

The puzzle assembled: Ediacaran guide fossil *Cloudina* reveals an old proto-Gondwana seaway

L.V. Warren^{1*}, F. Quaglio², C. Riccomini³, M.G. Simões⁴, D.G. Poiré⁵, N.M. Strikis³, L.E. Anelli³, and P.C. Strikis³

¹Departamento de Geologia Aplicada, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Avenida 24A, 1515, Rio Claro 13506-900, Brazil

²UNESPetro—Centro de Geociências Aplicadas ao Petróleo, Instituto de Geociências e Ciências Exatas, Universidade Estadual Paulista, Avenida 24A, 1515, Rio Claro 13506-900, Brazil

³Instituto de Geociências, Universidade de São Paulo (USP), Rua do Lago, 562, São Paulo 05508-080, Brazil

⁴Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Distrito de Rubião Júnior, Botucatu 18618-000, Brazil

⁵Centro de Investigaciones Geológicas (UNLP-Conicet), Calle 1,644, La Plata 1900, Argentina

ABSTRACT

During the Ediacaran the Clymene Ocean separated the Laurentia, Amazonia, and Río Apa cratons from several landmasses to the west forming the proto-Gondwana supercontinent. However, no clear evidence about the existence of Ediacaran epeiric seas over those landmasses has been found. Here we report and discuss the discovery of the Ediacaran guide fossil *Cloudina* sp. associated with other metazoan body and trace fossils in the Bambuí Group (central eastern Brazil). The Ediacaran age of the Bambuí Group and the paleogeographic position of *Cloudina*-bearing successions in Brazil, Antarctica, Namibia, and Argentina suggest a scenario of ocean connectivity among coeval intracratonic basins of South America, Africa, and Antarctica at the end of Neoproterozoic time. The new finding epitomizes one of the most important paleontological discoveries ever made in South America, helping to solve an old paleogeographic puzzle of the Gondwana supercontinent.

INTRODUCTION

The Bambuí Group crops out in central eastern Brazil, and is one of the most studied Neoproterozoic sedimentary successions in South America. It comprises an extensive, flat-lying cratonic cover in erosional contact with Paleoproterozoic and Archean basement rocks of the São Francisco craton. In its eastern and westernmost occurrences, the Bambuí Group is deformed and metamorphosed by the Brasília and Araçuaí mobile belts, respectively (Fig. 1A). The regional tectonostratigraphy has been interpreted as reflecting deposition in a foreland basin related to Gondwanan collisions involving the São Francisco craton (Pimentel et al., 2011).

The Bambuí Group (BG) overlies rocks of the Macaúbas Group and Jequitai Formation and the Carrancas conglomerate, units supposedly deposited during Sturtian glaciation. The unit is 700–1000 m thick (Misi et al., 2007) and comprises limestones and dolomites of the Sete Lagoas Formation at the base that grade upward to shales and siltstones of the Serra de Santa Helena Formation, followed by marls, siltstones, limestones, and sandstones of the Lagoa do Jacaré, Serra da Saudade, and Três Marias Formations (Fig. 1B).

The precise age of the BG is not well established, precluding accurate correlation with other supposedly coeval successions such as the Corumbá Group (Brazil), Itapucumi (Paraguay), Arroyo del Soldado (Uruguay), Sierras Bayas (Argentina), and Nama Group (Namibia). The presence of *Conophyton*, silicified microbial mats, rare fossilized algal phytolites and microphytolites, and other long-ranging microfossils, such as coccooid and filamentous cyanobacteria (Fairchild et al., 1996), do not contribute to accurate age determination (Nobre-Lopes and Coimbra, 2000). One specimen identified as an acanthomorphic acritarch suggests an Ediacaran age for the base of the BG (Cruz and Nobre-Lopes, 1992). The apparent absence of key index fossils has led to several attempts to determine the age

of BG and related units based on geochronologic and isotopic methods (Pedrosa-Soares et al., 2000; Misi et al., 2007; Babinski et al., 2007). It is currently accepted that the BG is entirely Neoproterozoic in age, ranging from the late Tonian to the early Ediacaran.

