PROTEROZOIC AND CAMBRIAN BIOEVENTS

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ABSTRACT

The modern ecosystems began to be formed in the Proterozoic Eon. The Proterozoic fossil record includes bacteria and cyanobacteria, heterotrophic and autotrophic protists, multicellular thallophytes, and metazoans. The gradual increase of the oxygen pressure in the atmosphere took place during the Proterozoic causing a great diversification of eukaryotic life and the origin of metazoans. The first autotrophic protists (acritarchs) originated in the Palaeoproterozoic and reached a high level of diversification in the early Neoproterozoic, when the first heterotrophic protists and biomineralized forms appeared. Several thallophytic groups may have originated during the Palaeoproterozoic, while the Rhodophyta probably radiated during the Mesoproterozoic, and Chlorophyta during the Neoproterozoic. The glacial episodes in the Neoproterozoic led to a mass extinction among protists. The Late Vendian ecosystems reveal deeply renewed assemblages of planktonic protists, problematic metazoan fauna (Ediacara Fauna), ichnofossils and slightly mineralized metazoans (*Cloudina*). The bioturbation characteristic for these ecosystems appears in form of small, simple and shallow burrows. The biotic turnover at the Neoproterozoic/Cambrian boundary is expressed by a mass extinction and the origin of new primary producers and consumers. The Cambrian rocks show a higher degree of bioturbation, suggesting a drastic change in the techniques of exploitation of the nutrients accumulated in the sediments.

Key words: Proterozoic, Cambrian, Protista, Thallophyta, metazoans, biomineralization, ichnofossils, oxygen, carbon, ecosystems evolution.

RESUMEN

Los ecosistemas modernos comenzaron a perfilarse en el Eón Proterozoico. Su registro fósil incluye bacterias y cianobacterias, protistas autótrofos y heterótrofos, talofitas multicelulares y metazoos. Durante el Proterozoico se produjo la oxigenación gradual de la atmósfera, que coincidió con la gran expansión y diversificación de la vida eucariota y posterior aparición de metazoos. Los primeros protistas autótrofos (acritarcos) aparecieron en el Paleoproterozoico, alcanzando un alto grado de diversificación (primeros heterótrofos y formas biomineralizadas) en el Neoproterozoico temprano. El origen de varios grupos de talofitas pudo haberse dado en el Paleoproterozoico, siendo el Mesoproterozoico un periodo de radiación de posibles rodofíceas y el Neoproterozoico de clorofíceas. Los episodios glaciares del Neoproterozoico produjeron una extinción masiva de protistas. El registro de los ecosistemas del Véndico Superior incluye asociaciones totalmente renovadas de protistas planctónicos, faunas problemáticas de metazoos (Fauna de Ediacara), icnofósiles y metazoos moderadamente mineralizados (*Cloudina*). La bioturbación característica de estos ecosistemas consistía en pequeñas madrigueras simples y poco profundas. Los cambios bióticos en el límite Neoproterozoico/Cámbrico se manifiestaron mediante una nueva extinción en masa y la aparición de nuevos productores primarios y consumidores. Las rocas cámbricas presentan un grado de bioturbación mucho más alto y avanzado, que sugiere un cambio drástico en la utilización de los nutrientes que se acumulaban en los sedimentos.

Palabras clave: Proterozoico, Cámbrico, protistas, talofitas, metazoos, biomineralización, icnofósiles, oxígeno, carbono, evolución de los ecosistemas.

LIFE IN THE PROTEROZOIC

The modern ecosystems began to be formed in the Proterozoic, a period in the Earth history that encompasses 2,000 million years (Ma), beginning at about 2,500 Ma ago and terminating at the base of the Cambrian Period (543 Ma). The fossil record of the Proterozoic Eonothem consists of cyanobacteria, the iron

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Figure 1. Spiral carbonaceous fossil *Grypania* sp. (2,200 Ma).

