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Evolution of Precambrian life in the Brazilian geological record

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Abstract: Precambrian rocks comprise nearly one-quarter of the surface of Brazil and range from Paleoarchean (ca. 3.6 Ga) to the latest Ediacaran (0.542 Ga) in age. Except for controversial phosphatized 'embryo-like' microfossils like those from the lower Ediacaran Doushantuo Formation, China and complex rangeomorphs, Brazilian research has revealed all major categories of Precambrian life forms described elsewhere – microbialites, biomarkers, silicified microfossils, palynomorphs, vase-shaped microfossils, macroalgae, metazoans, vendobionts and ichnofossils – but the paleobiological significance of this record has been little explored. At least four occurrences of these fossils offer promise for increased understanding of the following aspects of Precambrian biospheric evolution: (i) the relationship of microbialites in 2.1–2.4 Ga old carbonates of the Minas Supergroup in the Quadrilátero Ferrífero, Minas Gerais (the oldest Brazilian fossils) to the development of the early oxygenic atmosphere and penecontemporaneous global tectonic and climatic events; (ii) the evolutionary and biostratigraphic significance of Mesoproterozoic to Ediacaran organic-walled microfossils in central–western Brazil; (iii) diversity and paleoecological significance of vase-shaped heterotrophic protistan microfossils in the Urucum Formation (Jacadigo Group) and possibly the Bocaina Formation (Corumbá Group), of Mato Grosso do Sul; and (iv) insights into the record of skeletogenesis and paleoecology of latest Ediacaran metazoans as represented by the abundant organic carapaces of *Corumbella* and calcareous shells of the index fossil *Cloudina*, of the Corumbá Group, Mato Grosso do Sul. Analysis of the Brazilian Precambrian fossil record thus holds great potential for augmenting paleobiological knowledge of this crucial period on Earth and for developing more robust hypotheses regarding possible origins and evolutionary pathways of biospheres on other planets.

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Introduction

As postulated by many scientists (e.g. Schidlowski 2001; Javaux *et al.* 2003; Westall 2005), the search for life in the Cosmos depends on our understanding of modern and ancient life forms as well as past and present factors that affect the distribution of life and its interaction with the planet. Of necessity, therefore, the success of astrobiology will depend greatly upon the capacity of paleontology to identify connections among simple forms of past life on Earth as possible clues for recognizing life elsewhere. The Precambrian (4.56–0.542 Ga) paleobiology is especially important in this respect, because during this time life originated and evolved by way of a surprisingly small number of benchmark innovations that provided the basis for the present biosphere. Knoll & Bambach (2000) suggested that life has followed six mega-trajectories, each the result of a major biological breakthrough leading to a significant increase in the volume and complexity of ecospace over time. Of these steps, four occurred during the Precambrian: (i) the emergence of protolife certainly prior to 3.0–3.3 Ga (Brasier *et al.* 2006) or even 3.85 Ga (Allwood *et al.* 2006; Mojzsis *et al.* 1996, and also Nutman 2007), within the first billion years of Earth history; (ii) the evolution and success of the prokaryotic cell as the archetype of life on Earth, also prior to or around 3.5 Ga (Brasier *et al.* 2006; Schopf 2006; Wacey *et al.* 2011); (iii) the development of the eukaryotic cell by a complex series of endosymbiotic and other events, underway at least by 1.8 Ga (Porter 2004; Rasmussen *et al.* 2008); or possibly even by 2.6 Ga (Waldbauer *et al.* 2009); and (iv) the appearance of multicellular organisms in the seas, at least by 1.2 Ga (microscopic bangiomorph algae; Butterfield 2000) and possibly as early as 2 Ga (See Han & Runnegar 1992; Bengtson *et al.* 2007; Albani *et al.* 2010). Each of these major evolutionary innovations allowed life to diversify morphologically, metabolically and ecologically, limited only by a new set of constraints on size and complexity inherent to the innovation. In this way, each megatrajectory was added to previous ones, resulting in ever-increasing ecospace. Determining the chronology of these events from the record of Precambrian fossils not only elucidates the paths

Fig. 1. Map of Brazil showing the location of the Precambrian stratigraphic units mentioned in this paper. Conselheiro da Mata Group based on a bore hole. Based on *Mapa Geológico do Brasil, CPRM* (2003).

of terrestrial evolution but also furnishes potential temporal–ecological bases for searching for extraterrestrial life, both living and fossil.

Given that around two million square kilometres (25%) of Brazil is occupied by Precambrian rocks varying in age between 3.6 and 0.54 Ga (Schobbenhaus & Brito Neves 2003), data on fossils from these terrains (Figs 1 and 2) may provide valuable insights into biological and planetary evolution, applicable to the search for life in the Cosmos. Below, we review several key aspects of the Brazilian Precambrian fossil record that we judge of greatest potential interest to astrobiologists.

Nature of the Brazilian Precambrian fossil record

Although studies in Precambrian paleobiology in Brazil have essentially been descriptive, mostly dealing with new occurrences of fossils, morphological description and taxonomic identification, recent years have witnessed important initial advances in the application of these fossils to paleoenvironmental, biostratigraphical, paleoecological and evolutionary questions. In fact, with the exception of controversial phosphatized embryo-like microfossils, as in the Doushantuo Formation, China (Xiao *et al.* 2000; Chen *et al.* 2009; but see also Butterfield 2011; Huldtgren *et al.* 2011 for other interpretations) and rangeomorph fossils (Brasier & Antcliffe 2009), all categories of Precambrian fossils known elsewhere have also been recognized in the Brazilian fossil record, from the lower Paleoproterozoic (2.4 Ga) practically to the limit with the Phanerozoic at 0.54 Ga. These fossils include microbialites, silicified microfossils, palynomorphs (acritarchs), vase-shaped microfossils (VSMs), biomarkers, macroalgae, metazoans and ichnofossils (Fig. 2).

As elsewhere, the commonest and most widespread categories of Precambrian fossils in Brazil are microbialites, especially stromatolites, but also including oncolites and rare thrombolites. Although microbialites of Early Paleoproterozoic age comprise the oldest known fossils in Brazil, they are much commoner in late Mesoproterozoic and Neoproterozoic limestones, dolostones, phosphate and chert, in which they may represent the full range of settings within the photic zone, from relatively deep water (below storm wave base) to the supratidal. The Paleoproterozoic stratiform and columnar stromatolites, and possible oncolites of the Minas Supergroup, in Minas Gerais (Fig. 3), will be discussed below because of their great age (2.4 and 2.1 Ga) close to the advent of oxygenic atmosphere and the oldest widespread glacial events on Earth.

The second commonest category of Precambrian fossils in Brazil are microfossils (Fig. 4), presently known from 12 Mesoproterozoic to Neoproterozoic stratigraphic units in six tectonic domains. Most studies till now have dealt with silicified benthic, prokaryote-dominated, mat-forming microbiotas associated with stratiform, domical and columnar stromatolites. Fewer studies have focused on planktonic prokaryotes and eukaryotes (microalgae and acritarchs) in siliciclastic sequences, which have greater potential in paleoenvironmental and stratigraphic studies, including biostratigraphy. The importance of these microfossils and of vase-shaped microfossils is dealt with in greater detail below.

Perhaps the group of Brazilian Precambrian fossils of greatest paleobiological importance are the metazoan fossils *Corumbella* and *Cloudina* (Fig. 5(b)–(f)), which attest to the advent of skeletogenesis in latest Neoproterozoic metazoans. These fossils occur in the uppermost Ediacaran Tamengo Formation, Corumbá Group, Mato Grosso do Sul, and are associated with vendotaenids in both this formation and the overlying Guaicurus formation (Zaine 1991; Gaucher *et al.* 2003). The significance of the fossils of the Corumbá Group is discussed extensively further on.

