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Corumbella and *in situ Cloudina* in association with thrombolites in the Ediacaran Itapucumi Group, Paraguay

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ABSTRACT

An *in situ* assemblage of *Cloudina*, thrombolites and an ichnofossil (cf. *Archaeonassa*), together with fragments of *Corumbella werneri*, is reported here, from a tidally influenced, shallow, lagoonal setting on a carbonate ramp within the Itapucumi Group, Paraguay. The association of *Cloudina* with thrombolites is comparable to other terminal Neoproterozoic occurrences, but the coexistence of shelly fossils *in situ* with trace fossils and microbially induced sedimentary structures is apparently unique. This discovery extends the record of *Cloudina* and *Corumbella* in South America and further elucidates the diversity, distribution and palaeoecology of shelled organisms in late Ediacaran time.

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Introduction

Recent years have seen significant advances in our understanding of climatic, tectonic and evolutionary events that marked the end of the Neoproterozoic era. Low-latitude glaciation (Hoffman *et al*., 1998; Hoffman and Schrag, 2002) and the breakup of the supercontinent Rodinia (Hoffman, 1999; Li *et al*., 2008) set the stage for the appearance of increasingly varied macroscopic organisms (Grotzinger *et al*., 1995; Knoll and Carroll, 1999; Grey *et al*., 2003) and the subsequent escalation of the influence of the biosphere in the external dynamics of the Earth (Knoll and Bambach, 2000). It was within this context that the macroscopic organisms of the Ediacara biota appeared around 575 Ma (Narbonne and Gehling, 2003), followed at about 550 Ma by the worldwide advent of organisms capable of producing mineralized skeletal parts, putatively in response to the appearance of predators (Germs, 1972; Grant, 1990; Hofmann and Mountjoy, 2001; Bengtson, 2002). These innovations quickly led to a new plateau in ecological dynamics that ultimately resulted in the explosive radiation of shelly faunas at the beginning of the Cambrian.

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Initial access to this plateau, although widely recorded by bioclasts of the late Ediacaran calcareous tubular fossil *Cloudina* in grainstones from wave- and tide-dominated depositional settings, is most faithfully represented by associations of skeletal remains of *Cloudina* sp. plus *Namacalathus*, with or without biomineralized metazoan *Namapoikia* and possible calcareous algae, in microbial build-ups (stromatolites, thrombolites) in Namibia (Nama Group; Germs, 1972; Grant, 1990; Wood *et al*., 2002), Canada (Miette Group; Hofmann and Mountjoy, 2001), and Oman (Huqf Supergroup; Conway-Morris *et al*., 1990; Grotzinger *et al*., 2000), as well as by associations of *Cloudina* and *Corumbella* in Brazil (Corumbá Group; Hahn *et al*., 1982; Zaine and Fairchild, 1987) and *Cloudina* and *Sinotubulites* in China (Dengying and Gaojiashan formations, Wood *et al*., 2002; Hua *et al*., 2007). *Cloudina* apparently occupied low-energy settings protected by microbial build-ups or banks of ooids and surrounding areas, whereas *Namacalathus* inhabited the microbial bioherms themselves (Conway-Morris *et al*., 1990; Grotzinger *et al*., 2000; Hofmann and Mountjoy, 2001; Oliveira, 2010; Wood, 2011).

Hence, the discovery of thrombolitic biostrome outcrops and entire individuals of *Cloudina* apparently preserved in place, together with concentrated bioclasts of *Cloudina* and fragments of the supposed scyphozoan *Corumbella*, within the Itapucumi Group of eastern Paraguay not only confirms the previous report (Boggiani and Gaucher, 2004) of *Cloudina* in this country from limestone but also corroborates the observations mentioned above on the habitat of *Cloudina*, and significantly extends the geographical range in South America of *Corumbella* some 400 km to the south of its type-area in southwestern Brazil (Hahn *et al*.,1982; Zaine and Fairchild, 1985; Zaine, 1991; Gaucher, 2000; Gaucher *et al*., 2005). These observations, plus the presence of trace fossils and possible biomat structures within this association open an important new frontier in South America for research on life in the latest Ediacaran.