NEW BIOTA FROM THE SETE LAGOAS FORMATION

The Sete Lagoas Formation is ~100 m thick in the vicinity of the town of Januária (Fig. 1A), where it comprises laminated calcareous grainstone facies, followed by wavy and hummocky cross-stratified grainstones (Fig. 1B). Centimeter-thick beds of laminated microbial mats and asymmetrical domical thrombolites are intercalated in the grainstone facies (Fig. 1C). Centimeter-scale thrombolitic biostromes are made up of laterally extensive, relatively low (to 5 cm) domes and irregular nodules. Convolute layers, small desiccation cracks, and laterally interrupted microbial laminae are rarely observed in the mudstone and thrombolites.

Fossils occur in few layers of fine grainstones with wave ripples, microbial mats, and thrombolites in the middle portion of the Lagoa Santa Formation (Fig. 1C). Loosely packed *Cloudina* (Germs, 1972) shells and very rare *Corumbella weneri* (Hahn et al., 1982) fragments also occur in those layers (Figs. 2A–2J). Most *Cloudina* specimens are fragmented and disarticulated with poor size sorting and low roundness, mostly preserved parallel, perpendicular, or slightly oblique to bedding (Figs. 2A–2G). They range in size from 3 to 17 mm and consist of slightly elliptical to circular tubes that are 0.4–1.8 mm in cross section. Rare specimens show a bifurcated extremity with two tubes (clonal budding?) of smaller diameter (Figs. 2B and 2C). In basal cross sections, the eccentric to concentric tube-in-tube structure formed by thin walls with thicknesses of ~0.2 mm is relatively common (Figs. 2F and 2G). The lack of diagnostic character in most specimens, such as the apical portions of the funnels (Fig. 2E), is related to the fragmentation or intense recrystallization of their walls. Most tubes are filled by sparry calcite.

The sessile cnidarian scyphozoan *C. weneri* occurs as sparse, flattened, small fragments of 0.8–1.5 mm width and 1.5–2.5 mm length (Fig. 2H). The best preserved specimen is represented by articulated annular elements of submillimeter-scale rings with maximum thickness of 100 μ m, numbering 8/mm (Fig. 2H). Individual rings are composed of dark gray, very finely recrystallized calcite, suggesting organic composition of the original carapace. The rare fragments assigned to *C. weneri* occur in the same layer of the *Cloudina* fossils and represent <1% of the fossil assemblage.

Simple unbranched trace fossils are also associated with the thrombolites and fine grainstones. *Palaeophycus* ichnofossils are characterized by horizontally unlined, straight to sinuous burrows with elliptical to circular cross sections. Nonbifurcated excavations, horizontal to the bedding and filled by the same matrix of the rock (Fig. 2I), are 70.4–83.6 mm in length and 2.3–5.7 mm width. Well-preserved bilaterian trace fossils are also recognized as convex hyporeliefs and consist of slightly curved, unbranched, and linear horizontal burrows with a central depression that splits longitudinally into unequal lobes (Fig. 2J). Two flat raised lateral

*E-mail: warren@rc.unesp.br.

