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Notes

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L.V. Warren¹, M.L.A.F. Pacheco¹, T.R. Fairchild¹, M.G. Simões², C. Riccomini¹, P.C. Boggiani¹, and A.A. Cáceres³¹Instituto de Geociências, Universidade de São Paulo, Rua do Lago, 562, São Paulo 05508-080, Brazil²Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, Distrito de Rubião Júnior, Botucatu 18618-000, Brazil³Industria Nacional de Cemento (INC), Vallemí, Paraguay

ABSTRACT

Although the basic morphology of the Ediacaran metazoan *Corumbella weneri* (the type species of the genus) is well established, little is known about its skeletal tissue. Carbonaceous fragments of this fossil from the Itapucumi Group (Paraguay) reveal details of the ultrastructure of its carapace, providing an unprecedented opportunity to understand a paradigmatic issue of the evolution of skeletogenesis in early metazoans. *Corumbella* was a sessile predator whose carapace consisted of organic polygonal plates with pores and papillae similar to features observed in some conulariids. Its occurrence with the shelly fossil *Cloudina* suggests that the acquisition of protective structures in metazoans involved penecontemporaneous processes of biomineralization and secretion of organic walls.

INTRODUCTION

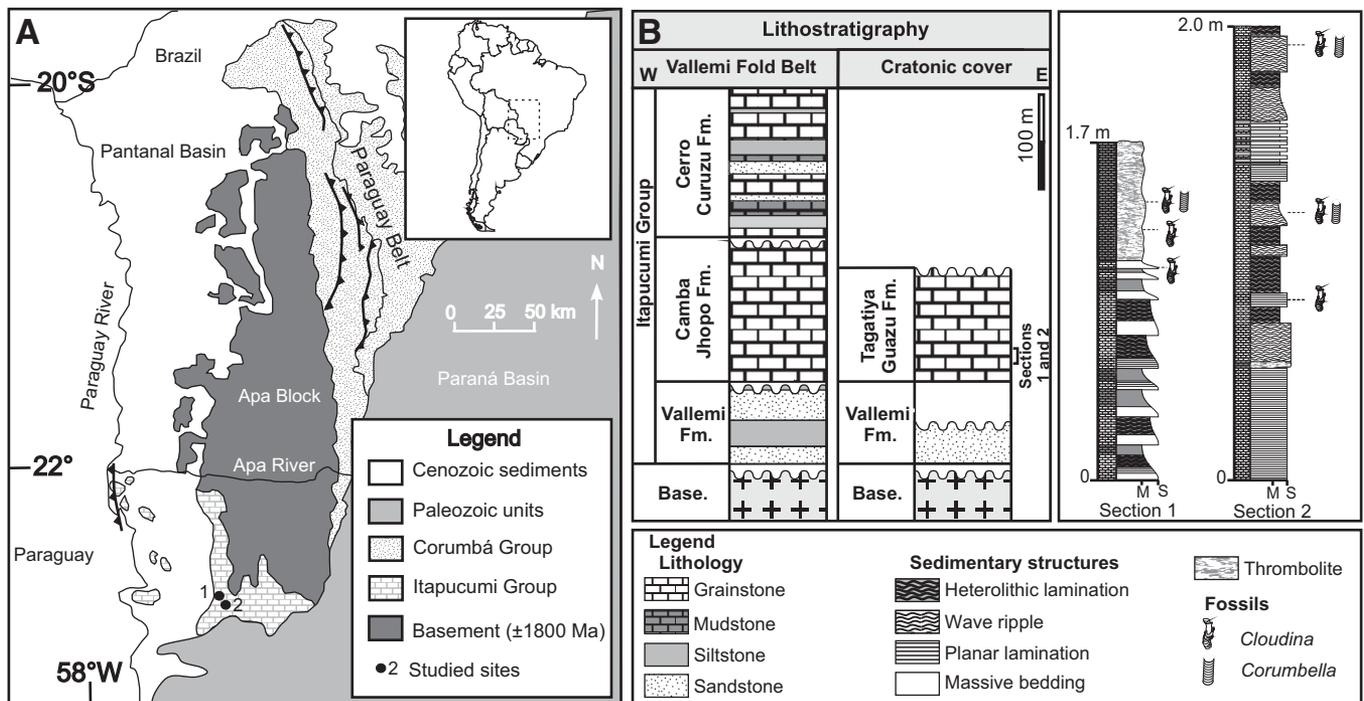
Within the context of the dramatic late Neoproterozoic climatic, tectonic, and paleoecological events, putative macroscopic metazoans appeared in the Ediacaran Period prior to 580 Ma (Yuan et al., 2011), followed ca. 550 Ma by the advent of macroscopic organisms with biomineralized skeletons. These innovations likely occurred in response to chemical changes in the oceans and the appearance of multicellular predators (Bengtson, 2002; Knoll, 2003; Hua et al., 2007), and ultimately triggered the Cambrian radiation of shelly faunas with all its ecological consequences.

