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PALEOBIOLOGIA DE CNDÁRIOS EDIACARANOS E PALEOZOICOS

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SUMÁRIO

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RESUMO

O Filo Cnidaria foi originado durante o Neoproterozoico. Estudos recentes de relógio molecular colocam a origem do Filo Cnidaria dentro do Período Criogeniano (cerca de 850-635 Ma), com a separação entre as duas subfamílias (Anthozoaria e Medusozoa) também ocorrendo durante este intervalo de tempo. No entanto, os macrofósseis cnidários mais antigos, todos medusozoa, ocorrem em rochas do Ediacarano tardio (cerca de 560-541 Ma). Os mais antigos cnidários fósseis conhecidos consistem em formas polipóides que não eram biomineralizadas ou fracamente assim. Um possível conulário pode primeiro ter aparecido na Formação Lantian (635-577 Ma), Sul da China. No entanto, uma nova ocorrência de *Paraconularia* sp., em associação com *Corumbella werneri,* no Ediacarano (c. 543 Ma), Formação Tamengo, Brasil, confirma a origem dos primeiros cifozoários no Neoproterozoico. Embora estes dados paleontológicos recentemente publicados tendem a corroborar a hipótese de que a Cnidaria tem uma história Neoproterozoica, o tempo de eventos de ramificação permanecem mal correlacionados com os resultados de análises de relógio molecular que indicam que Anthozoaria e Medusozoa podem ter se originado cerca de um bilhão anos atrás. Nesse sentido, é importante o estudo de detalhe da morfologia, das afinidades filogenéticas, da paleobiogeografia e das interpretações tafonômicas de cnidários fósseis, como conulários e *Corumbella.* As recentes interpretações filogenéticas indicam que, juntamente com os conulários, *Corumbella* fazia parte de um novo subgrupo dentro do Scyphozoa, os Paleoscyphozoa, um grupo irmão de Coronatae atuais. Nesse sentido, os paleocifozoários representariam os primeiros Scyphozoa conhecidos a partir do registro fóssil. Em relação à Família Conulariidae, a análise filogenética indicou que as subfamílias Conulariinae, Paraconulariinae e Ctenoconulariinae previamente reconhecidas não foram sustentadas como monofiléticas. Conulários são cnidários, extintos, com teca fosfática. Representantes desse grupo ocorrem em uma variedade de fácies sedimentares do Neoproterozoico ao Triássico. Conulários são característicos das faunas do Domínio Malvinocáfrico, sendo abundantes nas concentrações fossilíferas do Devoniano. Outras ocorrências são verificadas na Argentina, Peru, Paraguai, Uruguai e África do Sul. No Brasil, ocorrências de conulários são verificadas nas bacias do Amazonas, do Parnaíba e do Paraná e, mais recentemente, no Ediacarano, Formação Tamengo. Informações sobre a evidência de biomineralização em cnidários ediacaranos foram demonstradas no estudo com a carapaça de *Corumbella*. Corumbellídeos tinham uma teca flexível e provavelmente viviam com a sua parte basal ancorada no sedimento, assim como *Conotubus.* Quando considerados juntos, esses resultados sugerem que *Corumbella* foi um dos primeiros cnidários a construir um exoesqueleto, empregando uma microfábrica lamelar semelhante aos conulários. O aspecto de potencial organismo biomineralizador contribui para o entendimento das

características tafonômicas desse grupo e proporciona o entendimento sobre as condições paleoambientais em que viviam. A identificação de um horizonte de fragmentos de *C. werneri,* juntamente com fragmentos de *Cloudina lucianoi* pode contribuir para a indicação de limite entre parassequências. De fato, os dados tafonômicos são um importante complemento às análises estratigráficas, especialmente como evidência independente para as interpretações paleoambientais. Além disso, os dados tafonômicos contribuem também para o melhor entendimento da paleobiologia desses grupos de cnidários extintos, mostrando ser essa ciência ferramenta indispensável à análise do registro sedimentar.

Palavras-Chave: Cnidaria, Ediacarano, Conulatae, *Corumbella*, tafonomia.

ABSTRACT

The Cnidaria Phylum was originated during the Neoproterozoic. Recent molecular clock studies place the origin of the Cnidaria Phylum within the Cryogenic Period (about 850-635 Ma), with the separation between the two subfamilies (Anthozoaria and Medusozoa) also occurring during this time interval. However, the oldest cnidarian macrofossils, all medusozoa, occur in late Ediacaran Period rocks (about 560-541 Ma). The earliest known fossil cnidarians consist of polypoid forms that were non-biomineralized or weakly so. A possible conulariid may have first appeared (635-577 Ma) in the Lantian Formation, Southern China. However, a new occurrence of *Paraconularia* sp., in association with *Corumbella werneri*, in Ediacaran (c. 543 Ma), Tamengo Formation, Brazil, confirms the origin of the first Scyphozoa in the Neoproterozoic. Although these recently published paleontological data tend to corroborate the hypothesis that Cnidaria has a Neoproterozoic history, the time of branching events remain poorly correlated with the results of molecular clock analyzes that indicate that Anthozoaria and Medusozoa may have originated about one billion years ago. In this sense, it is important to study the detail of morphology, phylogenetic affinities, paleobiogeography and taphonomic interpretations of fossil cnidarians, such as conulariids and *Corumbella*. Recent phylogenetic interpretations indicate that, along with the conulariids ones, *Corumbella* was part of a new subgroup within the Scyphozoa, the Paleoscyphozoa, a current Coronatae sister group. In this sense, the paleoscyphozoans would represent the first Scyphozoa known from the fossil record. Regarding the Family Conulariidae, the phylogenetic analysis indicated that previously recognized Conulariinae, Paraconulariinae and Ctenoconulariinae subfamilies were not supported as monophyletic. Conulariids are extinct cnidarians with phosphate tecae. Representatives of this group occur in a variety of sedimentary facies from Neoproterozoic to Triassic. Conulariids are characteristic of the faunas of the Malvinocapric Realm, being abundant in the fossiliferous concentrations of the Devonian. Other occurrences are verified in Argentina, Peru, Paraguay, Uruguay and South Africa. In Brazil, occurrences of conulariids are verified in the basins of Amazonas, Parnaíba and Paraná and, more recently, in Ediacaran rocks of the Tamengo Formation. Information on the evidence of biomineralization in Ediacaran cnidarians was demonstrated in a *Corumbella* carapace study. Corumbellidae had a thick but flexible teak and probably lived with their basal part anchored in the sediment as well as *Conotubus*. When considered together, these results suggest that *Corumbella* was one of the first cnidarians to construct an exoskeleton, using a lamellar microfabric similar to the conulariids. The aspect of potential biomineralizing organism contributes to the understanding of the taphonomic characteristics of this group and provides an understanding of the paleoenvironmental conditions in which they lived. The identification of a horizon of fragments

of *C. werneri*, together with fragments of *Cloudina lucianoi* can contribute to the indication of the boundary between parassequences. In fact, taphonomic data are an important complement to stratigraphic analyzes, especially as independent evidence for paleoenvironmental interpretations. Moreover, the taphonomic data also contribute to a better understanding of the paleobiology of these groups of extinct cnidarians, showing that this science is an indispensable tool for the analysis of the sedimentary record.

Key words: Cnidaria, Ediacaran, Conulatae, *Corumbella*, taphonomy.