Figure 2. Colonial protist from the Belt Supergroup, North America (ca. 1,400 Ma).

and manganese bacteria and diverse microfossils of autotrophic and heterotrophic eukaryotes. The Neoproterozoic fossil record (1,000-543 Ma) provides evidence for the appearance of the first tallophytes (Hofmann, 1994) whose complex organization preceded the major ecological explosion at the Precambrian/Cambrian boundary. The Cambrian explosion has been a subject of a number of scientific hypotheses. From a biotic perspective, the increase of the oxygen pressure in the atmosphere during the Proterozoic Eon represented probably the most important environmental change caused by the organismic processes, i.e. the oxygenic photosynthesis. The free oxygen concentration in the atmosphere was due to the prior oxidation of the reduced iron stored in the oceans; this phenomenon took place during the Archean and a major part of the Proterozoic. The achievement of this critical state of oxidation allowed the oxygen release into the atmosphere, reaching high levels at about 1,600 Ma, as indicated by the first appearance of oxidized sediments in the geologic record. The process of increase of the oxygen pressure in the atmosphere continued throughout the Proterozoic Eon and coincided with a significant expansion and diversification of the eukaryotic life.

THE EUKARYOTIC LIFE

Recent Molecular Biology studies, based on the nucleotide sequences of subunits of the ribosomal RNA (rRNA), indicate that the eukaryotic organisms are of a great antiquity and that they probably share a common ancestor with the Archaeobacteria to which they are closely related. Thus, it is not surprising that the protein involved in the activation of the gene expression is practically identical in both Archaeobacteria and the eukaryotic organisms. This suggests that eukaryotes are probably related to Archaeobacteria, which are considered to be descendants of the most primitive unicellular life forms. On the other hand, the existence of eukaryotic protists lacking some organelles, such as *Giardia*, may suggest their great antiquity (Runnegar, 1994), since though having a nucleus they lack many functions and requirements of the typical eukaryotes. These reasons allow to interpret the spiral-shaped, carbonaceous fossil filaments attributed to *Grypania* (Fig. 1), and 2,200 Ma old, as possible primitive eukaryotes.

The origin of eukaryotes is not clearly discernible in the fossil record. Several lines of evidence are in favour of the endosymbiosis as a process leading to the origin of cells with nuclei (Margulis, 1981), and the existence of eukaryotic protists lacking some organelles argue for the polyphyletic and endosymbiotic origins of eukaryotes. This proposal is also supported by the sequences of nucleotides of the RNA in organelles (chloroplasts and mitochondria) of certain protists (Margulis *et al.*, 1990). According to this, mitochondria seem to have derived from Eubacteria, while chloroplasts from cyanobacterial ancestors.

Although the origin of eukaryotes is uncertain, the diversification in ecosystem formed by eukaryotic protists is broadly documented during the Palaeoproterozoic (1,700 Ma) (Fig. 2), and in particular during the Neoproterozoic (1,000-543 Ma; Mendelson and Schopf, 1992; Vidal and Moczydłowska, 1993; Vidal, 1994), by means of microfossils called acritarchs. Acritarchs are organic-walled cysts (Figs. 3, 4, 5), suggesting the existence of a sexual reproduction cycle clearly indicative of an eukaryotic organization comparable to that of some present-day Chlorophyta and Chrysophyta. On the other hand, a great variety of morphologies observed in the Neoproterozoic also suggests a higher rate of appearance of new species compared to the Palaeoproterozoic and Mesoproterozoic (Vidal and Knoll, 1982; Knoll, 1994).

Studies on nucleotide sequences in ribosomal RNA (rRNA) point to a major radiation of protists in the terminal Proterozoic and to appearance of major groups of photosynthetic protists during the same period of increased diversification (Perasso *et al.*, 1989). Except for

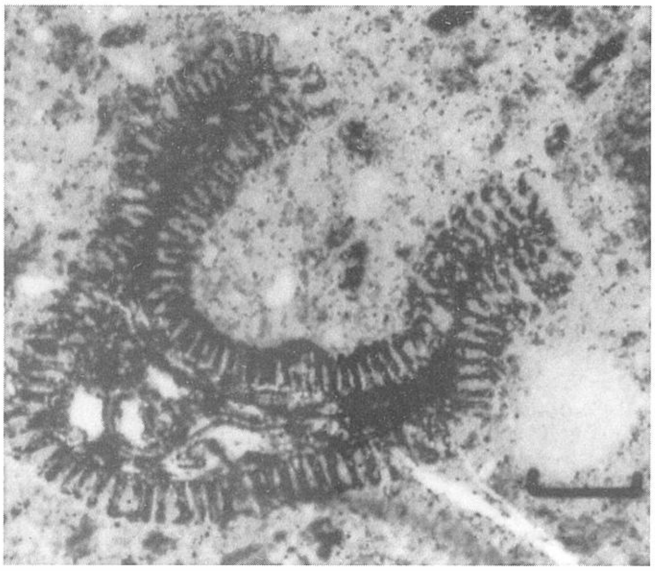

Figure 3. *Papillomembrana*, an acritarch ca. 600 µm in diameter, from the early Neoproterozoic of Norway.