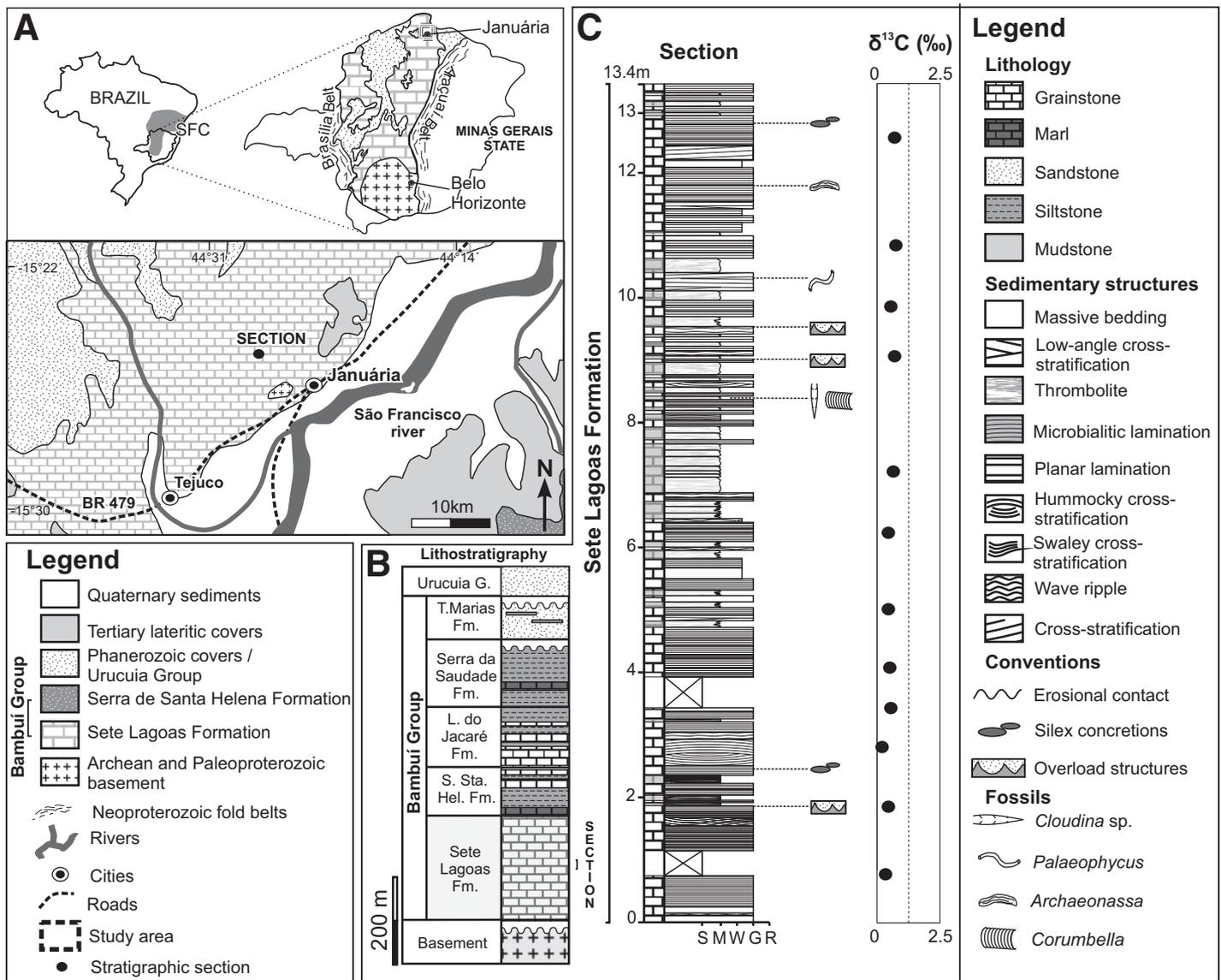


Figure 1. A: Location of São Francisco craton (SFC) and geologic map of Ediacaran Bambuí Group at Januária area, central Brazil. **B:** Lithostratigraphic column. G.—Group, Fm.—Formation, T.—Três, L.—Lago, S. Sta. Hel.—Serra de Santa Helena. **C:** Columnar section of peritidal facies deposits of Sete Lagoas Formation. S—shale, M—mudstone, W—wackestones, G—grainstone, R—rudstone.

ridges form the lower surface, and thinner transverse ridges, separated by a medial furrow, form a bilobed profile 30–108 mm long and 9.1–2.6 mm wide in cross section. In some cases, a terminal curve structure is preserved, interpreted as the forward portion of the horizontal trace.

PALEOENVIRONMENT, PALEOECOLOGY, AND AGE

The grainstone and thrombolitic facies suggest deposition under shallow-water conditions, in peritidal settings affected by waves during fair weather and occasionally by storms. Locally, subaerial exposure is indicated by desiccation cracks and interruption of the microbially induced laminae development.

The poor size sorting and absence of abrasion indicate that the *Cloudina* remains were not extensively reworked before being buried within their original life habitat. The geopetal structures filled by sparry calcite in *Cloudina* parautochthonous shells suggest that the presence of soft tissues after death of the organisms inhibited early infilling by sediments, resulting in a void that was later filled by calcite cement. The coexistence of *Cloudina* and *Corumbella* within shallow-water microbialitic facies suggests an environment similar to those described in other coeval

successions in Namibia, Oman, and Paraguay (Grotzinger et al., 1995; Amthor et al., 2003; Warren et al., 2011).