APRESENTAÇÃO

Essa Tese de Livre-Docência seguiu as normas especificadas no Edital de concurso de títulos e provas para a obtenção do Título de Livre-Docente no Departamento de Geologia Sedimentar e Ambiental, IGc/USP, sendo apresentada em forma de texto sumarizando parte da obra da candidata. Dessa forma, o documento apresentado está estruturado em um conjunto de artigos e capítulo de livro já publicados, bem como um artigo submetido e um texto inédito. A partir dos dados obtidos é apresentado um panorama sobre as pesquisas nos últimos anos a respeito dos cnidários ediacaranos e paleozoicos e as suas implicações paleoecológicas e paleoevolutivas.

No capítulo 1 é apresentado um artigo, publicado em 2014, sobre a Origem e diversificação de Cnidaria: Neoproterozoico ao Cambriano Inferior (*Origin and Early Diversification of the Phylum Cnidaria Verrill: Apparent Convergence of Molecular Phylogenies and the Fossil Record. Palaeontology, Frontiers in Palaeontology- Special Issue).* Esse artigo apresenta uma revisão sobre as ocorrências de cnidários no Neoproterozoico, incluindo fósseis brasileiros, bem como uma abordagem sobre a implicação dos cndários fósseis na filogenia do grupo.

A descoberta de um novo fóssil de *Paraconularia* sp. no Neoproterozoico do Brasil (Grupo Corumbá) e as suas inferências filogenéticas e evolutivas são apresentadas no Capítulo 2. Além disso, a análise filogenética dos conulários e a discussão das afinidades desse grupo junto aos Cnidaria e as implicações das ocorrências dos conulários na diversificação e paleogeografia durante o Paleozoico também são retratadas. Os resultados desses estudos são apresentados em um capítulo de livro, publicado em 2016 (*Origin and Early Diversification of Phylum Cnidaria: Key Macrofossils from the Ediacaran System of North and South America. In: S. Goffredo, Z. Dubinsky. (Org.). The Cnidaria, Past, Present and Future. 1ed.Cham: Springer International Publishing AG*), em um artigo de 2008 (*Cladistic analysis of the suborder Conulariina Miller and Gurley, 1896, Cnidaria, Scyphozoa; Vendian-Triassic, Palaeontology*) e em um artigo de 2015 (*Conulários do Devoniano do Brasil: importância paleobiogeográfica. Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais*).

O capítulo 3 inclui dois artigos sobre a paleoecologia, morfologia e afinidades filogenéticas de *Corumbella werneri*, um cnidário ediacarano que apresenta relações filogenéticas com conulários. Um dos artigos, foi publicado em 2015 (*Insights into the skeletonization, lifestyle, and affinity of the unusual ediacaran fossil* Corumbella. *Plos One*). O segundo artigo, submetido, aborda mais especificamente as relações filogenéticas de *Corumbella* entre os Cnidaria (*Phylogenetic position of the Ediacaran paleoscyphozoan fossil* Corumbella, *Corumbá Group, Brazil, among cnidarians*).

No capítulo 4, é apresentado um texto de dados inéditos sobre cnidarios ediacaranos como possíveis indicadores de limites estratigráficos. Esse texto foi derivado de uma dissertação de Mestrado, sob minha orientação, e faz parte de um artigo inédito que está sendo elaborado em conjunto com pesquisadores que abordarão a sedimentologia e estratigrafia de sequências das formações Bocaina e Tamengo (Grupo Corumbá).

Por fim, são apresentadas as principais conclusões e as perspectivas futuras sobre as pesquisas com cnidários fósseis, além de outras importantes novas ocorrências fósseis no Grupo Corumbá.

CAPÍTULO 1.

Origem e diversificação de Cnidaria: Neoproterozoico ao Cambriano Inferior

1.1. VAN ITEN, H.; MARQUES, A.C; LEME, J.M.; PACHECO, M.L.A.F; SIMÕES, M.G. 2014. Origin and Early Diversification of the Phylum Cnidaria Verrill: Apparent Convergence of Molecular Phylogenies and the Fossil Record. Palaeontology, Frontiers in Palaeontology (Special Issue) 1-14.

O Filo Cnidaria, um grupo monofilético de eumetazoários diploblásticos, consiste em cinco classes, nomeadamente Anthozoa (Kayal & Lavrov 2008, Kayal *et al.*, 2013) e as quatro classes de medusozoários - Cubozoa, Hydrozoa, Scyphozoa e Staurozoa (Daly *et al.*, 2007; este artigo, Fig. 1). A sinapomorfia de cnidários existentes é a presença de cnidae (Marques & Collins, 2004), que são organelas celulares microscópicas com diversas funções biológicas, incluindo a captura de defesa e presas. A anatomia relativamente simples e a organização de tecido de cnidários provavelmente surgiram precocemente durante a evolução animal (Dunn *et al.*, 2008; Ryan *et al.*, 2013), e há muito se pensou que o filo se originou e se diversificou em seus principais subclados durante o Proterozoico (ver, por exemplo, Shu *et al.*, 2014 e referências citadas). As relações filogenéticas entre as classes de cnidários historicamente foram sujeitas a interpretações divergentes, tendo duas hipóteses mais amplamente assumidas (1) que os cnidários portadores de septos gástricos, nomeadamente antozoários, cubozoários e cifozoários, formam um grupo monofilético que exclui hidrozoários; e (2) que os cnidários que exibem um estágio de vida medusóide, nomeadamente cubozoários, hidrozoários, cifozoários e estaurozoários, formam um grupo monofilético (o subfilo Medusozoa) que exclui os antozoários (Brusca e Brusca, 2003). No presente trabalho, parece que a última hipótese, baseada em evidências morfológicas e moleculares comparativas, é o paradigma preferido. Este artigo sintetiza evidências moleculares e paleontológicas novas sobre o momento da origem da Cnidaria e suas classes e discute hipóteses filogenéticas alternativas para o táxon. Quanto ao registro fossilífero, nos concentramos em descobertas no intervalo Ediacarano-Cambriano. Conforme discutido no artigo, alguns desses achados constituem a evidência paleontológica mais forte até agora documentada para a existência de cnidários coronados durante o Neoproterozoico.

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FRONTIERS IN PALAEONTOLOGY

ORIGIN AND EARLY DIVERSIFICATION OF THE PHYLUM CNIDARIA VERRILL: MAJOR DEVELOPMENTS IN THE ANALYSIS OF THE TAXON'S PROTEROZOIC–CAMBRIAN HISTORY

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Abstract: Diploblastic eumetazoans of the phylum Cnidaria originated during the Neoproterozoic Era, possibly during the Cryogenian Period. The oldest known fossil cnidarians occur in strata of Ediacaran age and consist of polypoid forms that were either nonbiomineralizing or weakly so. The oldest possible anthozoans, including the genus *Ramitubus*, may be related to tabulate corals and occur in the Doushantuo Lagerstätte (upper Doushantuo Formation, South China), the age of which is poorly constrained (approximately 585 Ma?). Conulariid scyphozoans may first appear as early as 635–577 Ma (Lantian Formation, South China). A definite conulariid, most similar to Palaeozoic species assigned to the genus *Paraconularia*, occurs in association with the possible scyphozoan, *Corumbella werneri*, in the latest Ediacaran (*c.* 543 Ma) Tamengo Formation of Brazil. Basal Cambrian (*c.* 540 Ma) phosphorites in the upper Kuanchuanpu Formation (South China) yield solitary polyps of the oldest probable anthozoan (*Eolympia pediculata*), which appears to have been a stem hexacorallian. This same formation contains fossils interpreted by some authors as pentaradial cubozoan polyps; however, both the oldest known cubozoans and the oldest hydrozoans, all medusae, may actually occur in the Cambrian (Series 3, *c.* 505 Ma) Marjum Formation (Utah, USA). Although these recently published palaeontological data tend to corroborate the hypothesis that Cnidaria has a relatively deep Neoproterozoic history, the timing of major internal branching events remains poorly constrained, with, for example, the results of some molecular clock analyses indicating that the two cnidarian subphyla (Anthozoaria and Medusozoa) may have originated as many as one billion years ago. Further progress towards elucidating the evolution and early fossil record of cnidarians may accrue from: (1) an intensive search for phosphatized soft parts in possible anthozoans from the Ediacaran Doushantuo Formation; (2) an expanded search for Ediacaran conulariids; and (3) additional detailed analyses of the taphonomy and preservation of Ediacaran and Cambrian cnidarians, including possible pentaradial cubozoan polyps from the Fortunian upper Kuanchuanpu Formation.