Geological setting

The Itapucumi Group (Harrington, 1950) crops out within the Rio Apa Block in an area 40 × 60 km east of and paralleling the Paraguay river in northeastern Paraguay (Fig. 1A). The western portion of this unit exhibits local low-grade (chlorite zone) metamorphism and intense deformation, with E-vergent reverse faults and inverted folds (Campanha *et al*., 2010). This succession (Fig. 1B) is made up of sandstones and siltstones of the Vallemi Formation that grade

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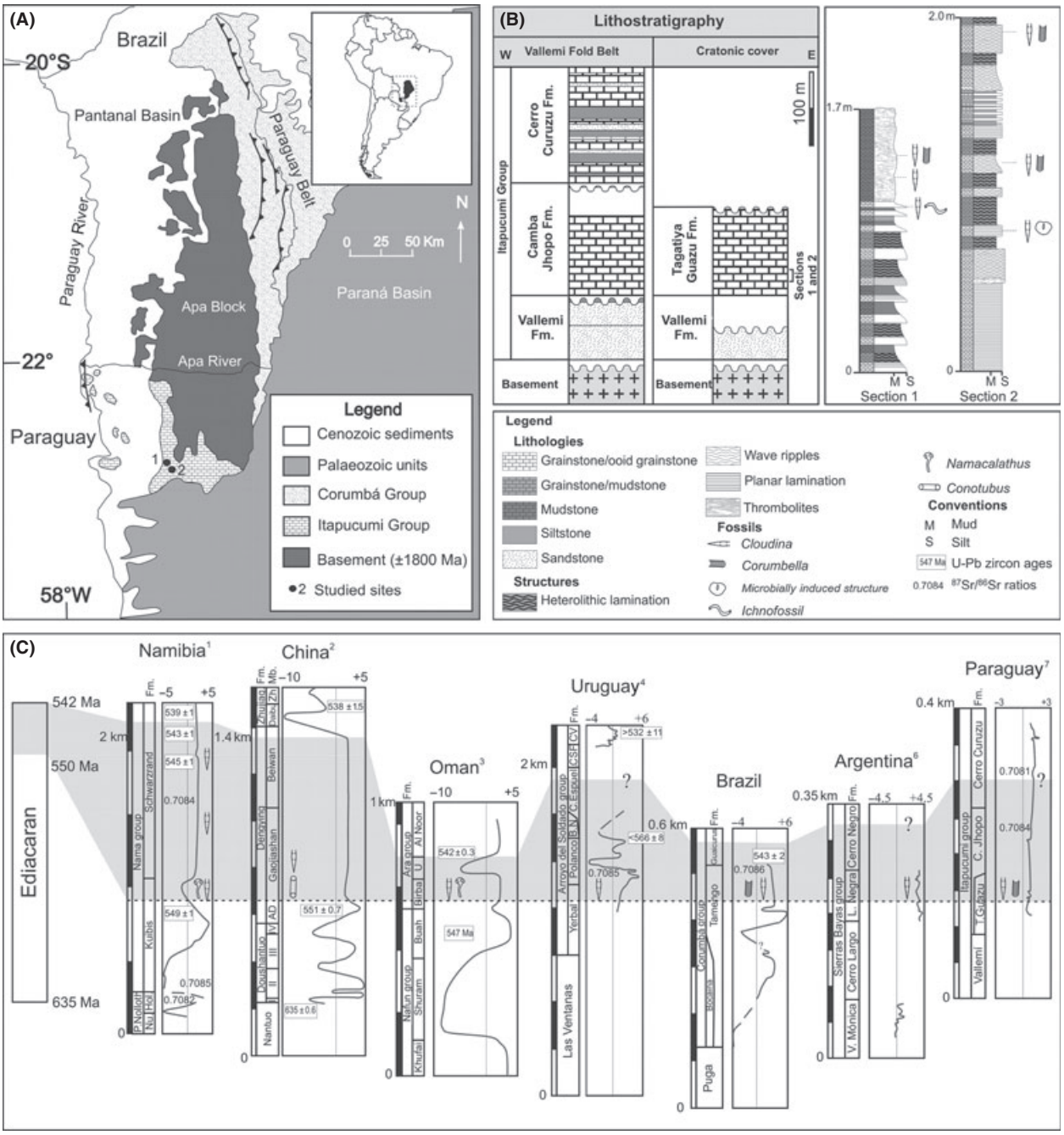