Ichnofossils have been identified in siliciclastic units of the Ediacaran to Lower Cambrian Itajaí Basin, state of Santa Catarina, Camaquã and Santa Bárbara basins, in the state of Rio Grande do Sul, and Camarinha Formation, in the state of Paraná. In the Itajaí Basin, Netto & Zucatti da Rosa (1997) originally identified the ichnogenera *Bifungites*, *Gordia* and *Oldhamia* in a turbidite setting, and Zucatti da Rosa (2005) later added the ichnogenus *Helminthoidichnites.* The ichnofauna of the Camaquã and Santa Bárbara basins includes nine ichnogenera preserved in two different assemblages, the older in marine and deltaic sediments and the younger in deltaic to eolian lithologies (Netto *et al.* 1992). In the Camarinha formation, the ichnogenera, *Gordia*, *Planolites* and *Skolithos* have been reported from turbidites (Ciguel *et al.* 1992). The presence of these trace fossils suggests the interesting possibility that the Precambrian–Cambrian transition may be present in these successions (e.g. Brasier *et al.* 1994).

Biomarkers were identified in Brazilian Proterozoic rocks in the Vazante Group, Minas Gerais, by Olcott *et al.* (2005) and interpreted within the context of Snowball Earth

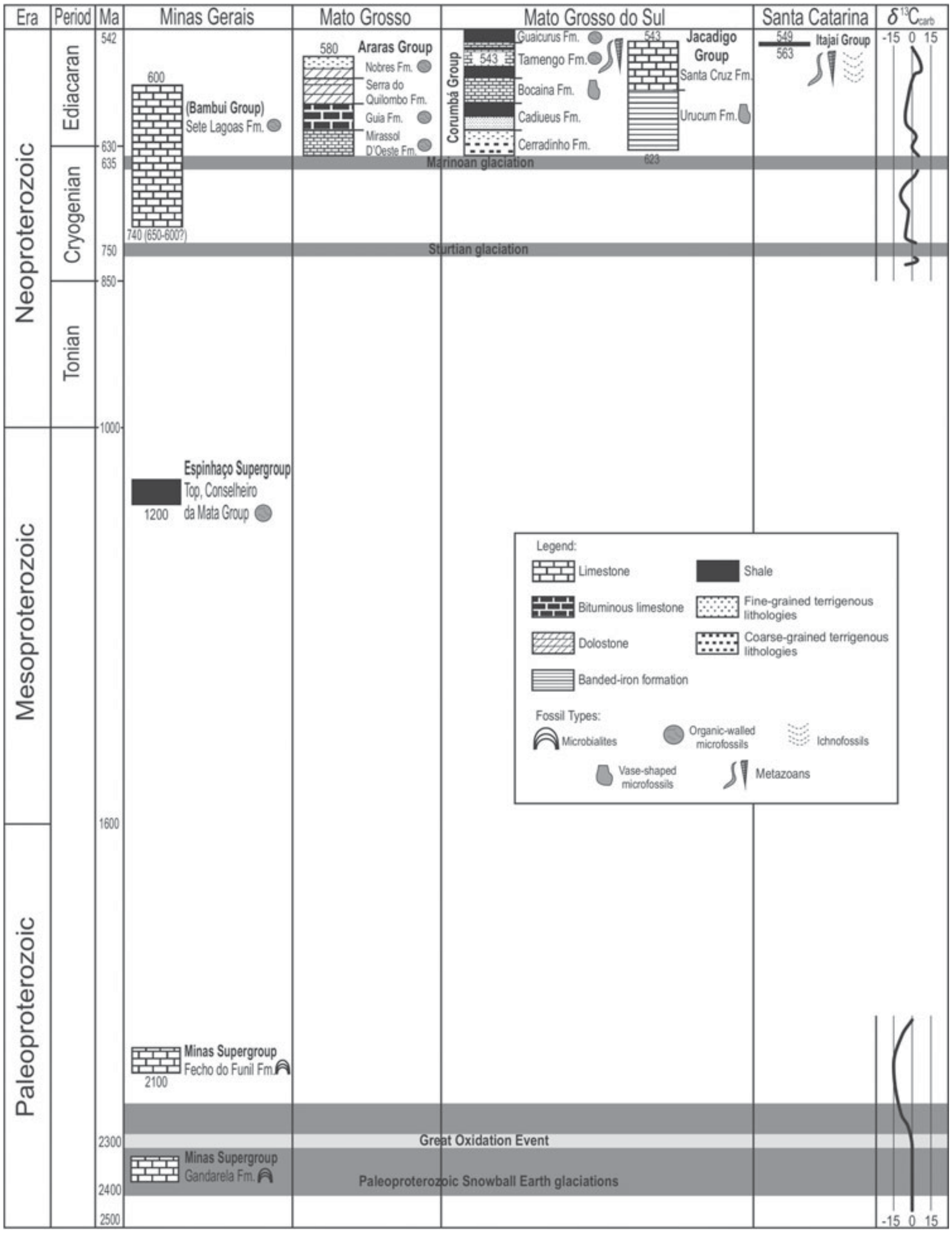

Fig. 2. Stratigraphic chart summarizing data on the fossiliferous stratigraphic units discussed in this paper. Age constraints indicated by numbers associated with schematic sections. The non-Snowball Gaskiers glaciation at 583 Ma is not indicated to avoid cluttering the image. Carbon isotope data based on Mills *et al.* (2011) for the Neoproterozoic and Bekker *et al.* (2001) for the Paleoproterozoic. Paleoproterozoic glaciations after Bekker *et al.* (2001). See text for details.

glaciation (Hoffman *et al.* 1998; Hoffman & Schrag 2002). Thinly laminated, organic-rich black shales overlying diamictite, rhythmic marls and carbonates in the Poço Verde Formation contain indigenous organic matter, which included 2-a-methylhopanes derived from cyanobacteria, alkylated 2,3,6-trimethylbenzenes derived from green sulfur bacteria, 3-b-methylhopanes derived from aerobic methanotrophs, gammacerane derived from protists, and steranes non-methylated at carbon 4 indicative of aerobic eukaryotes. If the Snowball Earth setting for this formation is correct, then these results would indicate that life was able to persist even under the harsh glacial conditions proposed in this hypothesis. Within the same snowball scenario, organic matter concentrated in bituminous limestone and shale overlying a Marinoan cap dolostone in the Araras Group in Mirassol d'Oeste, Mato Grosso, has yielded hydrocarbons that were deposited in a post-glacial, deep anoxic platform to slope setting (Nogueira *et al.* 2007). The nature and composition of these hydrocarbons, however, are still under investigation, and the results are anxiously awaited for comparison with the biogeochemical data of the apparently synglacial Poço Verde Formation.