Evidence indicates that organic carapaces preceded the rise of mineralized animal skeletons (Wood, 2011). The Ediacaran biota, for example, is traditionally characterized as consisting of soft-bodied organic-walled animals and vendobionts. Among the oldest known nonmineralized metazoan exoskeletons are thin-walled organic tubes, such as the Ediacaran conulariid *Vendoconularia* (Ivantsov and Fedonkin, 2002; Van Iten et al., 2005a), *Conotubus* (Hua et al., 2007), and the scyphozoan *Corumbella weneri* (Hahn et al., 1982). Exoskeletons of *C. weneri* have been likened to the chitinous peri-

derm tubes (Babcock et al., 2005) of modern coronate polyps (Scyphozoa, Cnidaria) (Jarms et al., 2002). Until recently, *Corumbella* was known only in marls of the Tamengo Formation (Corumbá Group), southwestern Brazil (Hahn et al., 1982), and in siliciclastic rocks of the Wood Canyon Formation, California (Hagadorn and Waggoner, 2000). Recently, carbonized specimens of *Corumbella* with well-preserved ultrastructural details were found in limestones of the Itapucumi Group (Paraguay). This discovery provides new insights into the nature of the *Corumbella* carapace, with significant paleoecologic and evolutionary implications.

LOCATION AND GEOLOGIC SETTING

The 300–400-m-thick Itapucumi Group occurs near the Paraguay River in northeastern Paraguay, within the Vallemí fold belt (Campanha et al., 2010), and as extensive, flat-lying cratonic cover in erosional contact on Paleoproterozoic basement rocks of the Apa Complex (Fig. 1A). In its eastern portion, it consists of 120 m of undeformed carbonates, designated as



the Tagatiya Guazu Formation (Fig. 1B). This unit contains an Ediacaran-age fossil assemblage including the index fossil *Cloudina*, *Corumbella*, and ichnofossils (Warren et al., 2011), and is composed of calcareous facies exhibiting massive, laminated to cross-stratified grainstones and heterolithic facies. Intercalated within these rocks are meter-thick beds of laminated microbial mats and domical thrombolitic biostromes, both associated with centimeter-thick beds of intraformational breccias. This facies association was deposited on a protected carbonate platform in a peritidal setting, probably in a shallow evaporitic lagoonal environment.

DESCRIPTION OF THE FOSSIL OCCURRENCES

Fossils of the Itapucumi Group include abundant fragments and many nearly complete specimens of *Cloudina* (Fig. 2A), as well as small fragments of *Corumbella*. *Cloudina* is found both as fragments in fine grainstone around thrombolitic biostromes (Fig. 1B), and as complete individuals in situ between thrombolitic domes (Warren et al., 2011). Similar associations of *Cloudina* with microbial buildups are also known in the Neoproterozoic of Namibia, Canada, and Oman (Conway-Morris et al., 1990; Grotzinger et al., 2000; Hofmann and Mountjoy, 2001). In Paraguay, *Corumbella* occurs as parautochthonous carbonized fragments (Figs. 2B–2D) together with intact *Cloudina* in a taphonomic setting different from that described in Brazil (Babcock et al., 2005). Differences in abundance and biostratigraphic signatures between these fossils in the Itapucumi Group are interpreted as reflecting differences in habitat, tegument composition, and taphonomic responses. *Cloudina* lived in shallow protected carbonate settings (Warren et al., 2011), whereas *Corumbella* occupied calm waters with terrigenous influx, to judge from its abundance in marls of the Tamengo Formation. In Paraguay, sedimentologic context suggests that these taxa occurred in environments with similar water depth, temperature, and salinity. *Corumbella* and *Cloudina* were buried as obrution deposits by fine calcareous sand, and their preservation indicates that under similar flow conditions, *Corumbella* shows a higher degree of disaggregation than *Cloudina*.