Fig. 1 (A and B) Locality map and stratigraphic sections from the Ediacaran-age Itapucumi Group, northeastern Paraguay. (C) Biostratigraphic, chemostratigraphic and geochronologic correlation between the Itapucumi Group and other terminal Neoproterozoic successions worldwide. The grey band corresponds to the *Cloudina* biozone (data from Grotzinger *et al*., 1995, 2000; Brasier *et al*., 2000; Amthor *et al*., 2003; Gaucher *et al*., 2003; Peral *et al*., 2007; Zhou and Xiao, 2007; Boggiani *et al*., 2010; Warren, 2011). (1) P.Nolloth, Port Nolloth Group; Nu., Numees Formation; Hol., Holgat Formation; (2) AD., Algal Dolomite; Zhuiaq., Zhujiaqing Formation; Zh., Zhongyicun Member; (4) BN, Barriga Negra; CSF, Cerros San Francisco; CV, Cerro Victoria; (6) V.Mónica, Villa Mónica; L.Negra, Loma Negra; (7) T.Guazu, Tagatiya Guazu; C. Jhopo, Camba Jhopo.

upward into grey oolitic limestones and dolostones of the Camba Jhopo Formation, culminating in the marls, pelites and dolostones of the Cerro Curuzu Formation (Warren, 2011). Further east, the Tagatiya Guazu Formation, considered the lateral equivalent of the Camba Jhopo Formation, comprises an extensive unmetamorphosed, undeformed cratonic sedimentary cover composed mainly of carbonates exhibiting mas-

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sive, cross-stratified grainstones and ooid grainstones, oncoids, mudstones and heterolithic facies intercalated with breccias and microbialites (Fig. 1B).

The fossils described here are from two outcrops 10 km apart in the Tagatiya Guazu Formation (Fig. 1B and C) in the eastern portion of the Itapucumi Group (22°46.18′S/57°29.10′W; 22°42.57′S/57°30.35′W). In both sections, massive and cross-stratified calcareous grainstones give way upward to heterolithic facies of grainstones and calcareous mudstones (Fig. 1B), exhibiting tidal bundles. Intercalated within these facies are centimetre-thick beds of intraformational breccias, including tepee structures, laminated microbialites plus thrombolitic biostromes (Fig. 2A and B), consisting of extensive, laterally continuous low domes up to 10 cm high relief and irregular nodules. The biostromes may be and are covered by lime mud containing dispersed grains of quartz sand (Fig. 2C) and platy intraclasts evidently eroded from nearby microbial mats and thrombolites with minimal abrasion and redeposited edgewise, without imbrication. The presence of convoluted and laterally interrupted stratiform microbialitic laminae (Fig. 2C and D), pseudomorphs of gypsum (Boggiani, 1998; Boggiani and Gaucher, 2004), tepee structures, intraformational breccias with mudstone curls and small desiccation cracks suggest sedimentation under evaporitic conditions with sporadic subaerial exposure of sediments and microbial mats. This facies association represents a shallow intertidal to supratidal setting on a rimmed carbonate ramp.

The presence of the *Cloudina*/*Corumbella* assemblage associated with thrombolites (Fig. 2D) in the eastern portion of the Itapucumi Group and the Tamengo Formation of southwest Brazil not only confirms the long-held view that these two units are lateral equivalents but also allows correlation with stratigraphic units in Uruguay and Argentina. In the Tamengo Formation, *Cloudina* occurs generally as bioclasts in grainstones or more rarely as fragments in poorly fossiliferous, thinly bedded fine grainstone/marl rhythmites. Shales in this formation harbour *Corumbella werneri* Hahn *et al.*, 1982; vendotaenids and a depauperate acritarch assemblage dominated by *Bavlinella* (Zaine, 1991; Gaucher *et al.*, 2003). In Uruguay, *Cloudina* has been described in siltstones of the Yerbal Formation, Arroyo del Soldado Group (Gaucher and Sprechmann, 1999; Gaucher, 2000), putatively in living position; better preserved, silicified specimens have been observed in limestones of the overlying Polanco Formation (Fig. 1C). Siltstones of the Yerbal Formation also host other skeletal fossils, most notably *Titanotheca coimbrae*, interpreted as an agglutinated foraminifera, and *Waltheria marburgensis*, purportedly possessing a phosphatic shell (Gaucher, 2000). *Cloudina* has also been reported from limestones of the Loma Negra Formation in Tandilia, Argentina (Fig. 1C, Gaucher *et al.*, 2005).

