (*N* = 300) counts of fossils within samples. Abundance was estimated using microfossil density within samples. Legend in upper left indicates percentage contribution of listed taxa to total fossil assemblage in each environment.

the bio- and chemostratigraphic breakpoints may not coincide precisely. The restricted facies distribution of distinctive early Mesoproterozoic acritarchs, however, suggests that biostratigraphic confidence will necessarily be tied to careful palaeoenvironmental characterization.

Process-bearing microfossils were once thought to be restricted to Phanerozoic strata. Two decades ago, their range was extended to the beginning of the Neoproterozoic era. Now, it is clear that process-bearing microfossils have been present for nearly half of life's recorded history. The Roper Group provides an unusually clear window on aspects of biology in the early Mesoproterozoic oceans, demonstrating that 1,500 Myr ago marine protists included cytologically sophisticated organisms that lived in ecologically differentiated communities. □

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The impact of ultraviolet radiation on the vertical distribution of zooplankton of the genus *Daphnia*

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The vertical migration of zooplankton into lower and darker water strata by day is generally explained by the avoidance of visually orienting predators, mainly fish^{1–4}; however, it is unclear why daily zooplankton migration has been maintained in fishless areas⁵. In addition to predation, ultraviolet radiation—a hazardous factor for zooplankton in the surface layers of marine and freshwater environments^{6–8}—has been suspected as a possible cause of daytime downward migration⁹. Here we test this hypothesis by studying several *Daphnia* species, both in a controlled laboratory system and under natural sunlight in an outdoor system. We selected *Daphnia* species that differed in their pigmentation as both melanin and carotenoids have been shown to protect *Daphnia* from ultraviolet light^{10,11}. All *Daphnia* species escaped into significantly deeper water layers under ultraviolet radiation. The extent to which the daphnids responded to this radiation was inversely linked to their pigmentation, which reduced ultraviolet transmission. These results suggest that ultraviolet avoidance is an additional factor in explaining daytime downward migration. Synergistic benefits might have shaped the evolution of this complex behaviour.

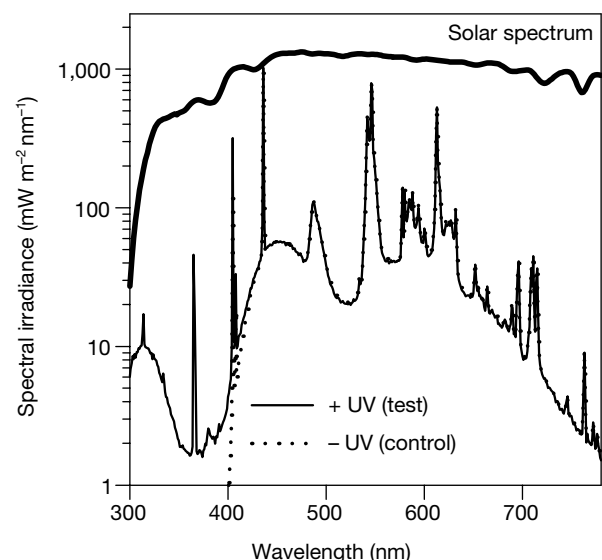


Figure 1 Spectral irradiation in mesocosms with (test) and without (control) ultraviolet radiation. Ultraviolet radiation above the water surface was lower than on a cloudless September day at noon in 1995 in Munich, when we performed the experiments under natural solar irradiation (solar spectrum).