For geological and paleobiological studies and of greatest relevance for astrobiology, the following four categories of

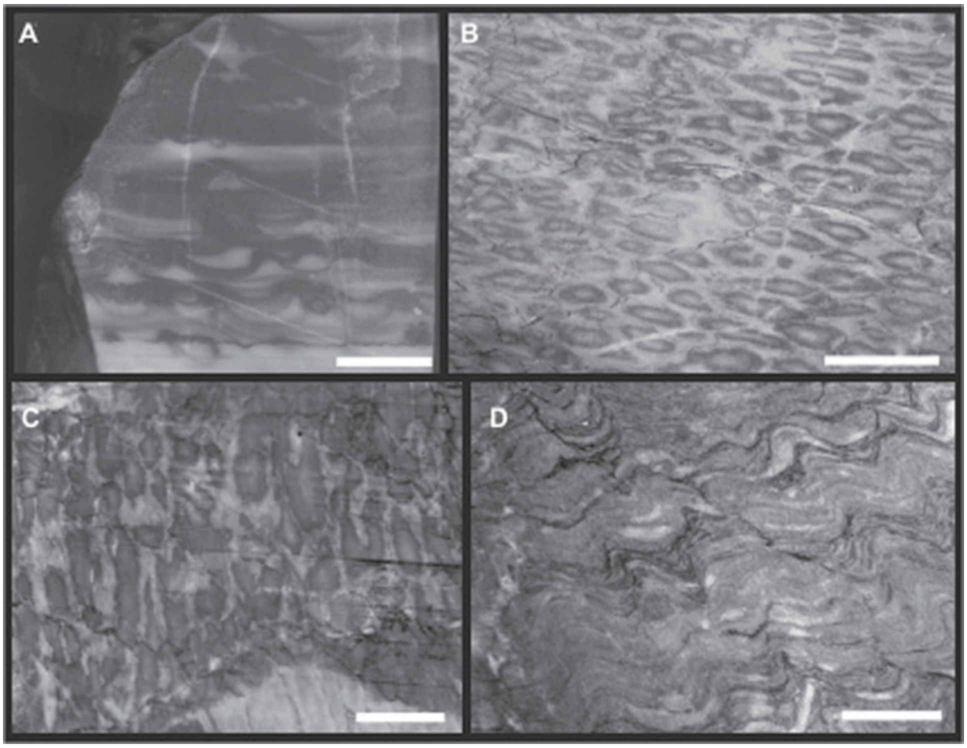

Fig. 3. Paleoproterozoic Brazilian microbialites from the Minas Supergroup, Quadrilátero Ferrífero, Minas Gerais. (A) Stratiform to domical stromatolites of the Gandarela Formation (2.4 Ga). Scale, 1 cm. (B–D) Stromatolites of the Fecho do Funil Formation (2.1 Ga), Cumbi quarry, near Ouro Preto, MG, Brazil. Images: E.A.M. Sanchez. (B) Transverse to slightly oblique sections of deformed columnar stromatolites. Low-grade metamorphism has destroyed most of the internal lamination. Scale, 5 cm. (C) Longitudinal sections of columnar stromatolites. Note parallel branching (centre–right). Scale, 5 cm. (D) Deformed, laterally continuous domical stromatolites. Scale, 5 cm.

Brazilian Precambrian fossils are of special interest: the ancient microbialites of the Minas Supergroup in Minas Gerais; vase-shaped protistan microfossils of the Jacadigo Group in Mato Grosso do Sul; the organic-walled microfossils of the Bambuí and Araras groups in Minas Gerais and Mato Grosso, respectively; and the early metazoans and associated fossils of the Corumbá Group in Mato Grosso do Sul (Figs 1 and 2).

Selected Brazilian Precambrian fossils of special interest

Paleoproterozoic microbialites of the Minas Supergroup

Although known especially for its huge deposits of banded iron formation (BIF), the Paleoproterozoic Minas Supergroup in the Quadrilátero Ferrífero of eastern Minas Gerais also includes microbialitic carbonates in the Gandarela and Fecho do Funil formations (Fig. 2), which comprise the oldest reliable record of Precambrian fossils in Brazil, dated at ca. 2.4 and ca. 2.1 Ga, respectively (Pb/Pb, Babinski *et al.* 1995). These fossils crop out in only four localities and have undergone low- to medium-grade metamorphism.

The older microbialites, in the Gandarela Formation, include laterally linked domical stromatolites with alternating dark and light grey laminae (Fig. 3(a)) and columnar stromatolites, in addition to stratiform mats and micritic oncoids (Souza & Müller 1984; Bertolino & Pires 1995). Bekker *et al.* (2003) interpreted them as having formed in high-energy intertidal to subtidal settings. However, only the stratiform mats have been adequately described and illustrated.

Although considerably deformed and recrystallized, the younger microbialites of the Fecho do Funil Formation, on the other hand, are much better known, because they were mined from a single quarry near Ouro Preto (Minas Gerais) that furnished flagstone for buildings throughout Brazil, including shopping malls (Sallun-Filho & Fairchild 2005), for more than 60 years. Within the now inactive quarry, large bioherms and biostromes of reddish to nearly white, densely packed branched columnar stromatolites (Fig. 3(b) and (c)) as well as subordinate laterally continuous domes (Fig. 3(d)) and oncolites are preserved in dolomitic lenses among highly folded phyllites (Dardenne & Campos Neto 1975). Lamination in these stromatolites has been nearly obliterated by metamorphism, but the tuberous to slender, parallel to divergently branching columnar form of these structures comprises convincing evidence that they are indeed stromatolites. The depositional setting of the Fecho do Funil Formation was interpreted as subtidal by Bekker *et al.* (2003).

In 2003, Bekker *et al.* studied the geochemistry and isotopic content of Minas Supergroup carbonates with the dual purpose of establishing their correlation with other units and establishing their significance with respect to key events, including glaciation, of the first-half of the Paleoproterozoic (Fig. 2). Values of $\delta^{13}C$ and $\delta^{18}O$ in the carbonates of the Gandarela Formation varied, in general, between -1.6 and

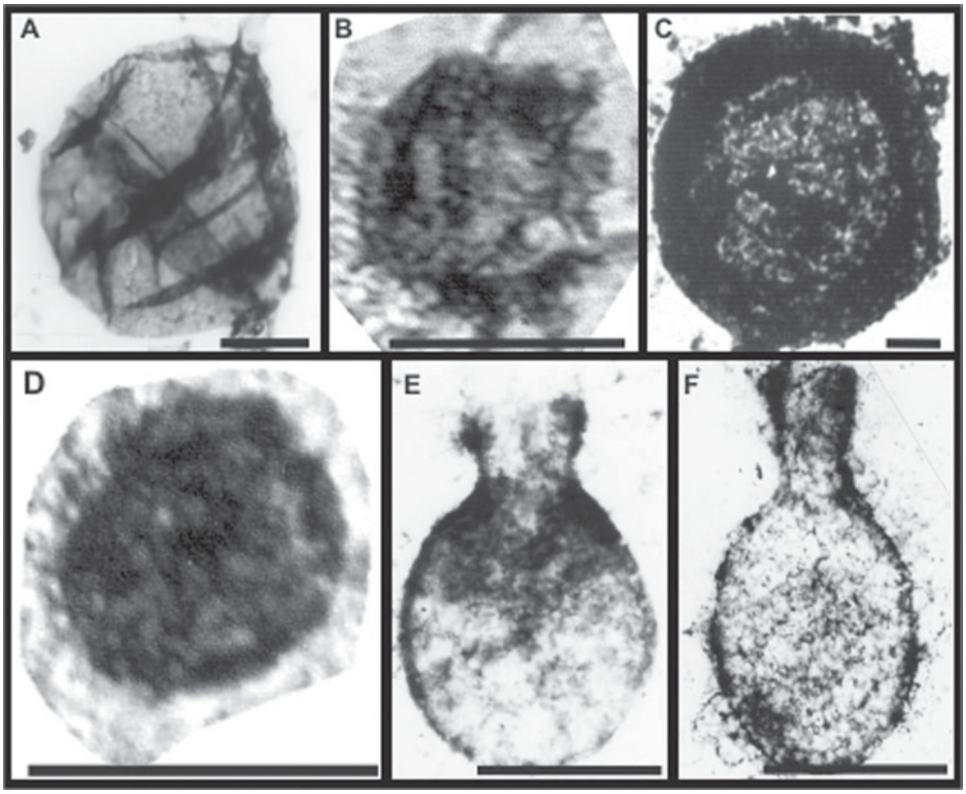

Fig. 4. Organic-walled microfossils. (A) *Leiosphaeridia* sp. from drill core sample, Conselheiro da Mata Group, Minas Gerais. Scale, 10 μm. Image from Simonetti, 1994. (B) *Trachyhystrichosphaera aimica*, Sete Lagoas Formation, Bambuí Group, Minas Gerais. Scale, 200 μm. (C) *Leiosphaeridia crassa*, Guia Formation, Araras Group, Mato Grosso. Scale, 25 μm. (D) Unidentified acritarch, Nobres Formation, Araras Group, Mato Grosso. Scale, 25 μm. (B–D) Images from Hidalgo (2007). (E–F) Vase-shaped microfossils, Urucum Formation, Jacadigo Group, Mato Grosso do Sul. Images from Zaine (1991). Scale, 50 μm in both figures.