The presence of the index fossil *Cloudina* (Grant, 1990) indicates a terminal Ediacaran age for these South American successions somewhere between 548 and 542 Ma (Grotzinger *et al.*, 1995; Amthor *et al.*, 2003), an age recently confirmed for the Tamengo Formation by geocronological and chemostratigraphical studies by Babinski *et al.* (2008) and Boggiani *et al.* (2010), respectively. The *Cloudina*-bearing units of South America are thus biostratigraphically equivalent to successions around the world (Fig. 1C) within the Nama Group (Namibia), Dengying Formation (China), Ara

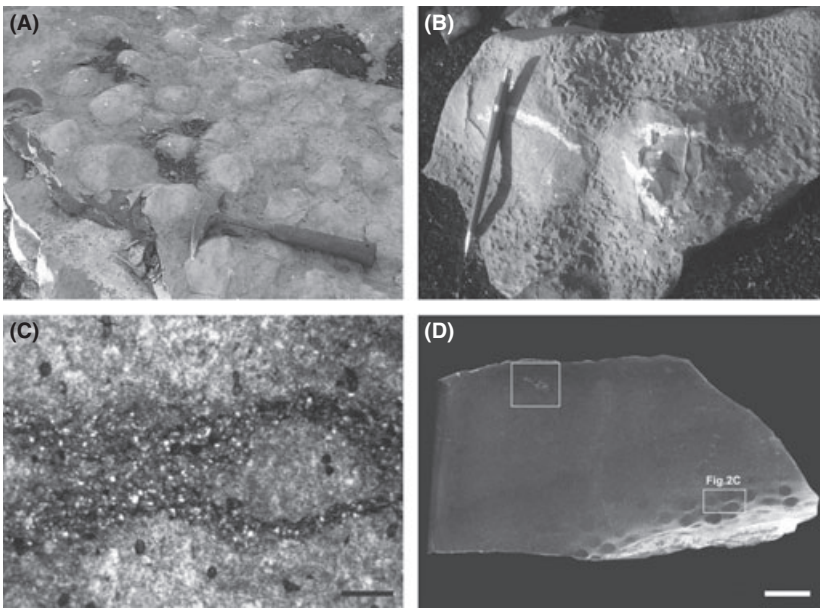

Fig. 2 (A and B) Domical thrombolites with small microbialitic intraclasts in the irregular depressions between domes. (C) Photomicrograph of thrombolite microstructure as seen in petrographic thin section. The light fragments are quartz grains. (D) Polished slab showing obliquely oriented shell of *Cloudina lucianoi* filled by sparry calcite cement (square at top) and mesoscopic clotted fabric (rectangle) at the lower right of the specimen. Scale bar represents 100 μm and 1 cm for C and D, respectively.

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Group (Oman), Miette Group (Canada), Ibor-Navalpino group (Spain, Cortijo *et al.*, 2010) and Kotodzha/Raiga Formations (Russia, Kontorovich *et al.*, 2008).

Description of the fossils

The fossils identified here as *Cloudina* in the Itapucumi Group are fragmented to entire, straight to markedly curved, generally cylindrical tubes, closed at their rounded proximal (basal) end and open at their distal (apical) end (Fig. 3A–C). The succession of nested, commonly eccentric ring-like wall segments observed in these specimens is typical of the genus *Cloudina* Germs, 1972. Wall segments do not always overlap regularly and may flare outward slightly at their distal ends (Fig. 3B and C), thus imparting an annular ornamentation to the tubes. In transverse cross-section, the tubes are slightly elliptical to circular with diameters from 1.0 to 3.5 mm (Fig. 3D). Complete specimens may reach 35 mm in length (Fig. 3A, G–I). Smaller than *C. hartmannae* Germs, 1972, and larger than *C. riemkeae* Germs, 1972, from Nambia, these fossils are comparable to the species *Cloudina lucianoi* Beurlen and Sommer, 1957, of the Tamengo Formation, to which they are assigned here (Beurlen and Sommer, 1957; Zaine and Fairchild, 1985). They are commonly filled by sparry calcite (Fig. 3E) and preserved parallel, perpendicular or oblique to bedding.