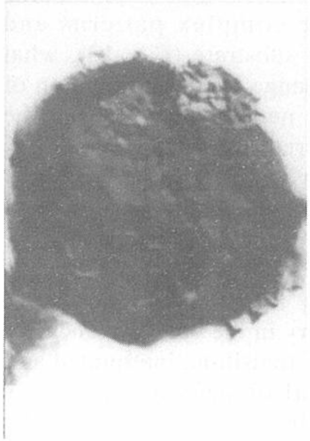

Figure 4. *Vandalosphaeridium*, an acritarch with appendices and operculum-shaped aperture, from the Chuar Group of Arizona, U.S.A. (ca. 800 Ma).

Figure 5. Acritarch with operculum-shaped, circular aperture, from the Chuar Group of Arizona, U.S.A. (ca. 800 Ma).

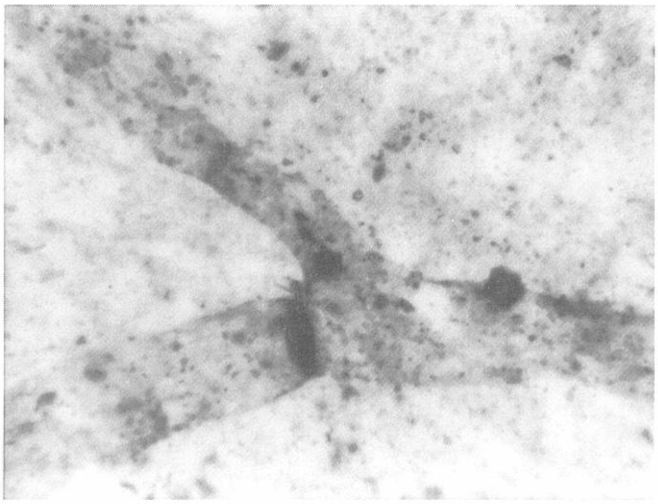

Figure 6. Rhodophytic algae of the Class Bangiales, from the early Neoproterozoic Svanbergfjellet Formation in Svalbard (800 Ma). (Thin section kindly provided by A. H. Knoll.)

the problematic fossil *Grypania* mentioned above (Fig. 1), the origin of several thallophytic groups could begin at about 1,700 Ma ago in the Mesoproterozoic, a period of radiation of possible Bangiophyceae (Fig. 6) and Rhodophyta (Butterfield *et al.*, 1988), and in the terminal Neoproterozoic, for possible Chlorophyta as *Tawuia* (Fig. 7) (Hofmann, 1994).

The two latest Proterozoic glacial events (650-600 Ma) seem to have affected a significant part of the Earth, since the glacial deposits are preserved in all continents. The glacial epoch coincides with a major extinction among Neoproterozoic protists (Vidal, 1983). The ecosystem that developed after this severe glacial period was dominated by planktonic protists (Fig. 8) that were morphologically very different from their predecessors, suggesting a new ecological radiation in the realm of the eukaryotic plankters. The reason for their extinction at the end of the Vendian Period (ca. 543 Ma) is still unknown. The Upper Vendian provides an evidence for the innovation of the problematic faunas (so-called Ediacara-type) that have received their name after the type locality of Ediacara in southern Australia (Fig. 9), although at the present they are known practically from all continents. At the same time, ichnofossils produced due to the activity of different groups of marine metazoans appeared, and they have a special significance in the Proterozoic of Spain.