STRUCTURE OF THE CARAPACE OF *CORUMBELLA WERNERI*

Fossils of *Corumbella* in Paraguay occur as black, flattened fragments of tubes, 1.4–2.9 mm wide and 3.0–4.6 mm long. The carapace exhibits marked annulations, with approximately four ring-like segments per millimeter of length (Figs. 2B–2E). Scanning electron microscopy (SEM) revealed the original features of the carapace in *Corumbella*. The rings consist of an irregular, tight-fitting mosaic of polygonal plates (lamellae?), 10–120 μm in maximum

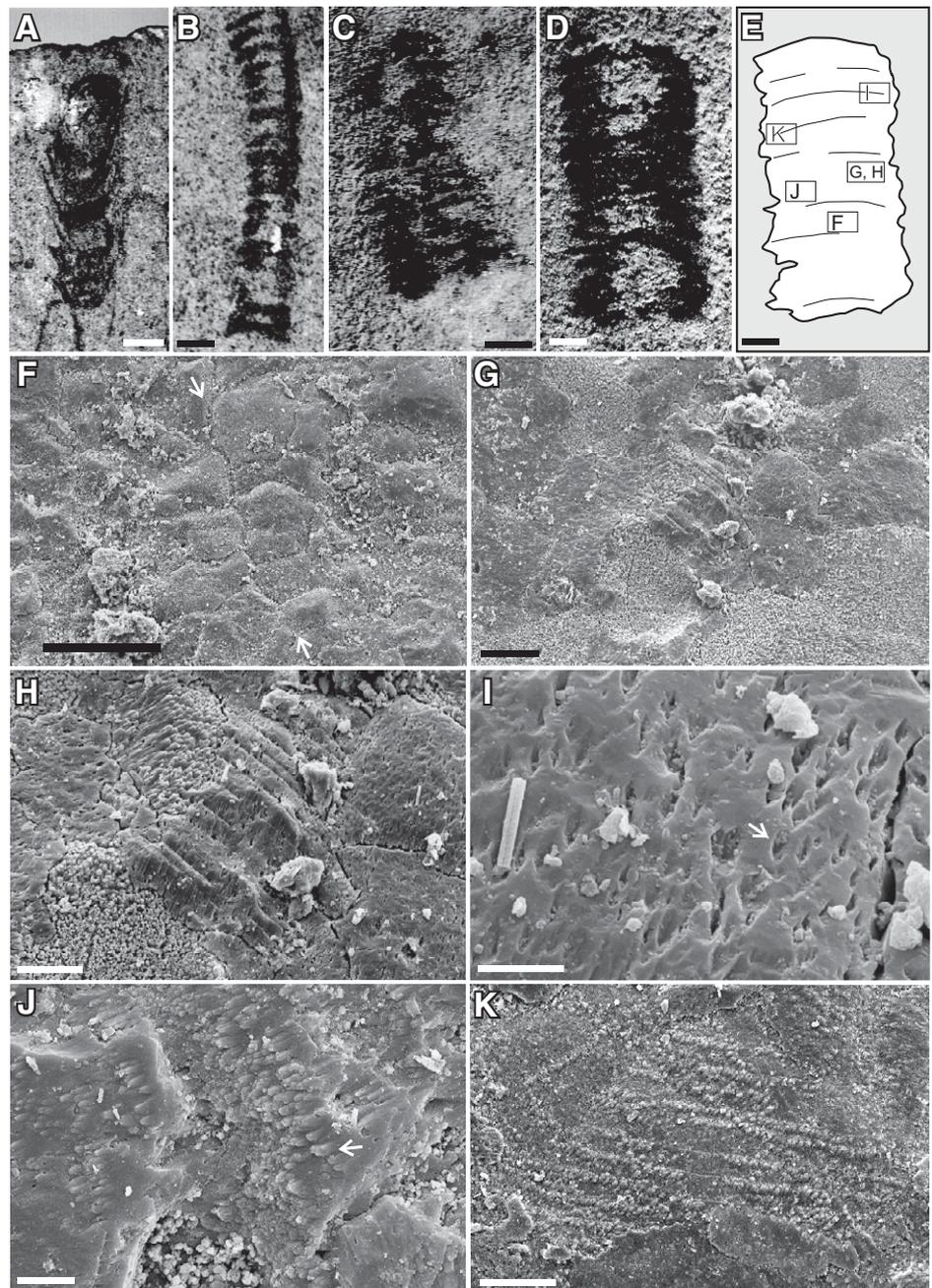


Figure 2. A: *Cloudina* sp. with typical cone-in-cone construction. B–D: Carbonized *Corumbella* carapaces. E: Sketch of specimen in D, showing locations of scanning electron microscopy images of *Corumbella* carapace in F to K. F, G: Views at different scales of mosaic of irregular polygonal plates in carapace of *Corumbella*. Arrows in F indicate principal suture. H: Polygonal plate mosaic with pores and papillae. I, J: Close-up views of papillae and pores. Arrows in I and J indicate pores and papillae, respectively. K: Detail of individual polygonal plate showing layered arrangement of papillae. Fossils are in Laboratory of Systematic Paleontology, Institute of Geosciences, São Paulo University, Brazil. Scale bars: 1 cm in C; 500 μm in A, B, D, and E; 100 μm in F; 20 μm in G, H, and K; 10 μm in I; 3 μm in J.

dimension and 5 μm thick (Fig. 2F). The mosaic is subtly divided by a principal suture, generally parallel to the annulations (Fig. 2F). The plates have straight edges with sharp contacts (Fig. 2G). The ultrastructure of *Corumbella* and the Ordovician scyphozoan *Sphenothallus* share similar patterns of organization. However, the lamellar microfabric seen in *Sphenothallus* (Van

Iten et al., 2005b) is not clearly developed in *Corumbella*. Moreover, unlike the lamellar surface of *Sphenothallus* sp. and the lamellar periderm of coronate scyphozoans (Chapman and Werner, 1972; Jarms et al., 2002), the plates in *Corumbella* are not smooth. Rather, they exhibit abundant small, shallow, elongate to elliptical pores, $\sim 1 \mu\text{m}$ across and 2 μm deep over most of

the surface (Figs. 2H and 2I) and domical structures, here designated as papillae (Fig. 2H and 2J). The papillae are bluntly conical to acicular, 3–15 μm long, and to 1 μm in diameter with rounded to flat terminations (Fig. 2J). Locally, groups of papillae are arranged in regularly spaced rows $\sim 3 \mu\text{m}$ apart (Fig. 2K).