A second metazoan in the Itapucumi Group occurs as fragments, 3.0–4.6 mm long and flattened, 1.4 and 2.9 mm wide, made up of articulated, non-phosphatic, non-calcare-

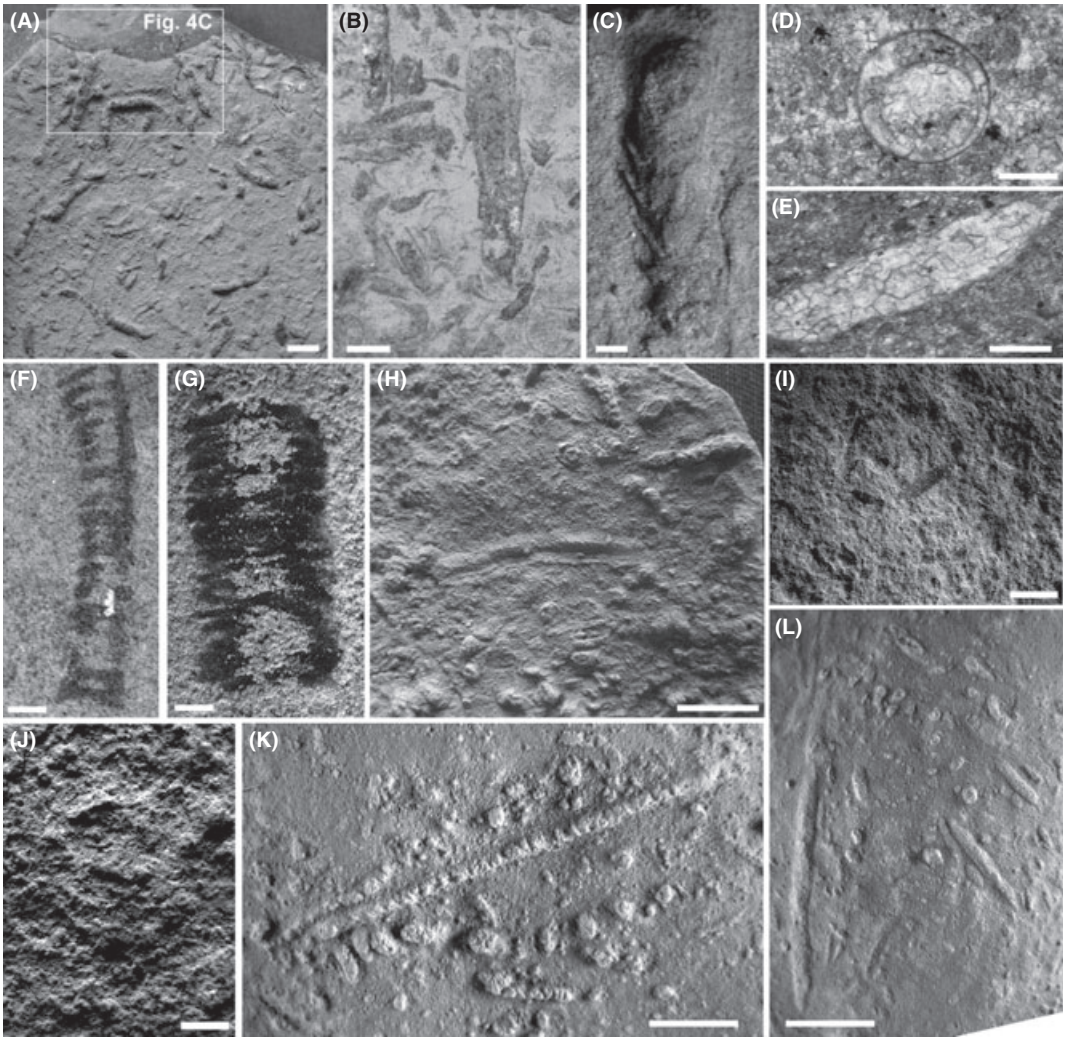

Fig. 3 Fossil assemblage of the Itapucumi Group. (A) Autochthonous assemblage of toppled specimens and in-place circular basal sections of *Cloudina lucianoi*. (B and C) *C. lucianoi* exhibiting typical cone-in-cone construction. (D) Photomicrograph of transverse section of *C. lucianoi* showing excentric emplacement of successive shell segments. (E) Photomicrograph of longitudinal section of *C. lucianoi* shell filled by sparry calcite cement. (F and G) Fragments of *Corumbella werneri*. (H) Bed-parallel trace fossil, cf. *Archaeonassa* (centre of photograph) associated with *in situ* specimens of *C. lucianoi*. (I and J) Discoidal pseudofossil exhibiting a small ellipsoidal central elevation interpreted as a rimmed microbially induced sedimentary structure (MISS of Noffke *et al.*, 1996). (K and L) Relatively long, nearly straight tubular structures. Note the subtle segmentation of the specimen in (K). Scale bar represents 1 cm for A and H; 5 mm for K and L; 2 mm for B, I and J; 1 mm for E; 500 μm for D, F and G; 300 μm for C.

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ous, apparently organic, narrow annular elements, approximately four per millimetre of length. These elements may also occur as submillimetric, lath-like fragments and isolated rings, no thicker than 0.25 mm (Fig. 3F and G) within the rock and possibly correspond to transverse rod-like skeletal elements that occur in conulariid scyphozoan cnidarians (Babcock *et al*., 2005). These fossils are attributed to *Corumbella werneri* (Hahn *et al*., 1982), described from the Tamengo Formation, rather than a possible second species, *Corumbella* sp., proposed by Hagadorn and Waggoner (2000) for rare specimens in sandstones from the Wood Canyon Formation, California, USA, because they are nearly identical in size, organization and preservation to the Brazilian species.