The metazoan level of organization is characterized by the presence of tissues, in which the collagen is a main constituent: "the tape & glue of the metazoan world" (Towe, 1981). The synthesis of collagen requires the

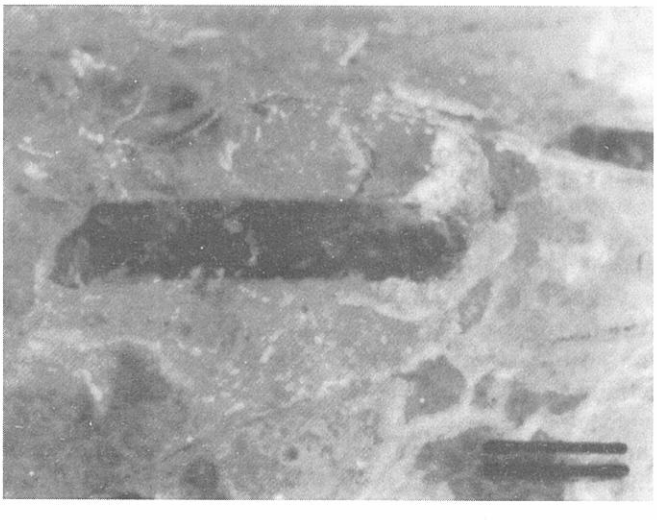

Figure 7. *Tawuia dalensis* Hofmann and Aitken, 1979, from the early Neoproterozoic of Siberia (ca. 800 Ma).

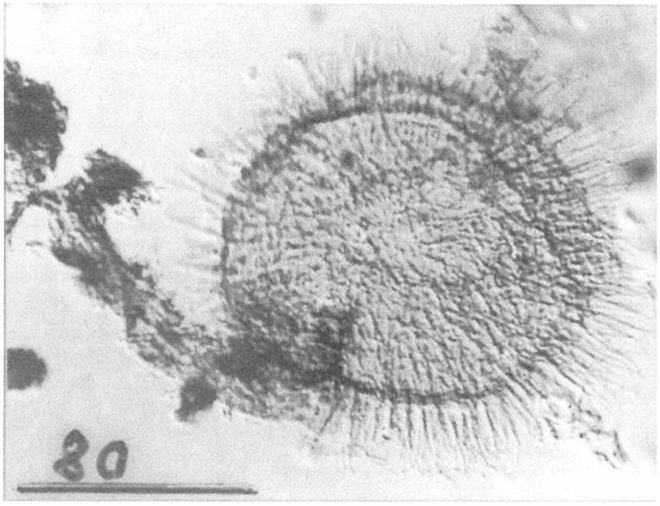

Figure 8. Acritarch from the Vendian of Siberia (640 Ma).

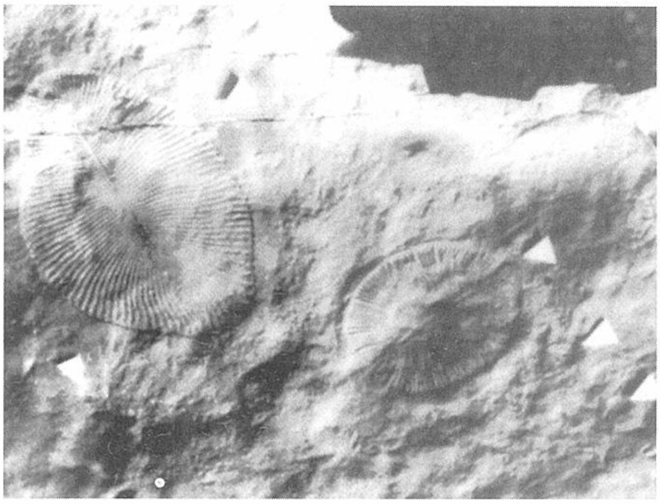

Figure 9. Ediacaran fossils from the Vendian of Australia.

oxygen concentration higher than 3% of the present atmospheric level (i.e., a concentration of 0.6% in relation to the present 21%). Uncertainty still exists concerning the dating of this episode in the evolution of life, but it seems that the appearance of ichnofossils produced by small marine metazoans took place not before 650 Ma ago. These fossils concur with the first appearance of organisms with a slightly mineralized shell attributed to *Cloudina* (Fig. 10), which are probably small cnidarians. In fact, *Cloudina* is probably, in terms of biomass, the most abundant Neoproterozoic fossil in the Iberian Peninsula. *Cloudina* is associated elsewhere with calcitic algae and primitive vendozoans, which are fossils of enigmatic marine organisms with a very strange anatomy, sometimes regarded as "life from another planet" or experiments of the evolutionary process that became extinct without leaving successors. In any case, some forms seem to belong to phylogenetic groups that reached the Palaeozoic times (Conway Morris, 1993; Crimes *et al*., 1995; Moczydłowska and Crimes, 1995).