The structure shown in positive hyporelief could be assigned to an undermat tunnel made by a bilaterian organism near the sediment-water interface (Chen et al., 2013). The traces are tentatively assigned to the bilobed ichnogenus *Archaeonassa* (Yochelson and Fedonkin, 1997). Simple burrows similar to feed ichnites such as *Palaeophycus* and *Planolites* are described in some Ediacaran successions, while the bilobate trace fossil *Archaeonassa* is reported from the early Ediacaran (Jensen, 2003), and structures described as truly metazoan trace fossil are considered no older than 560 Ma (Liu et al., 2010).

The newly found index fossil *Cloudina* confirms ages between 550 and 542 Ma (Grotzinger et al., 1995; Amthor et al., 2003) for the lower portion of the BG. In this way, we assume that the deposition of the middle portion of the Sete Lagoas Formation occurred in the late Ediacaran Period. The association with *Corumbella* also reinforces this age, since this scyphozoan is described only from the uppermost Ediacaran biozone in Brazil, the United States, and Paraguay (Hahn et al., 1982; Hagadorn and Waggoner, 2000; Warren et al., 2011). The $\delta^{13}\text{C}$ isotope data of peritidal

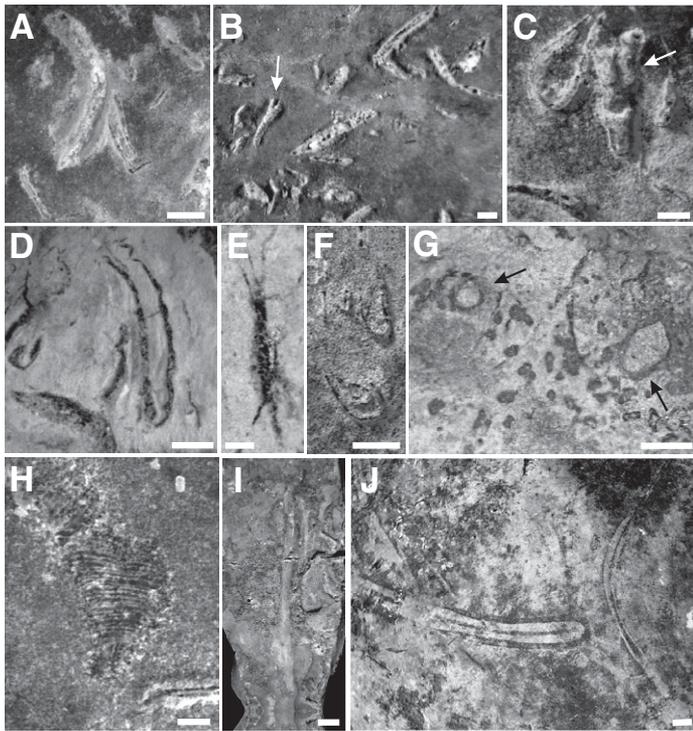


Figure 2. Fossil assemblage of Sete Lagoas Formation, Brazil. A: Tubular shells of *Cloudina* filled by sparry calcite. Scale bar is 2 mm. B: Complete and fragmented specimens of *Cloudina* varying in length and diameter. Scale bar is 2 mm. C: Close-up view of dichotomous branching (clonal budding?) of *Cloudina* specimens. Scale bar is 1 mm. Arrows in B and C indicate bifurcated specimens. D: Semicomplete longitudinal section of *Cloudina* shell filled by fine grainstones. Scale bar is 2 mm. E: Close-up view of recrystallized *Cloudina* shell with aligned crests. Scale bar is 1 mm. F: Basal section of *Cloudina* shell showing eccentric emplacement of funnels. Scale bar is 1 mm. G: *Cloudina* pavement including specimens oriented perpendicular to bedding (arrows). Scale bar is 1 mm. H: Fragment of *Corumbella*. Scale bar is 500 μm . I: Linear simple trace fossil *Palaeophycus* on upper surface of fine grainstone bed. Scale bar is 1 cm. J: Bed-parallel bilobed ichnofossil in positive hyporelief. Note longitudinal central linear depression and semicircular ending of traces. Scale bar is 1 cm.