Key words: Cnidaria, evolution, Neoproterozoic, Ediacaran, Cambrian, molecular phylogenetics.

PHYLUM Cnidaria Verrill, a monophyletic group of diploblastic eumetazoans, consists of five classes, namely Anthozoa (of disputed monophyly; Kayal and Lavrov 2008; Kayal *et al.* 2013) and the four medusozoan classes – Cubozoa, Hydrozoa, Scyphozoa and Staurozoa (Daly *et al.* 2007; this paper, Fig. 1). The synapomorphy of extant cnidarians is

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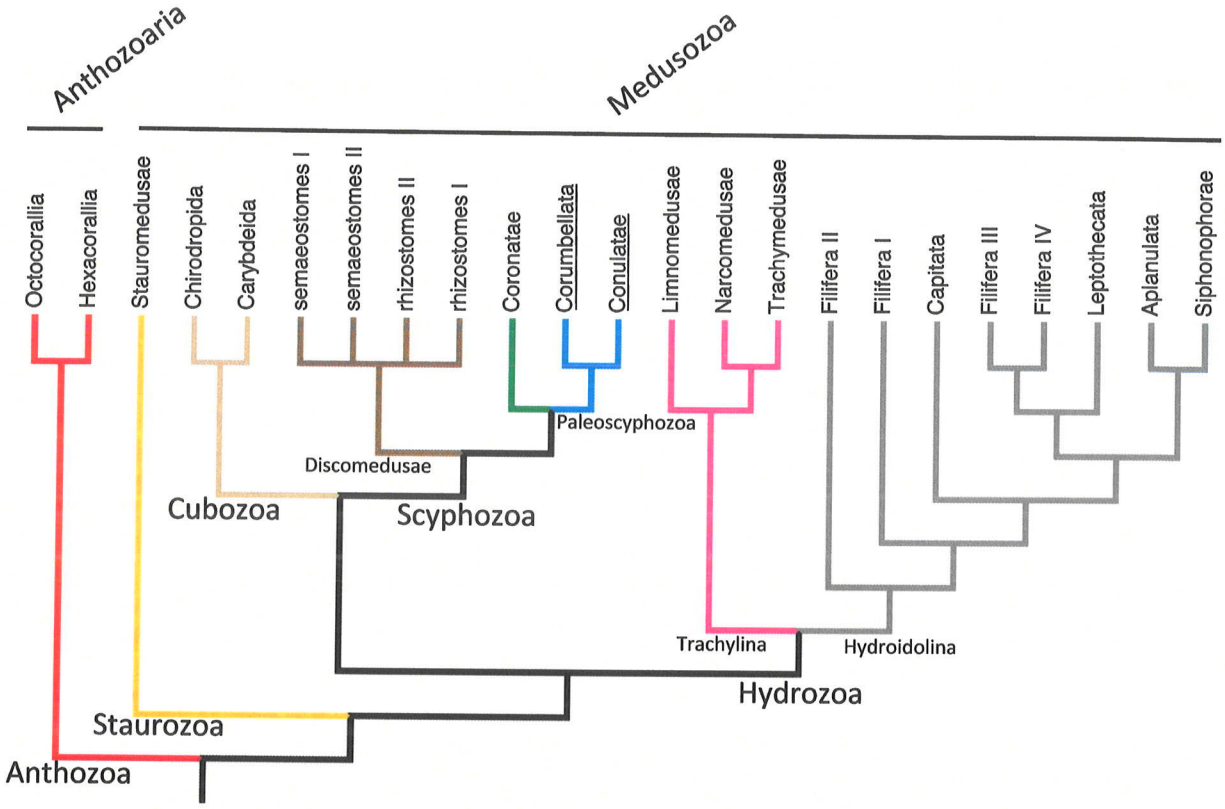


FIG. 1. Phylogenetic hypothesis for the phylum Cnidaria, showing an interpretation of relationships among major groups of cnidarians constructed by combining the previously published phylogeny of Collins *et al.* (2006), adopted here as the basic framework, with those of Cartwright *et al.* (2008), Collins *et al.* (2008), Bayha *et al.* (2010) and Bentlage *et al.* (2010) (for relationships among extant Hydroidolina, Trachylina and Scyphozoa). Placement of the two fossil groups (underlined), united here in a clade termed Paleoscyphozoa, based on the cladograms of Van Iten *et al.* (2006*a*) (for Conulatae) and Pacheco *et al.* (submitted; for Corumbellata, composed of the genus *Corumbella*).

the presence of cnidae (Marques and Collins 2004), which are microscopic cell organelles having diverse biological functions including defence and prey capture. The relatively simple anatomy and tissue organization of cnidarians presumably arose early during animal evolution (e.g. Dunn *et al.* 2008; Ryan *et al.* 2013), and it has long been thought that the phylum originated and diversified into its major subclades during the Proterozoic Eon (see e.g. Shu *et al.* 2014 and references cited therein). Phylogenetic relationships among the cnidarian classes historically have been subject to divergent interpretations, with the two most widely held hypotheses having been: (1) that cnidarians bearing gastric septa, namely anthozoans, cubozoans and scyphozoans, form a monophyletic group that excludes hydrozoans; and (2) that cnidarians exhibiting a medusoid life stage, namely cubozoans, hydrozoans, scyphozoans and stauromedusans, form a monophyletic group (the subphylum Medusozoa) that excludes anthozoans (Brusca and Brusca 2003). At present, it appears that the latter hypothesis, based both on comparative morphological and molecular evidence, is the preferred paradigm.

This article synthesizes new and particularly noteworthy molecular and palaeontological evidence bearing on the timing of the origin of Cnidaria and its classes and discusses alternative phylogenetic hypotheses for the taxon. Concerning the fossil record, we focus on major discoveries in the Ediacaran–Cambrian interval. As discussed below, some of these finds constitute the strongest palaeontological evidence thus far documented for the existence of crown group cnidarians during Neoproterozoic times.

PHYLOGENETIC RELATIONSHIPS

Relationships to other metazoan phyla

The phylogenetic position of Cnidaria within the metazoan tree of life, as well as the basal evolution of metazoans, appears to be far from settled (Dohrmann and Wörheide 2013). Classical hypotheses, for example, Coelenterata (Cnidaria as the sister group of Ctenophora),

Diploblastica vs Bilateria, and Ctenophora as the sister group of Bilateria, find diminished corroboration in recent data (e.g. Ryan *et al.* 2013), which suggest instead that Cnidaria is the sister group of Bilateria and that Ctenophora is the sister group of the rest of Metazoa. This hypothesis apparently is supported both by the presence of developmental genes and by phylogenomic analysis (see Ryan *et al.* 2013 and references cited therein). In short, then, fundamental questions of basal metazoan phylogeny and evolution remain open, but it is evident that a better understanding of cnidarians is of paramount importance to understanding the evolution of metazoans in general.