+0.4‰ and −13.5 to −6‰, respectively, but between −1 and −1.3‰ for the $\delta^{13}C$ signal in carbonate levels with microbialites. Total organic carbon showed values between 0.03 and 0.16 mg C g^{-1} and an isotopic record of $\delta^{13}C$ between +18.6 and +23.8‰. By comparison with similar results from other Paleoproterozoic units older than 2.32 Ga. The data for the carbonates of the Gandarela Formation were considered representative of the composition of Paleoproterozoic seawater, slightly altered by diagenesis and metamorphism.

Geochemical analysis of the Fecho do Funil Formation revealed values of +5.6 to +7.4‰ for $\delta^{13}C$ and −12.3 to −9.1‰ for $\delta^{18}O$ in the carbonates. Total organic carbon varied from 0.04 to 0.18 mg C g^{-1} sample and $\delta^{13}C$ for organic matter ranged from −24.8 to −14.4‰. The carbon isotopic results presented higher values than expected for Paleoproterozoic units of similar age, but the authors concluded that the values were, in fact, representative of seawater at that time.

What is missing in the Brazilian record of this period is evidence of glacial evidence of a Paleoproterozoic Snowball Earth scenario (Kirschvink *et al.* 2000; Bekker *et al.* 2003) as well as any evidence in the Gandarela Formation microbialites, for the methane atmosphere prior to the first glacial event, as proposed by Pavlov *et al.* (2000) and Kasting *et al.* (2001). However, the importance of the carbonates of the Gandarela and Fecho do Funil formations is that they register seawater conditions at two different moments of the Paleoproterozoic, first, when the putative supercontinent of that time was undergoing fragmentation which provoked changes in the dynamics of weathering, carbonate sedimentation and geochemical recycling of carbon, and second, when all these events, coupled with the rise of aerobic photosynthesis, resulted in an oxygenated atmosphere and a new biosphere (Kirschvink *et al.* 2000; Bekker *et al.* 2001, 2003; Bekker & Eriksson 2003; Knoll 2003).

Organic-walled microfossils

Organic-walled microfossils are the most abundant direct evidence of life in the Precambrian. Differences in their size, ornamentation and complexity have been employed in attempts to distinguish eukaryotic from prokaryotic microfossils and thereby identify the most ancient forms in the Precambrian record of microfossils. However, at the present time, steranes in rocks 2.4–2.6 Ga old of the Transvaal Supergroup (South Africa) are the oldest candidates for the earliest eukaryotic biomarkers in the geological record (Waldbauer *et al.* 2009), but it is wise to remember that similar, equally old biomarkers from the Pilbara Craton of Australia (Brocks *et al.* 1999) were later shown to be younger contaminants (Rasmussen *et al.* 2008). At present, then, the oldest reliable direct evidence of eukaryotes are compressed,

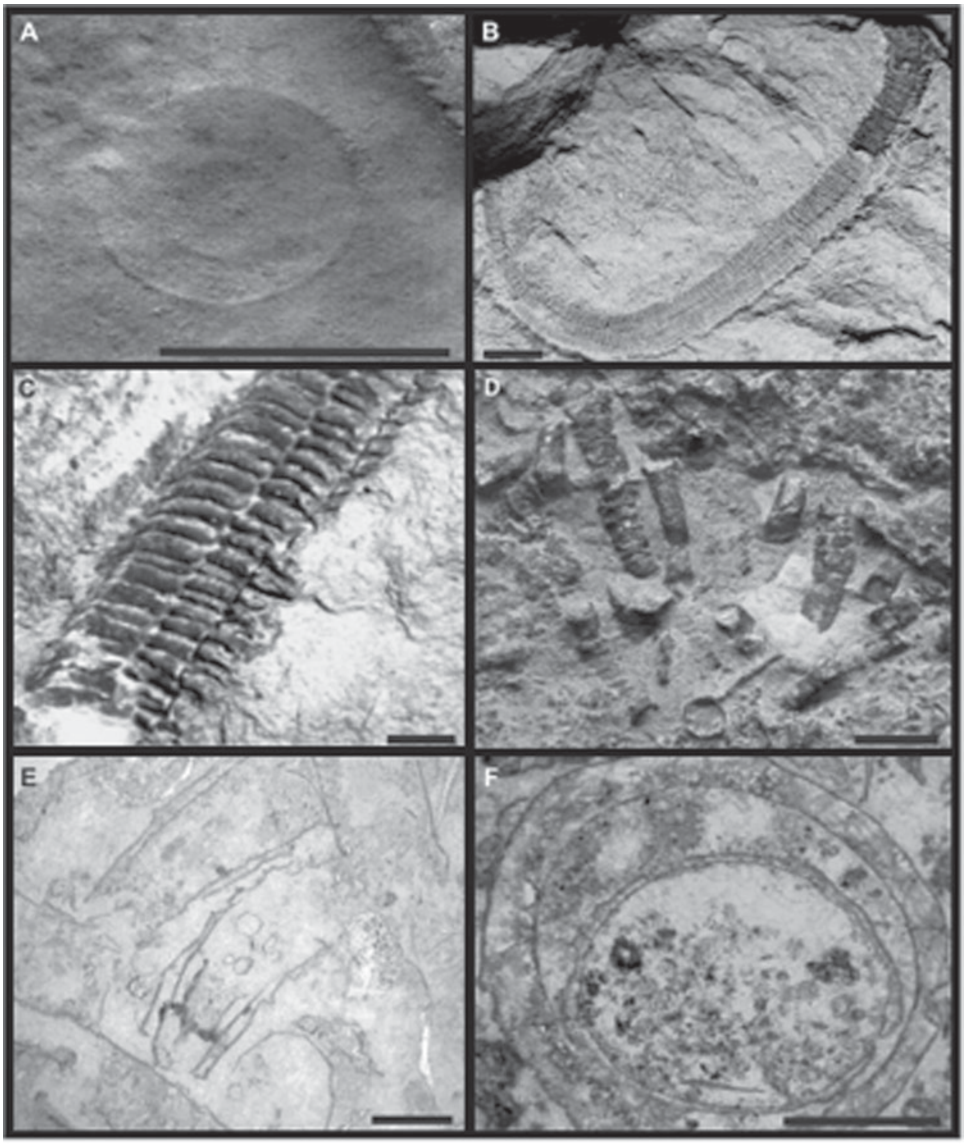

Fig. 5. Ediacaran macrofossils. (A) Discoidal impression (Itajaí Group, Santa Catarina) described as *Cyclomedusa* by Zucatti da Rosa (2005). Scale, 15 mm. Image from Zucatti da Rosa (2005). (B–F) Metazoan fossils, Tamengo Formation, Corumbá Group, Corumbá, Mato Grosso do Sul. (B–C) *Corumbella werneri*. (B) Internal cast, holotype (DGM-5601-I). Scale, 5 mm. (C) *Corumbella werneri*. Internal cast. Scale, 1 mm. (B–C) M.L.A.F. Pacheco. (D–F) *Cloudina lucianoi*. (D) Surface view of specimens, showing typical aspect of the wall. Scale 2.5 cm. (E) Longitudinal sections of *C. lucianoi* shells in petrographic thin section. Note nested truncated conical structures in central specimen. Scale, 1 cm. (F) Transverse section of *C. lucianoi* shells in petrographic thin section. Scale, 1cm. Images (D–F) from Meira (2011).

circular, elliptical and lanceolate organic-walled microfossils (acritarchs), from Paleoproterozoic rocks about 1.8 Ga old in the Changcheng Group, China, whose relatively large size and complexity exclude prokaryotic affinities (Hofmann & Chen 1981; Zhang 1986; Yan 1991; Huntley *et al*. 2006; Lamb *et al*. 2009; Peng *et al*. 2009).