carbonate succession in the Januária area (Fig. 1C) show values of 0.06‰ and 0.67‰, and an average of 0.37‰, consistent with previous data of the intermediate portion of the Sete Lagoas Formation (Misi et al., 2007). The positive excursions are apparently typical of the *Cloudina* interval biozone (Warren et al., 2011). Based on the fossil content and $\delta^{13}\text{C}$ results, we interpret that the lower portion of the BG has a terminal Ediacaran age, consistent with depositional ages of other South American and African carbonate units.

Caxito et al. (2012) recognized that the carbonate rocks of the basal Sete Lagoas Formation represent a postglacial cap dolostone, although the age of glacial deposits of the Macaúbas Group might be Sturtian or Marinoan. Zircon grains from the Macaúbas Group and Jequitaí and Bebedouro Formations indicate a maximum depositional age of 900 Ma and 874 ± 9 Ma, respectively (Pedrosa-Soares et al., 2000; Figueiredo et al., 2009), and detrital zircons from the middle and upper portions of the BG yielded ages of 650 and 616 Ma (Pimentel et al., 2011). Our interpretation of a late Ediacaran age for the middle portion of the Sete Lagoas Formation does not imply necessarily that the base of the unit exhibits the same age. Therefore, the interpretation that the basal dolomites overlying glacial deposits are post-Sturtian in age is still valid (Babinski et al., 2007).

NEOPROTEROZOIC PUZZLE ASSEMBLED

During the Ediacaran-Cambrian transition (550–496 Ma) the central elements of Gondwana (São Francisco–Congo, Kalahari, and Rio de la Plata cratons) were separated from the Amazonia–West Africa cratons by the short-lived Clymene Ocean (Trindade et al., 2006). Reconstructions of proto-Gondwana between 550 and 525 Ma assume that the São Francisco–Congo was connected to the Rio de La Plata, Kalahari, and Antarctic cratons (Fig. 3). The *Cloudina*-bearing units in the Nama Group (Namibia), Sierras Bayas Group (Argentina), Taylor Formation (Antarctica), and Arroyo del Soldado Group (Uruguay) are located in the eastern margins of those cratons, suggesting a connection of these basins by the Clymene Ocean (Fig. 3). During a regional transgressive event, open marine carbonate ramps and interior platforms were deposited in the intracratonic and marginal basins of the southeast portion of proto-Gondwana. The discovery of Ediacaran index fossils in the BG implies an intracontinental oceanic connectivity with the inner portions of the Congo–São Francisco craton. This seaway was probably linked eastward to the Clymene Ocean, covering parts of the Rio de la Plata, Kalahari, Paraná, and Antarctic cratons.

It is currently assumed that rocks of the BG were subject to folding and thrusting along the craton margins, presumably related to the Brazilian orogeny and the evolution of the surrounding Araçuaí, Brasília, and Rio Preto fold belts (Caxito et al., 2012). According to our paleogeographic reconstruction, the tectonic processes related to the evolution of the fold belts around the São Francisco craton are open to debate. The 800–650 Ma continent-continent convergent collision related to the formation of the Brasília fold belt (Pimentel, 2000) occurred at least 100 m.y. before the beginning of the BG deposition and long before the closure of extensive marginal and intracratonic basins that marked the final events of southwest Gondwana assembly in the Cambrian (Tohver et al., 2010). Thus, the idea that the deposition of the BG occurred in a foreland basin formed in response to tectonic stresses is flawed. Particularly for the Araçuaí belt, the hypothesis of evolution coeval with the closure of the Clymene Ocean in an intracontinental context cannot be ruled out.