Within-group relationships

Regarding phylogenetic relationships among major groups within Cnidaria, early hypotheses were inadequate because they were based on constraining scenarios (cf. Marques and Collins 2004) and/or taxonomical convenience (cf. Marques 2001). More recently, methodologically sound, objective seminal analyses have appeared, based either on DNA (e.g. Collins 2000) or on morphology (Marques 2001), but these studies still contain insufficiencies, mainly in taxon sampling (partial coverage of component taxa) and in sampling of characters (use of a single molecular marker such as the small subunit of the nuclear ribosome). The first comprehensive phylogenetic analysis combining morphological and natural history data for the subphylum Medusozoa, including the fossil group Conulatae, established the taxonomical framework of the five cnidarian classes that is widely accepted today (Marques and Collins 2004). However, Marques and Collins (2004) misinterpreted some of the characters of Conulatae, and their analysis was revised accordingly (Van Iten *et al.* 2006*a*). Concomitantly, a more robust DNA analysis, based on both the large (LSU) and small (SSU) subunits of the nuclear ribosome, was published by Collins *et al.* (2006), providing strong corroboration of the morphological topology of Van Iten *et al.* (2006*a*).

Less inclusive relationships among taxa were subsequently refined, both by adding taxa (viz taxa in Hydroidolina by Cartwright *et al.* 2008; taxa in Trachylina by Collins *et al.* 2008; taxa in Scyphozoa by Bayha *et al.* 2010; and taxa in Cubozoa by Bentlage *et al.* 2010) and by adding characters (viz incorporation of mitochondrial 16S rDNA in the analyses of Cartwright *et al.* 2008; Collins *et al.* 2008; Bentlage *et al.* 2010). Interestingly, certain traditionally accepted groups either presented disputable monophyly (viz Semaeostomeae and Rhizostomeae; Bayha *et al.* 2010) or were not recovered as monophyletic at all (viz 'Anthoathecata'; Cartwright *et al.* 2008). Several other classical groups were corroborated as monophyletic, but certain basic relationships remain unclear. Be that as it may, these studies have advanced our understanding of cnidarian evolution substantially and enable us here to present a revised interpretation of cnidarian phylogeny (Fig. 1).

Finally, recent mitogenomic analyses (Kayal *et al.* 2013, fig. 2; Osigus *et al.* 2013, fig. 3) have corroborated the monophyly of many cnidarian groups but paradoxically have also resulted in strongly contrasting views of cnidarian evolution. For instance, these studies reject the monophyly of Anthozoa (by associating Octocorallia with Medusozoa) and Scyphozoa (Coronatae are not related to Discomedusae) and reject Staurozoa as the sister group to all the other medusozoans; but support the sister group relationships of Staurozoa + Cubozoa and Hydrozoa + Discomedusae (Fig. 1). Even Cnidaria was found to be paraphyletic in one of the analyses (Osigus *et al.* 2013). However, we believe that the results of the mitogenomic analyses are not conclusive, as they are based on limited taxon sampling and are further handicapped by the inappropriateness of part of the mitogenome for addressing the phylogenetic questions involved (cf. Philippe *et al.* 2011). Data from phylogenomics are even scarcer, being restricted to one species for Scyphozoa, four for Hydrozoa and eight for Hexacorallia (see Ryan *et al.* 2013).

Timing of major branching events

Molecular analyses have also yielded divergent results concerning the times of origin of the major cnidarian groups, with the most recent studies (e.g. Erwin *et al.* 2011; Park *et al.* 2012) indicating that cnidarian taxa may be substantially older than currently suggested by their known fossil records (Fig. 2). The analysis of Erwin *et al.* (2011), based on seven different housekeeping genes from 118 metazoan taxa, suggests a Cryogenian origin for Cnidaria and an Ediacaran origin at least for Anthozoa. The study of Park *et al.* (2012), which focuses on the mitogenomes of anthozoans and scyphozoans, concludes that Cnidaria originated 819–686 Ma, Medusozoa 670–571 Ma and ancient anthozoan groups such as Hexacorallia 684–544 Ma. Studies based on other molecular markers place the origin of Cnidaria as far back as over one billion years ago (Waggoner and Collins 2004; Cartwright and Collins 2007; see also details in Park *et al.* 2012). All of these inferences are fairly conservative in their calibrations of the molecular clock, and recent fossil data such as those of Van Iten *et al.* (2013) for the Ediacaran System were not yet available then. Therefore, it is entirely plausible that the origin and early diversification of the major cnidarian clades occurred well before the Cambrian explosion, during the Ediacaran or even the Cryogenian periods.

EDIACARAN–CAMBRIAN FOSSIL RECORD

A number of fossil taxa of Ediacaran age, including many members of the classical soft-bodied Ediacaran biota, have been interpreted as cnidarian medusae or polyps (e.g. Glaessner and Wade 1966; see also summary in Young and Hagadorn 2010) or as diploblastic-grade metazoans possibly allied with cnidarians (cnidariomorphs; Kouchinsky *et al.* 2012). However, similarities between medusa-like fossils and extant jellyfish probably are nonhomologous (Young and Hagadorn 2010), and moreover, some of these fossils were holdfast structures originally embedded in bottom sediment (Gehling and Droser 2012; Laflamme *et al.* 2012). Likewise, similarities between the benthic rangeomorphs and extant colonial anthozoans or hydrozoan polyps are superficial (e.g. Narbonne 2004; Antcliffe and Brasier 2007; Brasier and Antcliffe 2009). *Eoporpita* from late Ediacaran strata of north-western Russia (White Sea region) has been interpreted both as a medusa and as a solitary anemone-like polyp (Wade 1972; see also Fedonkin *et al.* 2007), but except for an apparent radial symmetry we see no reason to interpret it as a cnidarian, much less as a member or close relative of a particular cnidarian clade. Two additional genera, *Cloudina* and *Namacalathus*, have been interpreted as calcareous cnidariomorphs (Kouchinsky *et al.* 2012), but how they might have been related phylogenetically to extant groups has not been specified. Be that as it may, recently discovered Ediacaran and Cambrian fossils, summarized by classes below, contribute important new information bearing on cnidarian origins and evolution. The stratigraphical occurrences of these fossil taxa are shown in Figure 2.