Over the time span of the Proterozoic, and especially in the Neoproterozoic, diversification and extinction among the eukaryotes (see Javaux *et al*. 2003; Huntley *et al.* 2006; Knoll *et al.* 2006) introduced sufficient diversity among unicellular micro-organisms as to permit the use of fossil microalgae and acritarchs in biostratigraphic correlation schemes in Australia (Zang 1995; Grey 2005; Willman & Moczydlowska 2008), Africa (Gaucher & Germs 2006; Couëffé & Vecoli 2011), Europe (Moczydlowska 2008a), China (Zhou *et al.* 2007; McFadden *et al.* 2009) and South America (Gaucher *et al.* 2003).

In Brazil, however, only Simonetti & Fairchild (2000), Gaucher *et al.* (2003) and Hidalgo (2007) have attempted to use Brazilian Precambrian microfossils for biostratigraphy. In the first case, Simonetti & Fairchild (2000) interpreted the low morphological diversity and small size (<200 μm) of the assemblage of organic-walled microfossils, dominated by *Leiosphaeridia* spp. (Fig. 3(a)) recovered from drill cores of siliciclastic rocks from the upper Conselheiro da Mata Group, Espinhaço Supergroup, Minas Gerais (Fig. 4(a)), as being typical of late Mesoproterozoic assemblages, a finding consistent with the ca. 1.2 Ga radiometric age for the group. These microfossils are still the oldest reported from Brazil.

Hidalgo (2007) analysed microfossils from the much younger Araras (< 635 Ma) and Bambuí (< 740 Ma) groups, in Mato Grosso and Minas Gerais, respectively, in an attempt to establish a biostratigraphic framework for the Neoproterozoic of Brazil and to identify possible effects of Snowball Earth glaciations upon the Brazilian fossil record. Despite the generally poor preservation of the microfossils, she identified nearly 20 taxa of Neoproterozoic acritarchs (Fig. 4(b)–(d)), including such biostratigraphically important forms as *Cymatiosphaeroides*, *Trachyhystrichosphaera* (Fig. 4(b)), *Leiosphaeridia minutissima*, *Leiosphaeridia crassa* (Fig. 4(c)) and *Tanarium*. Furthermore, she distinguished three different associations of acritarchs similar to those in biostratigraphic biozones proposed for the Neoproterozoic by Grey (2005) and Sergeev (2006), specifically, an older association in the Sete Lagoas Formation of the Bambuí Group and two younger ones in the Mirassol D́Oeste and Guia formations, and the overlying Nobres Formation (Fig. 4(d)), respectively, of the Araras Group. The results are consistent with the biostratigraphic proposal of Grey (2005) for the Neoproterozoic, based on morphological changes representative of evolutionary innovations.

The most ambitious correlation proposal for the Brazilian Neoproterozoic was made by Gaucher *et al*. (2003), who correlated the post-Marinoan Corumbá Group of Brazil with the Arroyo del Soldado Group of Uruguay on the combined basis of organic-walled microfossils, metazoans, stable isotopes and lithology. Three species of organic-walled microfossils, including cyanobacteria and acritarchs, occur in common in both units, but only two were considered biostratigraphically significant: *Leiosphaeridia tenuissima* and *Soldadophycus bossii*.

The studies by Gaucher *et al.* (2003) and Hidalgo (2007) have thus revealed the potential value of Brazilian Neoproterozoic microfossils for biostratigraphic correlation, both regionally and globally. With respect to important evolutionary issues, acritarchs from the Araras Group have provided tentatively significant data. Hidalgo (2007) found unornamented acritarchs at the bottom of the succession and, near the top, spiny forms, suggestive of a rapid change in composition (taxonomic replacement) after the Marinoan glaciation, possibly related to the appearance of metazoans (Peterson & Butterfield 2005; Willman & Moczydlowska 2008; Cohen *et al.* 2009).

Vase-shaped microfossils

The Jacadigo Group near Corumbá (MS) is well known for its commercially exploitable, Neoproterozoic Rapitan-like iron (and manganese) formation, which is much younger (< 623 Ma) than the Archean to Paleoproterozoic-banded iron formations that make up the world's major iron ores. However, near the base of this group, in the Urucum Formation, carbonate clasts within a massive diamictite deposited in a continental setting (Freitas *et al.* 2011) contain abundant vase-shaped microfossils, first identified by Fairchild *et al.* (1978) and later likened to *Melanocyrillium* sp. (Zaine 1991; Zaine *et al.* 1989) (Fig. 4(e) and (f)). These fossils consist of thin-walled, subspherical to ellipsoidal bodies, up to 108 μm in width and up to 143 μm in length, with a single, simple opening at one pole or at the end of a short to long neck-like extension, giving them their vase-shaped form. Walls are black, unornamented and carbonaceous. The thin wall, long neck and absence of a pylome differentiate these microfossils from the melanocyrillids of the Chuar Group (USA), with which they were compared by Zaine (1991).

Porter & Knoll (2000) and Porter *et al.* (2003) have demonstrated that Neoproterozoic VSMs are the oldest direct fossil evidence for heterotrophic protists. Since the original description in the Chuar Group (Bloeser *et al.* 1977), a variety of VSMs have been described, including agglutinated forms (Bosak *et al.* 2011) from Namibia and Mongolia that are similar in size but morphologically distinct from, and somewhat older than, the organic-walled Brazilian VSMs. In fact, the Urucum VSMs are seemingly different from practically all other described Proterozoic VSMs. Possible VSMs similar to thecamoebans present in phosphorites at the top of the stratigraphically younger Bocaina Formation of the Corumbá Group (Fontaneta 2012) considerably broaden the paleontological perspectives for this region and research on early protistan heterotrophs. All of these fossils are distinctly different from the supposedly agglutinated fossil foraminiferan test *Titanotheca coimbrae*, made up exclusively of rutile crystals, registered in these same phosphorites by Gaucher *et al.* (2003).

Metazoans

Two regions stand out in Brazil for their fossil evidence of complex megascopic organisms of Ediacaran age: the Itajaí Group in Santa Catarina and the Corumbá Group in Mato Grosso do Sul.