Despite several margins emerging after the Rodinia rifting process in the early Neoproterozoic, the appearance of shelly metazoans is probably more closely related to the proto-Gondwana amalgamation in the Ediacaran. The formation of extensive epicontinental seas covering this supercontinent may have provided appropriate environments for the establishment of microbial colonies and the flourishing and dispersion of the earli-

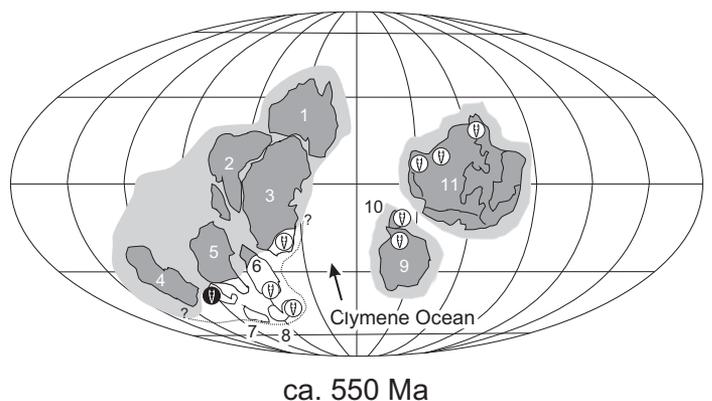


Figure 3. Paleogeographic reconstructions of Gondwana ca. 550 Ma highlighting main coeval *Cloudina*-bearing localities. Bambuí Group occurrence is in black. Dotted line indicates limits of intracratonic marine connection between southwest Gondwana. 1—Australia, 2—India, 3—Antarctica, 4—West Africa, 5—Congo–São Francisco, 6—Kalahari, 7—Paraná, 8—Rio de la Plata, 9—Amazonia, 10—Rio Apa, 11—Laurentia. All reconstructions based on Germs, 1972; Yochelson and Stump, 1977; Hagadorn and Waggoner, 2000; Trindade et al., 2006; Tohver et al., 2012; Gaucher et al., 2003; Warren et al., 2011.

est biomineralized metazoans. In the southwest Gondwana context, the absence of exclusively endemic faunas (Hagadorn and Waggoner, 2000), low diversity of few shelly organisms or species, and cosmopolitan character of the *Cloudina* genus were probably due to the absence of paleobiogeographic barriers between the newly formed basins. The extensive marine connection of the interior seas and marginal and oceanic basins (Fig. 3) provided the ideal conditions for the deposition of shallow carbonate facies and microbialites. A linked paleogeographic scenario also explains the homogeneous positive $\delta^{13}\text{C}$ excursion related to the *Cloudina* biozone in Brazil, Argentina, Namibia, Uruguay, and Oman carbonate successions (Grotzinger et al., 1995; Amthor et al., 2003; Boggiani et al., 2010; Bagnoud-Velásquez et al., 2013). The positive $\delta^{13}\text{C}$ values suggest high rates of organic productivity in those basins, probably due to microbialitic algae and cyanobacteria photosynthesis.

Because of the central position of the Congo–São Francisco craton at end of the Neoproterozoic, the BG is one of the most important pieces of the Gondwana paleogeographic and paleoecologic puzzle. The existence of a Gondwana seaway linking South America, Africa, and probably Antarctica elucidates the sedimentologic and isotopic similarities with other intracratonic and marginal carbonate units at the Proterozoic-Phanerozoic transition and reinforces the paleoecologic interconnectivity of Brazilian, Namibian, Argentinean, and Uruguayan basins.

ACKNOWLEDGMENTS

We thank the State of São Paulo Research Foundation (FAPESP grant 2010/19584-4) for financial support. This is a GEO-SEDEX contribution (no. 4), with institutional support of the University of São Paulo.

REFERENCES CITED

Amthor, J.E., Grotzinger, J.P., Schröder, S., Bowring, S.A., Ramezani, J., Martin, M.W., and Matter, A., 2003, Extinction of *Cloudina* and *Namacalathus* at the Precambrian-Cambrian boundary in Oman: *Geology*, v. 31, p. 431–434, doi:10.1130/0091-7613(2003)031<0431:EOCANA>2.0.CO;2.

Babinski, M., Vieira, L.C., and Trindade, R.I.F., 2007, Direct dating of the Sete Lagoas cap carbonate (Bambuá Group, Brazil) and implications for the Neoproterozoic glacial events: *Terra Nova*, v. 19, p. 401–406, doi:10.1111/j.1365-3121.2007.00764.x.