Contrary to pores in thecae of Paleozoic conulariids (Kozłowski, 1968; Bischoff, 1978; Van Iten, 1992; Van Iten et al., 2005b, 2006b), pores in *C. wernerii* occur in closely spaced rows with some degree of organization (Fig. 2I). The papillae are similar in shape (but differ in their pattern of organization) to structures observed on rods of some Phanerozoic conulariids (Van Iten et al., 2006a; John et al., 2010). The pores may correspond to papillae on opposite sides of plates, and rather than representing ornamentation, may have had structural and/or physiological functions.

The precise composition of the carbonized carapace *Corumbella* is not known. Neither chitin nor other organic polymers have been identified, but SEM–energy dispersive spectrometry analysis of a gold-coated *Corumbella* carapace (Fig. 3A) revealed the presence of carbon, calcium, silicon, aluminum, and oxygen (Fig. 3B). The chemical test for phosphate (1 dg of ammonium molybdate in reaction with 1:1 HNO_3) was negative, reinforcing the hypothesis of a nonmineralized carapace.

DISCUSSION AND CONCLUSION

As in the thecae of the modern and fossil coronate scyphozoans *Stephanoscyphistoma* (Scyphozoa, Cnidaria, Hahn et al., 1982; Jarms et al., 2002) and *Olivoooides* (Zhao and Bengtson, 1999), respectively, deformation in *Corumbella* (bent,

folded, compressed) points to an originally flexible rather than brittle, and most likely organic, carapace. *Corumbella* thus secreted a long, narrow, flexible tube (like scyphopolyps) of nearly constant diameter, with transverse rings, possibly analogous to ribs in conulariids (Babcock et al., 2005). The multiple plates in the *Corumbella* carapace is an additional characteristic shared with conulariids and coronate scyphozoans.

Corumbella occurs within the *Cloudina* range zone; hence, it may be assigned to the terminal Ediacaran between 549 and 542 Ma (Grotzinger et al., 1995; Amthor et al., 2003). The fossil assemblage in the Itapucumi Group and others worldwide, containing metazoan fossils such as *Namacalathus*, *Sinotubulites*, and vendotaenids (Grotzinger et al., 2000; Hua et al., 2007), attest to increasing ecological and behavioral complexity at the end of the Proterozoic. Predation was certainly one of the determining factors in the intense diversification of the Metazoa at this time (Vermeij, 1989). Sessile predators like *Corumbella* developed other adaptations, besides nonmineralized exoskeletons, such as toxin-release systems for capturing prey and protection. The coexistence of in situ *Cloudina* and parautochthonous *Corumbella* indicates a more complex paleoecological scenario for Ediacaran carbonate platforms than previously thought, with increasing complexity of intraguild nets.