Zircon crystals from volcanic tuffs have provided U/Pb (SHRIMP) ages of ca. 559–584 Ma for the Itajaí Group (Drukas & Basei 2009), and Guadagnin *et al*. (2010) reported U/Pb (LA-MC-ICP-MS) ages of 549 ± 4 Ma to 563 ± 3 Ma as the limits for the Itajaí Basin. The upper portion of the Itajaí Group, deposited in relatively calm waters below storm wave base in a prodeltaic marine setting has yielded enigmatic fossils interpreted as part of the benthic epifauna. These fossils were attributed to the sponge-like genus *Choia* and to possible Chancelloriida (Silva & Dias 1981; Da Rosa *et al.* 1997; Leipnitz *et al.* 1997; Paim *et al.* 1997), taxa previously considered to be exclusively Cambrian in age (Conway Morris 1992). Suspect medusoids, possibly *Cyclomedusa* (Fig. 5(a)) and *Charniodiscus* and rounded impressions or moulds of *Aspidella*, as well as faint, horseshoe-shaped impressions attributed to *Parvancorina* sp. (arguably related to the arthropods) have also been described (Zucatti da Rosa 2005), along with the ichnofossils *Bifungites*, *Gordia*, *Oldhamia* and *Helminthoidichnites* (Netto & Zucatti da Rosa 1997; Zucatti da Rosa 2005).

The Corumbá Basin in the southern part of the Paraguay Belt is made up of the Cadiueus and Cerradinho formations, at its base, reflecting deposition in an initial continental rift basin, and the Bocaina, Tamengo and Guaicurus formations, deposited in a stable marginal basin (Almeida 1984; Boggiani 1998; Alvarenga *et al.* 2000). Of these, the Tamengo Formation (543 ± 3 Ma U-Pb^{-1}; Babinski *et al.* 2006, 2008) is the most noteworthy in terms of its fossil content. Until recently, it was the only formation in the world containing abundant fossils of the early skeletal metazoans *Corumbella werneri* and *Cloudina lucianoi* (Zaine & Fairchild, 1987; Zaine 1991; Boggiani 1998; Nogueira *et al.* 1998; Babcock *et al.* 2005) (Fig. 5(b)–(f)), which are coeval with late members of the well-known Ediacaran soft-bodied biota (Hahn *et al.* 1982; Walde *et al.* 1982; Hahn & Pflug 1985; Zaine 1991; Babcock *et al.* 2005; Simon 2007; Pacheco *et al.* 2010a, b).

Corumbella werneri (Fig. 5(b) and (c)) was discovered in marls and shales of the Tamengo Formation in Ladário, just outside Corumbá, (Hahn *et al.* 1982). Later, two specimens of *Corumbella* sp. were described in sandstone from the similarly aged lower Wood Canyon Formation, in the Great Basin, USA (Hagadorn & Waggoner 2000), and very recently, parautochthonous fragments of *Corumbella* were found together with *in situ* specimens of *Cloudina* in calcareous grainstones and mudstones of the Itapucumi Group, in Paraguay, 360 km south of Corumbá (Warren *et al.* 2011).

C. werneri was originally reconstructed as a bipartite scyphozoan made up of a uniseriate primary polyp and a biseriate polypar, and placed within its own new subclass (Corumbellata) by Hahn *et al.* (1982). Zaine (1991) suggested rather that it may have been a vendobiont, an extinct group of megascopic organisms of uncertain biological affinity (Seilacher 1989; Buss & Seilacher 1994), possibly more closely related to the Protista than to the Metazoa (Seilacher *et al.* 2003; Seilacher 2007). Recent investigations, however, have revealed polarization and symmetry in *C. werneri* that permit its reconstruction as a quadrate tube made up of ring-like segments, similar to some modern coronate scyphozoans and possibly to the extinct conulariids as well, thereby assuring its place within the kingdom Metazoa (Babcock *et al.* 2005; Pacheco *et al.* 2010a, b, 2011a, b, Pacheco 2011).

The genus *Cloudina* was created by Germs (1972) for small, straight to sinuous, tubular calcareous shelly fossils (up to 6.5 mm in diameter and 35 mm long), open at the apex and closed at the base, found in limestones of the late Neoproterozoic Nama Group, Namibia (Germs 1972; Grant 1990). Characteristic of *Cloudina* are its short, partly overlapping segments having the shape of open truncated cones (Germs 1972; Zaine & Fairchild 1987; Grant 1990; Chen *et al.* 2008; Meira 2011) (Fig. 5(d) and (e)). Its walls are uniformly thick yet extremely thin (3–50 μm) (Fig. 5(f)), but early cementation between walls of successive segments appears to have strengthened the original shell (Grant 1990; Hua *et al.* 2003, 2005). *Cloudina* was immediately recognized as latest Neoproterozoic in age, thereby giving it the status of oldest known shelly metazoan fossil. Grant (1990) demonstrated that because of its widespread occurrence in rocks of identical age, it deserved to be considered an index fossil for the uppermost Ediacaran.

Cloudina is known from practically all the quarries and major outcrops of the Tamengo Formation in the Corumbá área (Zaine & Fairchild 1987; Meira 2011) and has been reported from Uruguay and Argentina (Gaucher *et al.* 2003, 2005) and, most recently, from Paraguay (Boggiani & Gaucher 2004; Warren *et al.* 2011). Outside South America, it occurs in Namibia (Germs 1972), Oman (Conway Morris *et al.* 1990), China (Conway Morris *et al.* 1990; Bengtson & Zhao 1992), Canada (Hofmann & Mountjoy 2001), Nevada (Hagadorn & Waggoner 2000), Spain (Palacios 1989) and Russia (Kontorovich *et al.* 2008).

Perspectives

The importance of the Brazilian fossils discussed above resides in their association with paradigmatic transitions and benchmark innovations in the evolution of the Proterozoic environment and biosphere.

For instance, the microbialites in the Paleoproterozoic Gandarela and Fecho do Funil formations of the Minas Supergroup are not just the oldest Precambrian fossils in Brazil: they were deposited, respectively, at about the same time as and not long after the 'Great Oxygenation Event' (GOE) (Holland 2002; Ohmoto 2003) around 2.3 Ga (Fig. 2), when free oxygen produced by aerobic photosynthesis finally began to accumulate in the atmosphere (Kirschvink *et al.* 2000; Bekker *et al.* 2001, 2003; Knoll 2003; Catling & Claire 2005). This event, coupled with continental breakup of the supercontinent Kernorland (Heaman 1997; Bekker & Eriksson 2003), led to profound changes in weathering, burial of organic carbon and geochemical cycling in general, resulting in major changes in climate (Paleoproterozoic Snowball Earth) and dominant metabolism in the biosphere (Kirschvink *et al.* 2000; Bekker *et al.* 2001, 2003; Anbar & Knoll 2002; Knoll 2003; Barley *et al.* 2005; Catling & Claire 2005; Kopp *et al.* 2005). Within this context, the microbialites of the older Gandarela Formation and the younger Fecho do Funil Formation bracket this period (Fig. 2), thereby providing an opportunity to explore possible changes in the relationships among paleoenvironmental and paleobiological factors within the atmosphere, hydrosphere and biosphere in response to the oxidation of atmosphere at this crucial time. The paper by Bekker *et al.* (2003) exploits this question, but hardly exhausts the subject.

A second field in which Brazilian fossils will certainly be useful is Neoproterozoic biostratigraphy. In the absence of megascopic index-fossils (animals, vendobionts and macroalgae) prior to about 580 Ma (Narbonne 2005; Yuan *et al.* 2011), recent Neoproterozoic biostratigraphic proposals have been based primarily on microfossils – acritarchs, microalgae and occasional other microfossils (such as VSMs, for example), whose abundance, complexity and diversity evolved in response to biological and environmental factors, once again related to continental breakup (Rodinia) and Snowball Earth scenarios and their consequences (Hoffman *et al.* 1998;

Hoffman & Schrag 2002; Knoll 2003). Several authors (Moczydlowska 2005, 2008a, b; Huntley *et al.* 2006) allege that changes, especially in paleoclimate, were responsible for both an increase in diversity and extinction among eukaryotes. The palynological study by Hidalgo (2007) in post-glacial Neoproterozoic successions in Brazil is consistent with this interpretation.