Bagnoud-Velásquez, M., Spangenberg, J.E., Poiré, D.G., and Gómez Peral, L.E., 2013, Stable isotopes (S, C) and hydrocarbon biomarkers in Neoproterozoic sediments of the Sierras Bayas Group, Argentina: *Precambrian Research*, v. 231, p. 388–400, doi:10.1016/j.precamres.2013.04.001.

Boggiani, P.C., Gaucher, C., Sial, A.N., Babinski, M., Simon, C.M., Riccomini, C., Ferreira, V.P., and Fairchild, T.R., 2010, Chemostratigraphy of the Tamengo Formation (Corumbá Group, Brazil): A contribution to the calibration of the Ediacaran carbon-isotope curve: *Precambrian Research*, v. 182, p. 382–401, doi:10.1016/j.precamres.2010.06.003.

Caxito, F.A., Halverson, G.P., Uhlein, A., Stevenson, R., Dias, T.G., and Uhlein, G.J., 2012, Marinoan glaciation in east central Brazil: *Precambrian Research*, v. 200–203, p. 38–58, doi:10.1016/j.precamres.2012.01.005.

Chen, Z., Zhou, C., Meyer, M., Xiang, K., Schiffbauer, J.D., Yuan, X., and Xiao, S., 2013, Trace fossil evidence for Ediacaran bilaterian animals with complex behaviors: *Precambrian Research*, v. 224, p. 690–701, doi:10.1016/j.precamres.2012.11.004.

Cruz, N.M.C., and Nobre-Lopes, J., 1992, Microfósseis do Grupo Bambuí na região de Arcos, Minas Gerais: *Anais da Academia Brasileira de Ciências*, v. 64, p. 420.

Fairchild, T.R., Schopf, J.W., Shen-Miller, J., Guimarães, E.M., Edwards, M.D., Lagstein, A., Li, X., Pabst, M., and Melo-Filho, L.S., 1996, Recent discoveries of Proterozoic microfossils in south-central Brazil: *Precambrian Research*, v. 80, p. 125–152, doi:10.1016/S0301-9268(96)00009-5.

Figueiredo, F.T., Almeida, R.P., Tohver, E., Babinski, M., Liu, D., and Fanning, C., 2009, Neoproterozoic glacial dynamics revealed by provenance of diamictites of the Bebedouro Formation, São Francisco Craton, central eastern Brazil: *Terra Nova*, v. 21, p. 375–385, doi:10.1111/j.1365-3121.2009.00893.x.

Gaucher, C., Boggiani, P.C., Sprechmann, P., Sial, A.N., and Fairchild, T.R., 2003, Integrated correlation of the Vendian to Cambrian Arroyo del Soldado and Corumbá Groups (Uruguay and Brazil): Palaeogeographic, palaeoclimatic and palaeobiologic implications: *Precambrian Research*, v. 120, p. 241–278, doi:10.1016/S0301-9268(02)00140-7.

Germis, G.J.B., 1972, New shelly fossils from Nama Group, south west Africa: *American Journal of Science*, v. 272, p. 752–761, doi:10.2475/ajs.272.8.752.

Grotzinger, J.P., Bowring, S.A., Saylor, B.Z., and Kaufman, A.J., 1995, Biostratigraphic and geochronologic constraints on early animal evolution: *Science*, v. 270, p. 598–604, doi:10.1126/science.270.5236.598.

Hagadorn, J.W., and Waggoner, B., 2000, Ediacaran fossils from the southwestern Great Basin, United States: *Journal of Paleontology*, v. 74, p. 349–359, doi:10.1666/0022-3360(2000)074<0349:EFFTSG>2.0.CO;2.

Hahn, G., Hahn, R., Leonardos, O.H., Pflug, H.D., and Jung, D.H.G., 1982, Körperlich erhaltene Scyphozoen-Reste aus dem Jungpräkambrium Brasilien: *Geologica et Palaeontologica*, v. 16, p. 1–18.

Jensen, S., 2003, The Proterozoic and earliest Cambrian trace fossil record; patterns, problems and perspectives: *Integrative and Comparative Biology*, v. 43, p. 219–228, doi:10.1093/icb/43.1.219.