By the end of the Ediacaran Period, ocean water had become enriched in NaCl, with neutral pH and major ion composition similar to Phanerozoic seawater. Despite the relative increase of $\sim 36 \text{ meq/L}$ in Ca^{2+} ion concentration (Hardie, 2003), the advent of animal biomineralization ca. 550 Ma is probably more closely related to adaptations to varied carbonate envi-

ronments and the ecological pressure of predation, rather than to global geochemical modifications in seawater (Hua et al., 2007).

Corumbella figures as one of the few Precambrian animals capable of producing a fossilizable organic exoskeleton. Its cooccurrence with shelly fossils in the Itapucumi Group is further evidence that the acquisition of protective structures in metazoans at the end of the Ediacaran involved nearly synchronous processes of biomineralization and organic skeletogenesis. This scenario supports the hypothesis that the advent of skeletogenesis was probably related to increased predation pressure and conquest of new niches rather than to geochemical changes in environmental conditions.

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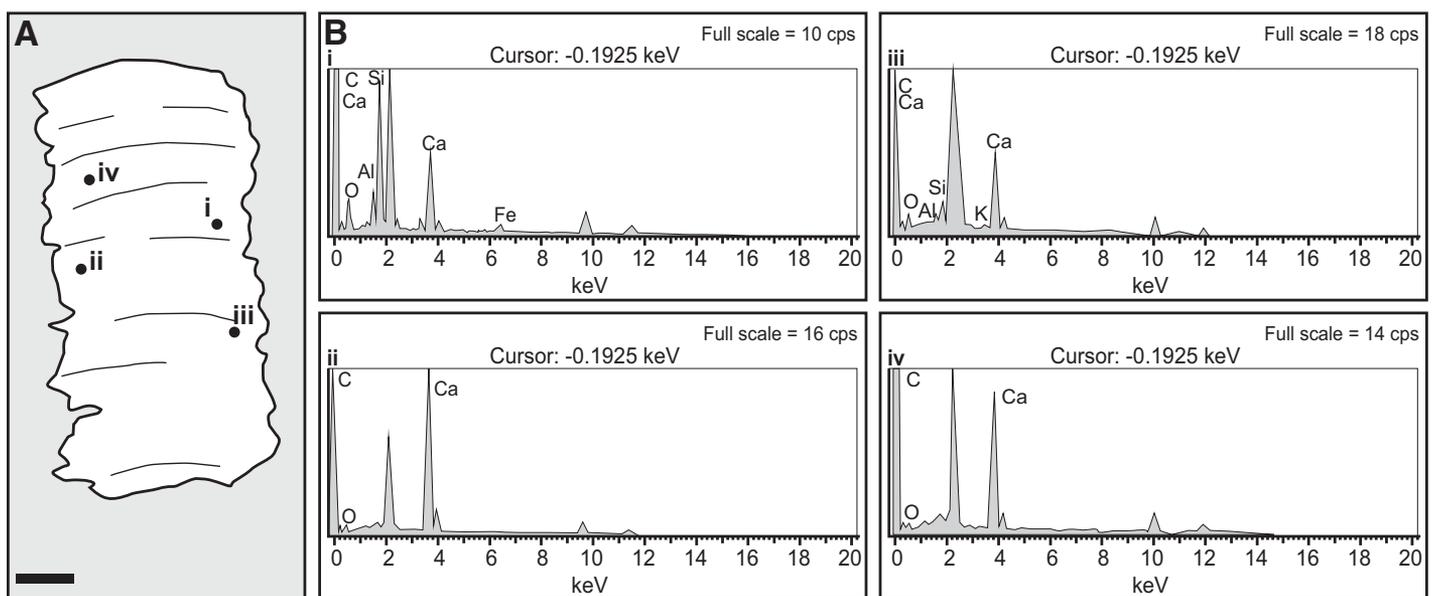


Figure 3. A: Location of scanning electron microscopy (SEM) and energy dispersive spectrometry (EDS) analyses (i–iv in B) in sample shown in Figure 2D. Scale bar = 500 μm . B: SEM-EDS element spectra of gold-coated carapace of *Corumbella*.

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