Recent geochronological and sedimentological analyses, however, suggest alternative interpretations for the age of a supposed cap carbonate at the base of the Bambuí Group (Sete Lagoas Formation), which Hidalgo studied, and for the glacial origin of diamictites in the Corumbá region. In the former case, Pimentel *et al.* (2009) suggested a maximum age for deposition between 650 and 600 Ma based on U/Pb (SHRIMP) ages obtained for detrital grains of zircon at the top the Sete Lagoas Formation. This significantly challenges the long-standing idea that deposition of the Bambuí Group began after 740 Ma, following the older (Sturtian) of the Neoproterozoic snowball glaciations (Vieira *et al.* 2007), rather than the younger Neoproterozoic (Marinoan) glacial event at ca. 635 (Fig. 2). Nevertheless, based on the biostratigraphic considerations of Sergeev (2006), the acritarch assemblage identified from this formation by Hidalgo (2007) favours the older, traditional view.

The vase-shaped microfossils in the Jacadigo Group comprise a third group of Precambrian fossils from Brazil that merit special attention, in this case because of their potential paleoecological/paleoenvironmental importance. This is because they occur in limestone clasts of apparently non-marine origin within a diamictite deposited prior to the Rapitan-like iron formation of the same group that has been associated with Neoproterozoic glacial conditions (see Gaucher *et al.* 2003) (Fig. 2). In their recent detailed sedimentological study of the Jacadigo Group, however, Freitas *et al.* (2011) found no convincing evidence of glacial conditions during any phase of deposition this group. Hence, these VSMs may offer a rare view of non-marine Ediacaran life outside the context of Snowball Earth. They are also important because they differ from other VSMs, as summarized by Porter (2011), and thus add to a growing body of evidence for considerable morphological variety among Neoproterozoic heterotrophic protists (Porter *et al.* 2003; Porter 2004; Bosak *et al.* 2011) related to changes in trophic complexity (Karlstrom *et al.* 2000).

The fourth important group of Precambrian fossils are the late Ediacaran Brazilian metazoans (and associated fossils), which represent a critical phase of one of the most profound events in the evolution of the biosphere – the emergence of animal life. Metazoans arose much earlier than the Early Cambrian explosion of life (Fedonkin 2003), probably before the first records of the soft-bodied Ediacara biota (Shen *et al.* 2008; Yuan *et al.* 2011), and even earlier than the extreme climatic changes and increase in oxygen levels of the latter half of the Neoproterozoic (Brain *et al.* 2012). Molecular clock evidence points to an origin for crown group demosponges and cnidarians at about 700 Ma (Conway Morris 2000; Erwin *et al.* 2011). In face of the sparse, problematical record of early metazoan fossils worldwide, e.g., controversial 600 Ma-old phosphatized 'metazoan embryos' from the Doushantuo Formation, China (Xiao & Knoll 2000; Chen *et al.* 2004; Huldtgren *et al.* 2011), 635 Ma-old sponge biomarkers in the Huqf Supergroup in Oman (Love *et al.* 2009), and 760–550 Ma-old Ma sponge-like fossils from the Otavi and Nama Groups in Namibia (Brain *et al.* 2012), the Brazilian (and South American) Precambrian fossil record represents a largely untapped, potentially major source of significant new finds regarding early metazoan evolution.

Carbon and sulfur isotopic data suggest that Neoproterozoic oceans prior to a major oxygenation event near the end of the Ediacaran period (Canfield 1998; Holland 2009; Shields-Zhou & Och 2011), like those before the 'Great Oxygenation Event' at 2.32 Ga (Holland 2002; Ohmoto 2003) (Fig. 2), may have been anoxic and probably iron- and sulfur-rich (Halverson *et al.* 2009), hardly suitable for the diversification of macroscopic metazoans (Catling *et al.* 2005). Both of these global oxygenation events were accompanied by widespread deposition of banded iron formations, when anoxic deep waters with large amounts of ferrous iron in solution came into contact with oxygenated surface waters (Pierrehumbert *et al.* 2011). The disappearance of these unusual deposits from the rock record, if not due to oxygenation of the oceans, may have occurred when the deep oceans became sulfidic, rather than oxic (Canfield 1998), producing deep seawater that may have become more reducing rather than more oxidizing, despite the rise in atmospheric oxygen. Yet it is possible, however, that even in the context of widespread Neoproterozoic oceanic anoxia, metabolic versatility in early stages of animal evolution may have been a key factor in the emergence and establishment of the group (Budd 2008; Shields-Zhou & Och 2011), while later oxygenation allowed significant increase in the size, complexity and mobility among the Metazoa (Catling *et al.* 2005).

Diversity of eukaryotic plankton crashed during the break-up of Rodinia in the mid-Neoproterozoic (Nagy *et al.* 2009). It is likely that in the Cryogenian glacial interval between ca. 720 and 635 Ma, the first animal lineages diverged from ancestral eukaryotic unicellular populations and/or communities (Peterson *et al.* 2008), probably in close proximity with the anoxic, ferruginous, icy environments of the ocean (Canfield *et al.* 2008). The oldest concrete evidence of the dawn of animal life is younger than this, represented in the fossil record by complex macroscopic multicellular organisms of the Mistaken Point ($\leqslant 575$ Ma, Canada) and Lantian (> 579 Ma, China) assemblages of the Ediacaran biota (Narbonne 2005; Shen *et al.* 2008; Yuan *et al.* 2011). Thus, the macroscopic biosphere that continues to this day had its origin soon after the Marinoan glaciation (Xiao & Laflamme 2009; Yuan *et al.* 2011), and quite probably under anoxic conditions (Narbonne 2011).

Within this new, macroscopic biosphere, a significant number of the classical 'soft-bodied' Ediacaran organisms may not have been metazoans at all, but rather members of the extinct Vendobionta (Seilacher 1989; Buss & Seilacher 1994), an extinct major group of organisms characterized by flexible bodies built up of hollow, tubular subunits in serial or fractal arrangements and having an organic cuticle (Buss & Seilacher 1994; Seilacher 2007). The varied frond-like and quilted benthic forms, typical of vendobionts, show no evidence of a mouth or gut (Fedonkin *et al.* 2007) and were incapable of moving about. Some of them may have been osmotrophic, feeding off dissolved organic carbon in seawater (Laflamme *et al.* 2009), while others may have digested the abundant microbial mats typical of the shallow sea bottom before the evolution of grazing and burrowing animals (Erwin & Tweedt 2011).

While the taxonomic status of the Vendobionta remains phylogenetically unresolved, even at the level of kingdom (Seilacher *et al.* 2003), the most recent and parsimonious explanation for the taxonomic composition of the other elements of the Ediacaran biota is that some of the fossils represent real metazoans – especially those with bilateral symmetry, such as *Kimberella* (Fedonkin & Waggoner 1997; Dzik 2003; Fedonkin *et al.* 2007) and early skeletal taxa like *Cloudina* and *Namacalathus* (Grotzinger *et al.* 2000). These early metazoan fossils are found together with soft-bodied Ediacaran fossils throughout the world but always in different, but often coeval facies (in carbonates and siliciclastic rocks, respectively) and never on the same bedding plane (Germs 1972, 1983; but see Warren *et al.* 2011), clear evidence of a robust and varied late Ediacaran ecosystem.