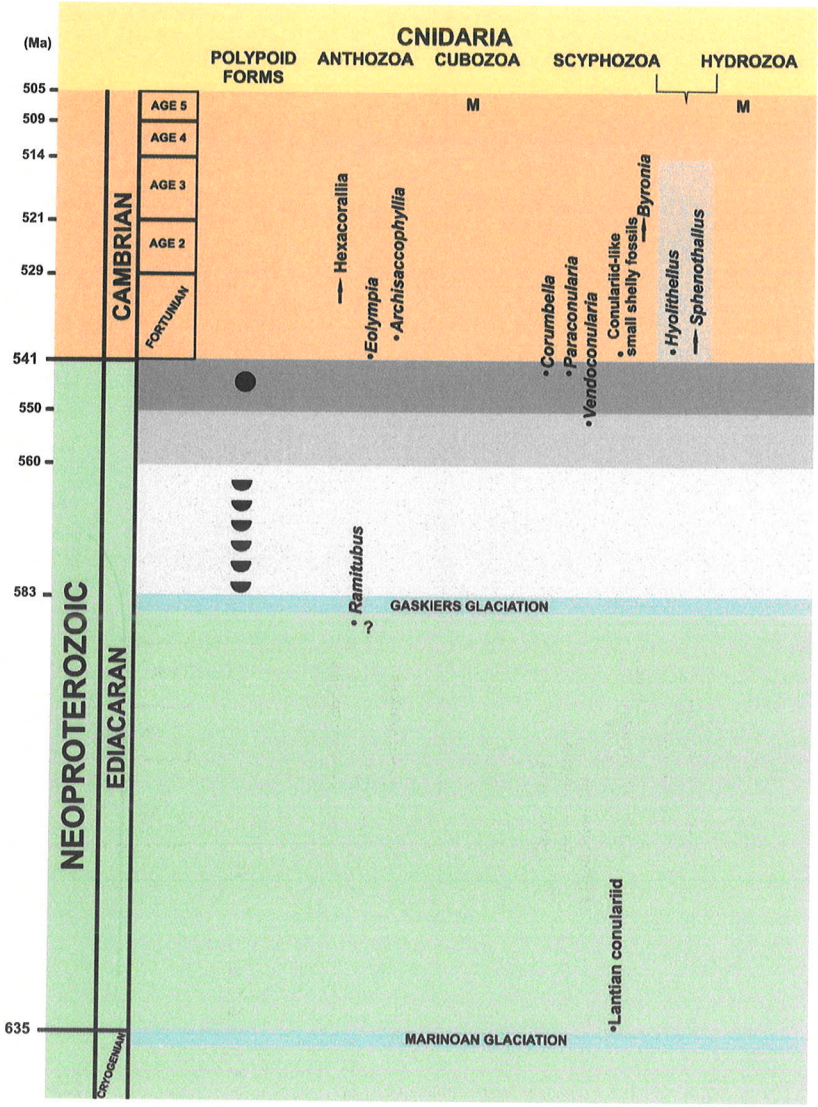


FIG. 2. Stratigraphical distributions of key fossil genera and other cnidarian groups, arranged by classes, discussed in the present paper. The letter M in the uppermost part of the chart (Cambrian Age 5) stands for medusae. The Ediacaran time intervals 583–560, 560–550 and 550–541 Ma have been equated, respectively, with the Avalon, White Sea and Nama fossil assemblages (e.g. Narbonne *et al.* 2012); however, Grazhdankin (2014) has shown that these faunal groupings actually are biofacies and should not be used as formal chronostratigraphical units.

Anthozoa

Possible Ediacaran anthozoans. Dolomitic phosphorites in Unit 4 of the Doushantuo Formation (Weng'an, Guizhou Province, South China) host the extraordinary Weng'an biota, which includes possible metazoan eggs and embryos, and skeletonized eumetazoans (Budd 2008; Liu *et al.* 2008; Shu *et al.* 2014). The age of this Lagerstätte is poorly constrained but may lie close to 585 Ma (i.e. prior to the Gaskiers glaciation; see e.g. Liu *et al.* 2008, text-fig. 1 and Narbonne *et al.* 2012, fig. 18.2). Among the putative eumetazoans are four genera of possible anthozoans: *Crassitubus*, *Quadratitubus*, *Ramitubus* and *Sinocyclocyclicus* (Xiao *et al.* 2000; Liu *et al.* 2008). All four taxa consist of a very small (diameter <1 mm), cylindrical or tetragonal tubule exhibiting closely spaced, internal transverse cross-walls that may be complete, incomplete or perforated. Specimens found thus far are fragmentary and appear to have been nonbiomineralizing (their ultrastructure has not been determined but may have been lamellar). In *Ramitubus*, the outer surface of the tubule is annulated, and some specimens exhibit multiple dichotomous branching. Additionally, some tubules occur in clusters and may have been colonial. Liu *et al.* (2008) compared *Ramitubus* and the other three genera with filamentous cyanobacteria, algae and polypoid cnidarians, concluding that they were neither bacteria nor algae, nor (apparently) any other organisms save possibly anthozoans. To be sure, internal cross-walls that may be incomplete or perforate also occur in the calicles of certain chaetetid-type sponges (e.g. Vacelet 1991); however, at least some chaetitids produce spicules, and such structures apparently are not present in the Doushantuo tubules (see the photomicrographs in Liu *et al.* 2008). Although features that can be homologized with the septa, mural pores or dissepiments of Phanerozoic corals also are absent, Liu *et al.* (2008) concluded nevertheless that the external transverse annulations, dichotomous branching and internal cross-walls of *Ramitubus* are most similar, respectively, to the external growth lines, mode of asexual reproduction (axial increase) and tabulae of tabulate corals.

If any of the genera reviewed above are in fact anthozoans or stem anthozoans, then their presence in the Doushantuo Lagerstätte suggests that this group splits from its most recent common ancestor with the medusozoans prior to 580 Ma.

Cambrian (Fortunian Stage) anthozoans. Numerous species of calcareous anthozoans of the subclass Hexacorallia, many of them bearing septa and/or tabulae, have been discovered in Terreneuvian ('early' Cambrian) strata throughout the world (see Hicks 2006 and references cited therein). Most recently, exquisitely preserved phosphatized specimens of the earliest definitely known anthozoan, probably a hexacorallian or stem taxon of this group, have been recovered from basal Cambrian (*c.* 540 Ma) strata in the upper part of the Kuanchuanpu Formation (Shaanxi Province, South China; Han *et al.* 2010; see also see Han *et al.* 2013, fig. 6). *Eolympia pediculata* is a minute (<1 mm long), solitary soft-bodied polyp exhibiting 18 mesenteries, including bilaterally arranged directive mesenteries, as well as 18 tentacles and a stalk-like pedicle. Computer-aided microtomographic analysis has revealed additional anatomical structures within the body, including lumens in the tentacles, a gastric cavity and an actinopharynx.

Yet another minute polyp from the upper Kuanchuanpu Formation, first described by Steiner *et al.* (2004) and interpreted by these authors as an anthozoan, probably is a scyphozoan polyp undergoing polydisc strobilation (see Han *et al.* 2010, fig. S1).

Younger (Cambrian Age 3) strata in the Qiongzhusi Formation (Yunnan Province, South China), which hosts the Chengjiang Lagerstätte, yield *Archisaccophyllia kunmingensis*, a solitary soft-bodied polyp most similar to extant actiniarians (Hou *et al.* 2005; see also Lei *et al.* 2014). Well-preserved specimens, which average about 20 mm long, exhibit features interpretable as a single row of 12 unbranched tentacles, an oral disc with oval mouth and pharynx, longitudinal mesenteries, a pedal disc and possible acontia.

At present then, exceptionally preserved, (originally) soft-bodied anthozoan fossils recently discovered in Fortunian strata of South China indicate that the hexacorallians split from their most recent common ancestor with the octocorallians no later than earliest Cambrian times (about 540 Ma).