A single, slightly curved, unornamented, unbranched, linear horizontal structure preserved in positive epirelief (Fig. 3H) amidst abundant fragments of *C. lucianoi* is interpreted as a trace fossil similar to *Archaeonassa* (Yochelson and Fedonkin, 1997). The structure is 27.1 mm long and varies in width from 2.5 mm at one extremity to 5.3 mm at the other. A slightly offset flat central depression separates the structure longitudinally into two narrow raised lobes (Fig. 3H). This mark is interpreted as a feeding trace of a soft-bodied worm-like organism or a locomotion trace of a mollusc-like animal made near the sediment–water interface (Valentine, 1995; Jensen, 2003).

Figure 3I and J shows an elliptical structure measuring 6.6×8.6 mm with slightly elevated borders 1.7 mm wide and a central, slightly elevated elliptical structure, 3.8×1.3 mm, preserved in positive hyporelief in a fine grainstone. Although similar to moulds of soft-bodied medusoid cnidarians reported from the Ediacaran, such as *Nimbia occlusa* (Fedonkin, 1980; Hagadorn and Waggoner, 2000), this simple structure is known from a single, poorly preserved specimen in the Itapucumi Group and more likely represents a microbially induced sedimentary structure (MISS; Noffke *et al*., 1996; Grazhdankin and Gerdes, 2000).

Millimetric to centimetric fragments of elongate, roughly cylindrical structures with tapering terminations were observed in depressions between thrombolitic domes (Fig. 3K and L). Some specimens present a subtle segmentation suggestive of equally spaced ring-like structures (Fig. 3K). Although possibly representing poorly preserved *C. lucianoi*, their length-to-diameter ratio, straightness and apical termini suggest other affinities, perhaps calcareous algae.

Discussion

Fossils in the Itapucumi Group include abundant fragments and complete specimens of *Cloudina*, much less abundant, short segments of *Corumbella* and single specimen of a suspected trace fossil and a pseudofossil interpreted here as a MISS (Noffke *et al*.,1996).