At the same time that the vendobionts became extinct (Seilacher 2007), metazoans diversified and began to dominate ecosystems near the Ediacaran–Cambrian boundary (Erwin & Tweedt 2011). This signal event may have been caused by great changes in environmental conditions related to supercontinent breakup (McKerrow *et al.* 1992), variations in sea level (Hallam 1984), nutrient crises, fluctuations in atmospheric oxygen (Shields-Zhou & Och 2011) and/or carbon dioxide levels (Brasier 1992), changes in ocean chemistry (Lowenstein *et al.* 2001), re-engineering of ecosystems, or, most likely, by a combination of these factors.

Within this context, the varied fossils in the Jacadigo and Corumbá groups comprise a practically unique assemblage within the Ediacaran period. Recent research (Meira 2011; Pacheco 2011; Pacheco *et al.* 2011a; Warren *et al.* in press) and new studies will certainly broaden knowledge of the latter phases of eukaryotic evolution in the Ediacaran. The ichnofossils from the Itajai Basin (Zucatti da Rosa 2005; Drukas & Basei 2009) will provide a further complementary view of this record. These studies, particularly those of the Jacadigo and Corumbá groups, will have global implications (Boggiani 1998; Gaucher *et al.* 2003), given the important occurrences of VSMs in the former group and, in the latter group, stromatolites, possible VSMs and phosphorite in the Bocaina Formation, and shelly fossils of *Cloudina* and organic carapaces of *Corumbella* in the Tamengo Formation (Fig. 2). The recent questioning (Freitas *et al.* 2011) of the glacial origin of the Rapitan-type iron formation in the Jacadigo Group and the diamictites of the Puga Formation, beneath the Corumbá Group near Corumbá (Urban *et al.* 1992; Alvarenga *et al.* 2009; Boggiani *et al.* 2010) will certainly force re-examination of basic aspects of the sedimentary dynamics and evolutionary implications of the Snowball Earth hypothesis.

Temporal synchroneity of these units with other successions worldwide, which also present similar fossils and unusual lithologies may be established via chemostratigraphical correlation using C and Sr isotopes. For example, as observed in other carbonates in the latter part of the Ediacaran (after the Gaskiers glaciation at 583 Ma), two negative $\delta^{13}C$ excursions associated with the Shuram–Wonoka anomaly of Oman and Australia at ca. 551 (Burns & Matter 1993; Pell *et al.* 1993), just below the disappearance of typical early Ediacaran large spiny acritarchs on a global scale and the first occurrence of *Cloudina* shells and the disappearance of typical early Ediacaran large spiny acritarchs on a global scale, also appear to be recorded in the Tamengo Formation (Fig. 2). This global $\delta^{13}C$ variation has been attributed to the oxidation of vast amounts of dissolved organic carbon with extremely negative values in deep oceanic waters (Rothman *et al.* 2003; Shields-Zhou & Och 2011). A ubiquitous feature of the upper Tamengo Formation, on the other hand, is a positive $\delta^{13}C_{carb}$ plateau around +3 to +5‰, associated with the occurrence of *Cloudina* and *Corumbella* (Boggiani *et al.* 2010). These values have been interpreted as indicating high rates of production and burial of organic carbon (with low $\delta^{13}C_{org}$) and subsequent deposition of carbonate with high $\delta^{13}C$ values, coupled with increased release of oxygen to the atmosphere (Shields-Zhou & Och 2011).

The positive $\delta^{13}C$ plateau is thus consistent with the idea that favourable conditions for the origin or expansion of macroscopic metazoans existed around the time of deposition of the carbonates of the upper Tamengo Formation. Hence, it may not be merely coincidental, in this respect, that a firm organic or weakly mineralized skeleton in *Corumbella* (Pacheco 2011; Pacheco *et al.* 2011a; Warren *et al.* 2012), and that the earliest evidence of possibly predatory borings in thin-walled, biomineralized shells of *Cloudina* (in China) (Bengtson & Zhao 1992; Bengtson 1994; Hua *et al.* 2003, 2005) first appear at this time, although other causes (protistans, worms and mineral grains) have been suggested (Bengtson & Zhao 1992). Therefore, of the four groups of Brazilian Precambrian fossils highlighted in this paper, it is the Corumbá Group that perhaps offers the best (and possibly a unique) opportunity to investigate a major issue in biospheric evolution, i.e., initial ecological relationships among early skeletal metazoans and the possible consequences of the introduction of competition and predation among macroscopic organisms upon trophic net complexity (Clapham & Narbonne 2002; Droser *et al.* 2006; Wood 2011; Warren *et al.* in press).

Final considerations

Despite the vast area occupied by Precambrian rocks in Brazil, the corresponding fossil record has been relatively little exploited. Traditionally, most papers dealing with this subject have focused on description and taxonomy rather than on paleobiological inference or biostratigraphical interpretation. Meanwhile, worldwide, in just the past few years, a series of new techniques has been applied to the study of very ancient fossils, especially microfossils and chemical fossils – Raman spectroscopy and imagery, confocal laser scanning microscopy (Schopf & Kudryavtsev 2009), synchrontron X-ray microtomography (Chen *et al.* 2009), nanoSIMS (Oehler *et al.* 2009), micro-FTIR spectroscopy (Igisu *et al.* 2009), chemostratigraphy and others – that has elevated Precambrian paleobiological research to a new level of sophistication. Much of the technological development of many of these techniques have been directly stimulated by the concrete prospect of actually searching for fossil evidence of an ancient alien biosphere on Mars within a few decades. The needs of astrobiology in this endeavour require not only knowledge of Earth's most ancient life forms, but a well-founded understanding of paleontological practices and paleobiological concepts.

We have mentioned in this paper four different kinds of Brazilian Precambrian fossils of potential value for understanding biological evolution and the transformation of Earth's surface and atmosphere over time as well as for application to practical problems of geology, as in biostratigraphy. With respect to the Paleoproterozoic microbialites of the Quadrilátero Ferrífero, for instance, Bekker *et al.* (2003) conducted an initial geochemical investigation designed to test hypotheses regarding the atmosphere, oceanic chemistry and glacial events around the time of the Great Oxygenation Event at 2.3 Ga. Yet much remains to be done.

Few workers have investigated the organic-walled planktonic microfossils of the Brazilian Proterozoic, so that only the surface of their paleobiological and biostratigraphical significance has been touched. A first step forward in this regard would be the independent corroboration by other workers of the results that do exist and initiation of systematic formation-by-formation, basin-by-basin research programmes in Precambrian palynology.

Understanding of the paleobiology and global significance of the Ediacaran fossils in the Jacadigo (VSMs and microfossils) and Corumbá groups (microbialites, microfossils, macroalgae and metazoans) in the Corumbá region is already benefiting from recent detailed stratigraphic analyses (Oliveira 2010; Freitas *et al.* 2011; Warren 2011) and the application of such modern techniques as X-ray tomography (Pacheco and Leme in collaboration with Professor Cláudio Campi de Castro, Universidade de São Paulo), synchrontron X-ray microtomography (Pacheco and colleagues, in collaboration with the team of Professor Franz Pfeiffer, Technical University of Munich) and Raman spectroscopy (Sanchez & Fairchild 2012, and other works in collaboration with Drs Douglas Galante, Fabio Rodrigues, Professor Dalva Faria, Universidade de São Paulo, and Professor Dr Airton Martin, UniVap, São José dos Campo, SP).

The application of these and other techniques to the Precambrian Brazilian fossils discussed here offers great promise for delving more deeply into the biological affinities and ecological aspects of Precambrian life (Fedonkin & Waggoner 1997; Seilacher 1999; Narbonne 2004), with implications for the astrobiological search for basic life forms outside the limits of the terrestrial biosphere.

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