Cubozoa

The Cambrian (Series 3) Marjum Formation (Utah, USA; *c.* 505 Ma) has yielded exceptionally preserved specimens of probable crown group jellyfish (Cartwright *et al.* 2007; Young and Hagadorn 2010), including possible box jellies or cubozoans (Cartwright *et al.* 2007, figs 10, 11). Additionally, the basal Cambrian upper Kuanchuanpu Formation has yielded superbly preserved ontogenetic series, including embryonic stages and hatchlings that have been interpreted most recently as minute cubozoans (Dong *et al.* 2013; Han *et al.* 2013; Yasui *et al.* 2013). These fossils, generally referred to as *Olivooides multisulcatus* or *Punctatus emeiensis*, exhibit a pentaradial symmetry, although similar fossils from the same formation have been described as tetramerous (viz *Quadrapyrgites*; cf. Li *et al.* 2007; Liu *et al.* 2009). Chen (2004) and Steiner *et al.* (2010) assigned the pentaradial specimens to

Echinodermata or Scalidophora, respectively, but these two hypotheses have since been rejected (Dong *et al.* 2013; Han *et al.* 2013). A third hypothesis that these fossils are related to Cnidaria (Bengtson and Zhao 1997; Zhao and Bengtson 1999) has received substantial attention, based on new data from environmental scanning electron microscopy, conventional scanning electron microscopy and synchrotron radiation X-ray tomographic microscopy. Zhao and Bengtson (1999) proposed that these fossils represent crown group scyphozoans, mainly because of their internal anatomy and the presence of a putative budding ephyra in their life cycle. However, Bengtson and Zhao (1997) proposed that these fossils represent a unique lineage potentially unrelated to Cnidaria, differing from extant cnidarians in having a spacious body cavity separating ectoderm from endoderm, an anatomy that is incompatible with a cnidarian affinity (Yasui *et al.* 2013). Most recently, Dong *et al.* (2013) argued that the pentamerous specimens represent crown group scyphozoans, based both on their internal anatomy and on the putative presence of a budding ephyra in their life cycle. Alternatively, and based again on features of the internal anatomy, Han *et al.* (2013) proposed that these fossils were pentaradial cubozoans having a life cycle that differed from that of extant species. However, we find it difficult to reconcile current knowledge of the anatomy and life history of extant cubozoans, all of which show tetrameral radial symmetry, with this hypothesis (see also discussion below).

Hydrozoa

Putative fossil chondrophores (family Porpitidae) have been reported from Ediacaran and Cambrian strata at various localities (see Cartwright *et al.* 2007 and references cited therein). Also, at least some of the polyp-like fossils (e.g. *Sphenothallus*) from Terreneuvian strata may be thecate hydrozoans (Van Iten *et al.* 1992). Most recently, possible narcomedusan medusae, with preserved tentacles that insert above the umbrella margin, have been recovered from the Marjum Formation (Young and Hagadorn 2010). The oldest probable hydrozoan medusae, belonging possibly to the extant orders Anthomedusae or Leptomedusae, occur in the Late Ordovician (late Katian) William Lake Lagerstätte (Stony Mountain Formation, Williams Member) of Manitoba, Canada (Young *et al.* 2007; Young and Hagadorn 2010).

Scyphozoa

Possible early Ediacaran conulariid. Black shales in Member II of the Ediacaran Lantian Formation (southern Anhui Province, South China) host the oldest (635–577 Ma) known assemblage of morphologically complex fossil eukaryotes (Shu *et al.* 2006; Yuan *et al.* 2011). Preserved as carbonaceous compressions, the Lantian biota is dominated by probable macroscopic algae (Yuan *et al.* 2011, fig. 2) but may also include the oldest cnidarians or cnidarian-like diploblasts (Yuan *et al.* 2011, fig. 3; Van Iten *et al.* 2013). Van Iten *et al.* (2013) proposed that one specimen in particular, shown here in Figure 3A–B, may be a conulariid scyphozoan. The specimen can be interpreted as a polyp consisting of a nonmineralized, three- or four-sided, steeply pyramidal periderm having sulcate corners and apertural lappets similar to those of many Palaeozoic conulariids. Extending from the putative apertural end of the specimen are approximately eight ribbon-like structures that may represent circumoral tentacles. The narrow apical end is broken, and one prediction of the conulariid hypothesis is that it originally tapered to a near point or to a rounded apical wall (schott). Problems with the cnidarian polyp hypothesis include the identity of ribbon-like structures within or beneath the putative periderm, although as noted in Van Iten *et al.* (2013) these may correspond to endodermal canals. Additionally, the fossil appears to lack features that can be interpreted as homologous to conulariid nodes or transverse ribs. Most recently, Grazhdankin (2014) proposed that this and other Lantian fossils may not have been cnidarians or algae, but rather 'bulbous holdfast structures' of frondomorphs such as *Mawsonites*. Be that as it may, the conulariid hypothesis (Van Iten *et al.* 2013) implies, again, that the anthozoan–medusozoan split occurred no later than about 580 Ma and suggests as well that the first thecate scyphopolyps were nonbiomineralizing.

Latest Ediacaran scyphozoans. The latest Ediacaran (*c.* 543 Ma) Tamengo Formation (Corumbá Group) of Mato Grosso do Sul, Brazil, contains abundant specimens of *Cloudina lucianoi* and *Corumbella werneri*, two of the oldest known skeletonized eumetazoans (Fairchild *et al.* 2012; Kerber *et al.* 2013). The genus *Cloudina*, known throughout the world (e.g. Gaucher *et al.* 2003; Kontorovich *et al.* 2008; Cai *et al.* 2014) and originally interpreted as a calcareous tubiculous annelid, has since been reinterpreted as a possible cnidarian polyp, based on comparisons of gross morphology, microstructure, biomineralization and mode of asexual reproduction (Vinn and Zatoń 2012). *Corumbella werneri* is a tetrameral tube, very steeply pyramidal in shape and composed of polygonal 'rings' that are approximately square in transverse cross-section (Fig. 4). The 'rings' articulate along their edges and alternate along the facial midline (Pacheco *et al.* 2011), in a manner similar to that of the transverse ribs of the Palaeozoic conulariid genus, *Climacoconus* (see Van Iten 1992; Leme *et al.* 2008). The midline of each side or face of the skele-

ton is sulcate, forming a low continuous carina on its inner surface. In these respects, *Corumbella* is most similar to conulariid scyphozoans and to thecate scyphopolyps of the order Coronatae and may have been a scyphozoan most closely related to these two groups (Hahn *et al.* 1982; Babcock *et al.* 2005; Pacheco *et al.* 2011; Warren *et al.* 2012).

Most recently, a 2-m-thick shale bed in the middle part of the Tamengo Formation yielded a single specimen of a conulariid (Fig. 3C–D), the oldest definitely known representative of this extinct group of scyphozoans (Leme *et al.* 2013). The Tamengo Formation conulariid, which occurred about 20 m below the topmost occurrence of *Cloudina* in the host section, is most similar to Palaeozoic species assigned to the genus *Paraconularia*, previously thought to range from the Lower Devonian to the Triassic (Babcock and Feldmann 1986). *Paraconularia* generally are characterized by finely nodose, adaperturally arcuate transverse ribs that terminate in the corner sulcus, where they bend towards the apertural end of the periderm and alternate with the ends of the transverse ribs from the adjacent face. The nodes commonly exhibit spine-like extensions (adapertural spines; Babcock and Feldmann 1986) that project adaperturally, part way across the interspace. The Tamengo Formation conulariid exhibits all of these gross anatomical features, though unlike most Palaeozoic conulariids its periderm appears to have been predominantly organic in composition (as indicated by results of Raman spectrometry; J. M. Leme, H. Van Iten, M. L. A. F. Pacheco, M. G. Simões, T. R. Fairchild, P. Boggiani, F. Rodrigues and D. Galante, unpub. obs.). Recent cladistic analyses of phylogenetic relationships among conulariid genera (Leme *et al.* 2008; Van Iten *et al.* 2014) indicate that *Paraconularia* is a relatively apical branch among conulariids. The presence of this genus in the Ediacaran System is therefore remarkable, as the cladogenic event that originated Paleoscyphozoa (= Conulatae + Corumbellata; Fig. 1) occurred after those that produced anthozoans, staurozoans, hydrozoans, cubozoans and even discomedusans. Thus, and in agreement with the most recent molecular estimates (e.g. Erwin *et al.* 2011; Fatka *et al.* 2012; Erwin and Valentine 2013), the fossil record of scyphozoans indicates that there must have been a fairly long interval of cnidarian evolution prior to latest Ediacaran times.