Cloudina may be preserved parallel, perpendicular or oblique to bedding and occurs in three different ways within the Itapucumi Group: (1) as thin, lenticular coquinas in shallow tidal channels and in troughs between low-amplitude dunes and current ripples (Fig. 4A and B); (2) as fragments (fine bioclasts) in very fine grainstones between thrombolitic domes; and most importantly, (3) as articulated segments and prostrate whole specimens apparently *in situ* and associated with thrombolites (Figs 2D, 3A and 4C–G). Several spar-filled tubes of *Cloudina* oblique or perpendicular to the bedding appear to be the basal portions of relatively long, nearly

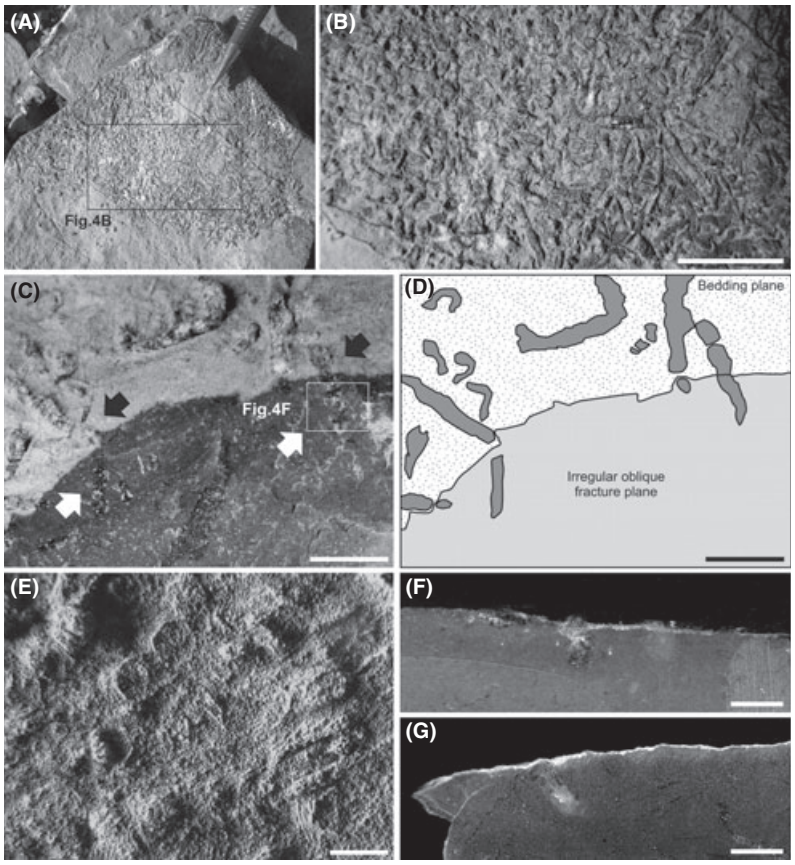

Fig. 4 Autochthonous *Cloudina lucianoi*. (A and B) Overview (A) and detail of coquina of *C. lucianoi* in a shallow trough. Note random arrangement of the shells in B. (C and D) Oblique view of sample (A) and graphic interpretation (B) showing sparry internal moulds in relief parallel to bedding plane (light grey) and normal to bedding (arrows) on the nearly vertical broken margin (darker grey). (E) Bedding plane view of transverse cross-sections of several specimens of *C. lucianoi* oriented perpendicular to bedding. (F and G) Side views of a polished carbonate slab showing spar-filled tubes of *Cloudina* in presumed living position in the sediment. Scale bar represents 1 cm for B, C and D; 5 mm for E, F and G.

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complete, prostrate shells lying upon the suprajacent bedding surface (Fig. 4 C–G). Many of the circular sections of shells observed on bedding planes (Fig. 4E) may represent a similar situation. In several of the prostrate specimens, the upper margin of some of the shell segments flares outward from the axis of the shell as a very delicate rim. Any transport would have easily broken and abraded these rims and disarticulated the longer specimens of *Cloudina*. Hence, these fossils were most likely preserved in place as obrution deposits, possibly when unconfined suspended lime mud and fine calcareous sand washed over natural barriers, smothering the protected areas where thrombolitic domes and *Cloudina* flourished. The depositional history was much different for *Cloudina* in the coquinas and as comminuted bioclasts in grainstones, and evidently involved differing degrees of transport, jostling, breakage and abrasion directly related to their respective short and long residence times within the taphonomically active zone.