THE CAMBRIAN EXPLOSION

The marine sedimentary rocks predating the major Cambrian radiation do not contain distinctive acritarchs. Furthermore, these rocks show rather little activity of organisms (bioturbation). This has been interpreted as a result of gradual colonization of the marine environments, beginning in the late Neoproterozoic in shallow marine shelves and later invading deeper slopes, as the oxygen concentration allowed it (Crimes, 1989, 1992). After this, several palaeobiological questions arise: Was the colonization of deep water environments in the terminal Proterozoic the result of drastic changes in the concentration of the oxygen?, or was it, on the contrary, due to the transportation of oxygen towards deeper environments through the establishment of a previously absent oceanic circulation system? Data from the sedimentary successions of the Iberian Peninsula suggest that the second alternative is more likely (Vidal, Jensen and Palacios, 1994). The characteristic ichnofossils of the Neoproterozoic consists of shallow and simple burrows (Fig. 11), while Cambrian rocks are much more bioturbated, showing more complex patterns and reaching deeper levels in the substrate (Fig. 12), what evidently suggests a drastic change in the exploitation of the organic remains and other nutrients deposited in the sea floor. Evidently these materials were also exploited in the Proterozoic marine ecosystems, but mainly by organotrophic bacteria and fungi. The appearance of filter-feeders, detritus-feeders and grazers modified drastically the cycle of the organic carbon in marine ecosystems. This is probably reflected by the change detected in the carbon chemistry in the oceans coinciding with the Proterozoic/Cambrian transition, interpreted as a drastic change in the burial of organic carbon in sediments and in the lithosphere (Hayes *et al*., 1992; Logan *et al*., 1995).

Besides its most spectacular aspect, the burst in production of the mineralized skeletons during the Early

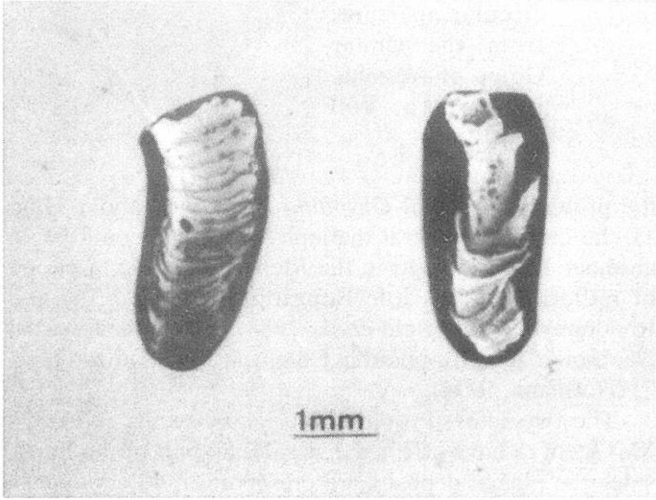

Figure 10. *Cloudina*, calcareous conical fossil from the latest Neoproterozoic of China. (Figure kindly provided by S. W. F. Grant.)

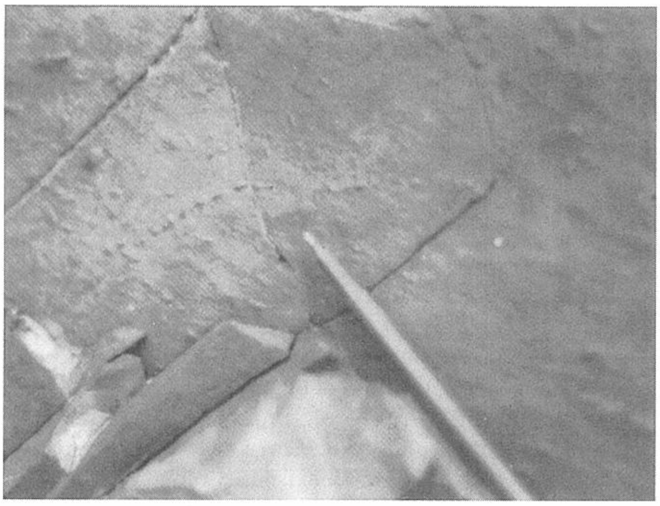

Figure 11. Simple trace fossils from the latest Neoproterozoic Cíjara Formation, Extremadura, western Spain. (Figure kindly provided by T. Palacios.)