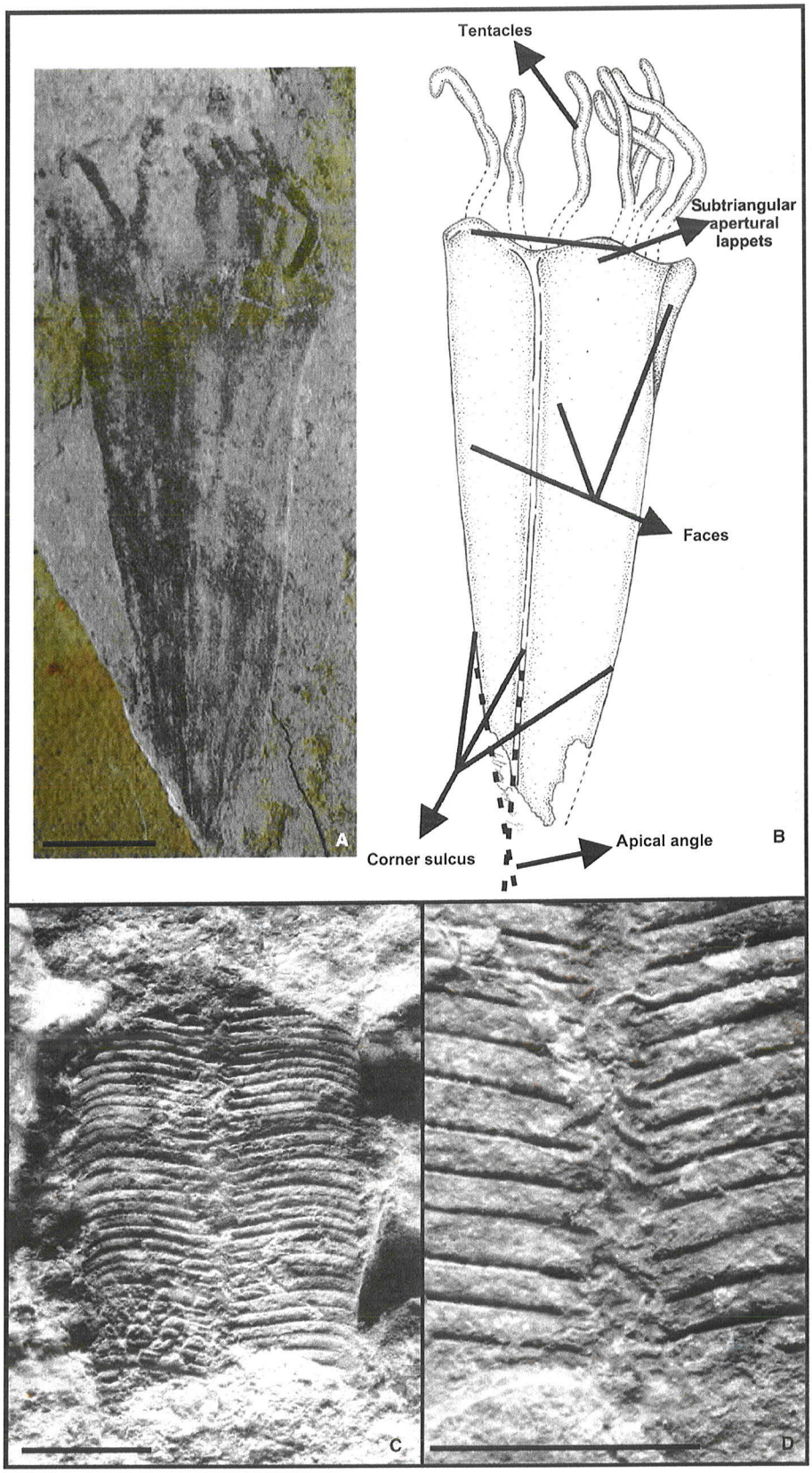
One additional Ediacaran taxon has been interpreted as a conulariid. This is *Vendoconularia triradiata* (Fig. 5), currently known from the Erga and Ust-Pinega formations (late Ediacaran) of north-western Russia (Ivantsov and Fedonkin 2002; Van Iten *et al.* 2005; Grazhdankin 2014). Originally described (Ivantsov and Fedonkin 2002) on the basis of a single sandstone steinkern measuring about 50 mm long and showing hexaradial symmetry (six faces), *Vendoconularia* exhibits intriguing gross anatomical similarities to *Metaconularia* (Van Iten *et al.* 2005), the oldest currently known species of which range into the Lower Ordovician. Alternatively, Grazhdankin (2014) suggested that *Vendoconularia* may have been related to tribrachiomorphs, which are possible stem group eumetazoans showing three-fold symmetry.

Finally, strata of Terreneuvian age contain a variety of possible and/or probable, thecate medusozoan polyps, including conulariid-like small shelly fossils, *Byronia*, *Hyolithellus* and *Sphenothallus* (e.g. Conway Morris and Chen 1992; Zhu *et al.* 2000; Van Iten *et al.* 2010; this paper, Fig. 2).

SUMMARY AND RECOMMENDATIONS

Understanding of the early evolution and Ediacaran–Cambrian fossil record of phylum Cnidaria has changed dramatically since the advent of molecular phylogenetics and the initial discovery of medusa- and polyp-like fossils of the classical Ediacara biota. At present, the oldest probable fossil cnidarians, the non- or weakly biomineralizing medusozoans *Corumbella werneri* and *Paraconularia* sp., occur in strata (Tamengo Formation, Brazil) of latest Ediacaran age. Again, though, an even older conulariid may occur in the Lantian Formation (South China; 635–577 Ma). Possible remains of nonbiomineralizing anthozoans, related perhaps to tabulate corals, occur in the Doushantuo Lagerstätte (South China; *c.* 585 Ma?). The oldest known hexacorallian anthozoan (*Eolympia pediculata*) is earliest Cambrian (*c.* 540 Ma) in age, and middle–late Fortunian strata may contain medusozoan polyps (e.g. conulariid-like small shelly fossils, *Hyolithellus* and *Sphenothallus*). The oldest known hydrozoans and cubozoans are represented by medusae in the Cambrian (Series 3) Marjum Formation (Utah, USA; *c.* 505 Ma). Based solely on current knowledge of the fossil record, then, the split between the anthozoan subclasses Hexacorallia and Octocorallia can be dated at no later than about 540 Ma (based on *E. pediculata*), and the split between the medusozoan classes Cubozoa and Scyphozoa can be dated at no later than about 543 Ma (based on *Paraconularia* sp.). Again, because the branching event that originated Cubozoa and Scyphozoa occurred after those that produced Anthozoa, Hydrozoa and Staurozoa (Fig. 1), these palaeontologically based dates suggest that cnidarians actually originated much earlier in the Proterozoic Eon, in agreement with the results of molecular studies (e.g. Park *et al.* 2012), which estimate that Cnidaria and its major groups originated as early as the Cryogenian Period. To help guide future research on the problem of the origin and early diversification of this phylum, we offer the following four recommendations:

1. The simple morphology of possible anthozoans (e.g. *Ramitubus*) in phosphorites in the upper Doushantuo Formation makes it difficult to present a compelling


Tentacles
Subtriangular apertural lappets
Faces
Corner sulcus
Apical angle
A
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D