A large number of *Cloudina* shells are filled by sparry calcite (Figs 3E, 4F and G), not only in the Itapucumi Group but also in the coquinoid tempestites within the Corumbá Group. Given the thinness of the shell segments in *Cloudina* (perhaps no more than 50 μm according to Grant, 1990), it is surprising, first, that these fossils were not fragmented or crushed during transport and, burial and, second, that they were not immediately filled by sediment once they were buried. We believe that many of these spar-filled shells were originally occupied by the *Cloudina* animal smothered during obrution or killed by the tempest responsible for their rapid transport and concentration in storm beds. The carcass of the animal would have effectively inhibited breakage during transport and blocking infilling of the shell by sediment until decomposition of the tissues resulted in a void that was later filled by sparry calcareous cement.

Corumbella, on the other hand, occurs as rare fragments and degraded, disarticulated segments along with fragments of *Cloudina,* a situation also described, but very rare, in the Tamengo Formation (Zaine, 1991). Differences in abundance and biostratinomic signatures between *Cloudina* and *Corumbella* in the Itapucumi Group may be related to differences in their respective habitat preferences, i.e. nearby protected carbonate settings for *Cloudina,* and distant shaley settings for *Corumbella werneri,* as registered in the type locality in the Tamengo Formation (Zaine, 1991; Babcock *et al*., 2005), as well as to the rigidity of the calcareous shells of *Cloudina* and the plasticity of the apparently organic skeleton. For these reasons, *Corumbella* occurs as flattened, often degraded parauchthonous/alocthonous bioclasts and *Cloudina*, as whole shells and broken fragments are apparently preserved within or very near to its natural habitat.

The Itapucumi Group thus provides the sixth example of coquinoid limestones containing *Cloudina* plus at least one other skeletal fossil in association with microbial buildups on Neoproterozoic carbonate platforms, albeit on a smaller stratigraphic scale than in that registered in Namibia, Canada, Oman, Brazil, Spain and Russia. For example, in Namibia and Oman, and probably in Canada (Hofmann and Mountjoy, 2001) as well, the *Cloudina-Namacalathus*–thrombolite-stromatolite, association extends for several kilometres as bioherms/biostromes, tens to hundreds of metres in thickness. Given the distance between the two sections reported here, the microbialites and skeletal fossils in the Itapucumi Group may be as extensive as some of the examples cited above. The presently known thickness of these deposits, however, is on the order of 10 m, but this may merely reflect the very limited size of the fossiliferous outcrops. Despite the influence of currents in the reef-like buildups in Namibia and their effect upon the shapes of platey stromatolites and bioherms in Canada, the commonly good preservation of the thin-walled calcareous shells at all four localities suggests that *Cloudina* (and *Namacalathus*) either grew within the buildups themselves or were derived from nearby protected areas.

Conclusions

The Paraguayan fossil occurrences described in this article are sedimentologically, taphonomically and palaeontologically comparable to similar Ediacaran successions worldwide. The presence of MISS structures (Noffke *et al*., 1996), thrombolites and specimens of *Cloudina* preserved *in situ* suggests a shallow marine carbonate environment in which the substrate, in part organic, was colonized by sessile and vagile benthos. *Cloudina* apparently lived as a flexible mat-sticker rising above the seafloor by partially anchoring itself in the sediment or attaching itself to small thrombolite domes. This life style surely provided greater efficiency for feeding, whereas the presence of a mineralized organic-rich exoskeleton protected the organism from possible predators (Hua *et al*., 2007; Wood, 2011). The co-occurrence of shells of *Cloudina* and fragments of the cnidarian *Corumbella werneri*, reported here for only the second time outside its type area, suggests that these organisms shared analogous or nearby environmental settings and colonized similar substrates. Furthermore, the presence of an ichnofossil identified as *Archaeonassa* preserved among *in situ Cloudina* specimens shows that soft-bodied organisms inhabited the same environment. These observations suggest that at least locally there were no ecological barriers impeding the co-occurrence of organic substrate, benthic microbial communities and soft-bodied and shelly organisms within the same environment. Hence, the lack of similar fossil assemblages in the palaeontological record may possibly reflect sedimentological or taphonomical biases.

The assemblage reported here significantly extends the geographical range of the *Cloudina–Corumbella* association in South America, indicating that *Corumbella* is more common in the *Cloudina* biozone in western Gondwana than previously registered. Thus, the Itapucumi assemblage represents a potential landmark in South American palaeontology that promises to provide important new perspectives on late Ediacaran palaeoecology.

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