Liu, A.G., McLroy, D., and Brasier, M.D., 2010, First evidence for locomotion in the Ediacara biota from the 565 Ma Mistaken Point Formation, Newfoundland: *Geology*, v. 38, p. 123–126, doi:10.1130/G30368.1.

Misi, A., Kaufman, A., Veizer, J., Powis, K., Azmy, K., Boggiani, P.C., Gaucher, C., Teixeira, J.B.G., Sanches, A.L., and Iyer, S.S.S., 2007, Chemostratigraphic correlation of Neoproterozoic successions in South America: *Chemical Geology*, v. 237, p. 143–167, doi:10.1016/j.chemgeo.2006.06.019.

Nobre-Lopes, J., and Coimbra, A.M., 2000, Microfítólitos associados a construções estromatólíticas do Grupo Bambuí, Proterozóico Superior, região de Arcos - MG: *Revista Brasileira de Geociências*, v. 30, p. 589–592.

Pedrosa-Soares, A.C., Cordani, U.G., and Nutman, A., 2000, Constraining the age of Neoproterozoic glaciation in eastern Brazil: First U-Pb SHRIMP data of detrital zircons: *Revista Brasileira de Geociências*, v. 30, p. 58–61.

Pimentel, M.M., 2000, Basement of the Brasília Fold Belt and the Goiás Magmatic Arc, in Cordani, U.G., et al., eds., *Tectonic evolution of South America: 31st International Geological Congress*, p. 190–229.

Pimentel, M.M., Rodrigues, J.B., DellaGiustina, M.E.S., Junges, S., Matteini, M., and Armstrong, R., 2011, The tectonic evolution of the Neoproterozoic Brasília Belt, central Brazil, based on SHRIMP and LA-ICPMS U-Pb sedimentary provenance data: A review: *Journal of South American Earth Sciences*, v. 31, p. 345–357, doi:10.1016/j.jsames.2011.02.011.

Tohver, E., Trindade, R.I.F., Solum, J.G., Hall, C.M., Riccomini, C., and Nogueira, A.C., 2010, Closing the Clymene Ocean and bending a Brasiliano belt: Evidence for the Cambrian formation of Gondwana, southeast Amazon craton: *Geology*, v. 38, p. 267–270, doi:10.1130/G30510.1.

Tohver, E., Cawood, P.A., Rossello, E.A., and Jourdan, F., 2012, Closure of the Clymene Ocean and formation of West Gondwana in the Cambrian: Evidence from the Sierras Australes of the southernmost Rio de la Plata craton, Argentina: *Gondwana Research*, v. 21, p. 394–405, doi:10.1016/j.gr.2011.04.001.

Trindade, R.I.F., D'agrella-Filho, M.S., Epof, I., and Neves, B.B.B., 2006, Paleomagnetism of Early Cambrian Itabaiana mafic dikes (NE Brazil) and the final assembly of Gondwana: *Earth and Planetary Science Letters*, v. 244, p. 361–377, doi:10.1016/j.epsl.2005.12.039.

Warren, L.V., Fairchild, T.R., Gaucher, C., Boggiani, P.C., Poiré, D.G., Anelli, L.E., and Inchausti, J.C.G., 2011, *Corumbella* and in situ *Cloudina* in association with thrombolites in the Ediacaran Itapucumi Group, Paraguay: *Terra Nova*, v. 23, p. 382–389, doi:10.1111/j.1365-3121.2011.01023.x.

Yochelson, E.L., and Fedonkin, M.A., 1997, The type specimens (Middle Cambrian) of the trace fossil *Archaeanassa* Fenton and Fenton: *Canadian Journal of Earth Sciences*, v. 34, p. 1210–1219, doi:10.1139/e17-097.

Yochelson, E.L., and Stump, E., 1977, Discovery of Early Cambrian fossils at Taylor Nunatak, Antarctica: *Journal of Paleontology*, v. 51, p. 872–875.

Manuscript received 19 November 2013

Revised manuscript received 13 February 2014

Manuscript accepted 16 February 2014

Printed in USA