Cambrian, the process of biomineralization was not a prerogative of the Cambrian Period: protists had already developed the unicellular biomineralization in the early Neoproterozoic, preceding the Varangerian glaciation (ca. 800 Ma; Vidal, 1994). Sedentary primitive metazoans as *Cloudina* did not only build slightly biomineralized shells (Grant, 1990), but they were also the first organisms capable of producing biostructures, as shown in their huge accumulations found in Namibia or in Spain.

In contrast to the most popular view, the biotic changes around the Neoproterozoic/Cambrian boundary are expressed not only by the appearance of consumer organisms, either detritus-feeders, filter-feeders or grazers (Butterfield, 1994) (Fig. 13), but rather by the appearance of completely new forms of primary producers. After the Precambrian/Cambrian boundary, the duration of such biotic assemblages of planktonic primary producers and consumers is quite ephemeral. The radiometric calibration of these assemblages is ongoing, based on the ratios of the uranium and lead isotopes in single zircons formed during volcanic events (Bowring *et al.*, 1993; Isachsen *et al.*, 1994), thus gauging the relative ages obtained from fossils (Vidal *et al.*, 1995). The base of the Cambrian System has been dated to ca. 543 Ma, and thus the Cambrian biotic explosion has been shorter in duration than previously inferred, not exceeding the time interval between 9 and 12 million years (Vidal, Palacios *et al.*, 1994).

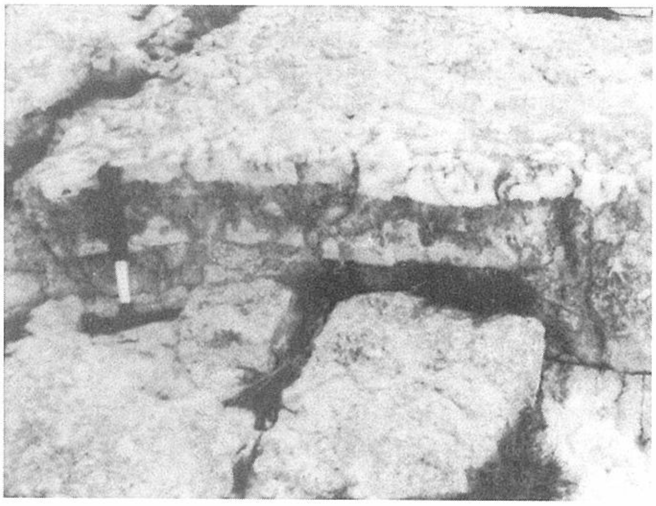

Figure 12. Heavily bioturbated strata from the Lower Cambrian Hardeberga Formation, Sweden.

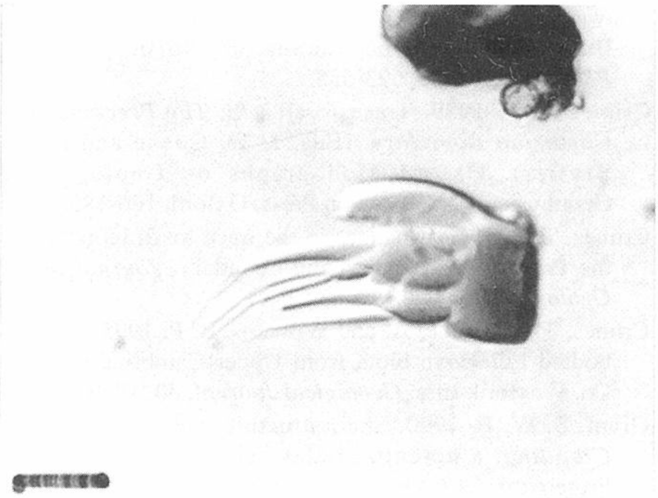

Figure 13. Probable branchiopod leg from the Lower Cambrian Lingulid Sandstone, Sweden.

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