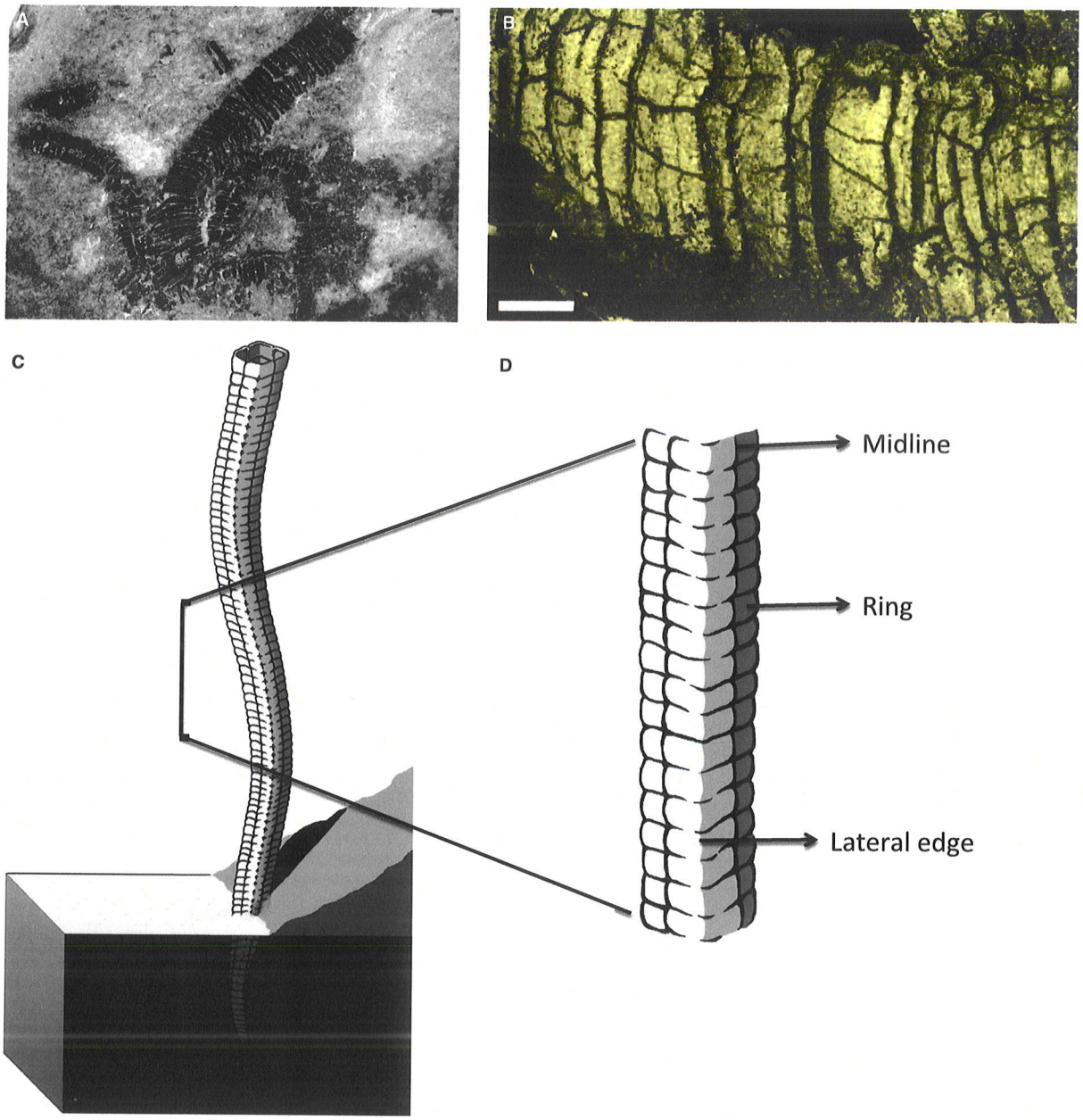

FIG. 4. *Corumbella werneri* (latest Ediacaran; Brazil, Paraguay and Nevada, USA). A, possible gregarious specimens (all incomplete) from the Tamengo Formation of Brazil; B, micro-CT scan of a portion of a *Corumbella* exoskeleton, showing multiple small fractures; C, reconstruction of the periderm of a solitary polyp in its original life orientation and with its apical region embedded in bottom sediment (figure drawn by P. Busana and modified from Pacheco *et al.* 2011); D, detail of C, highlighting the sulcate midline and nonsulcate corners. Both scale bars represent 1 mm.

FIG. 3. A–B, possible conulariid from the early Ediacaran Lantian Formation (Lantian biota, Anhui Province, South China). A, photograph of the entire specimen, preserved as a carbonaceous compression and consisting of a tapered portion and multiple ribbon-like structures; B, line drawing showing how this fossil can be interpreted as a conulariid or conulariid-like cnidarian. Scale bar represents 3 mm (figure modified from Van Iten *et al.* 2013, fig. 1). C–D, *Paraconularia* sp. (latest Ediacaran; Tamengo Formation, Corumbá Group, Mato Grosso do Sul, Brazil; specimen number GP-1T 2301, Paleontology Collection, Universidade de São Paulo, Instituto de Geosciências). C, full view of two partial faces of the flattened specimen. Scale bar represents 10 mm; D, detail of the corner groove between the two faces shown in C. Scale bar represents 7 mm.

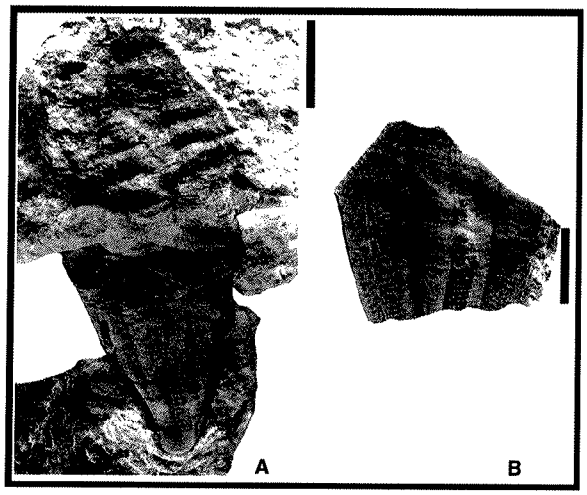

FIG. 5. *Vendoconularia triradiata* (late Ediacaran, Erga and Ust'Pinega formations; north-western Russia). A, side view of the holotype, a sandstone steinkern; B, detail of one of the six faces showing the paired brown lines interpreted by Van Iten *et al.* (2005) as possible traces of a pair of low internal carinae flanking the midline. Scale bar represents 13 mm in A and 10 mm in B. Figure modified from Ivantsov and Fedonkin (2002, pl. 1).

case for homology with skeletons of Palaeozoic and younger members of this class. However, the Doushantuo Formation tubules occur in strata that yield minute soft-bodied fossils interpreted as phosphatized metazoan eggs and embryos. Therefore, continued collection of associated tubular fossils may eventually yield specimens preserving both the apertural end of the skeleton and phosphatized remains of the (originally) soft-bodied polyps, similar in form to those already discovered in presumably isotaphonomic, basal Cambrian phosphorites of South China.

2. The definite occurrence of an advanced conulariid (*Paraconularia* sp.) near the top of the Ediacaran System suggests that it might be worthwhile to extend the search for these fossils, one of only a handful of eumetazoan groups that cross the Ediacaran–Cambrian boundary, into still older rock units. In the case of the Lantian biota, if it can be shown that specimens interpreted (Van Iten *et al.* 2013) as possible conulariids do in fact terminate in a pointed apex or rounded schott-like structure, or exhibit nodes and/or transverse ribs, then the case for a conulariid affinity for such ancient macrofossils will be strengthened considerably. Because Ediacaran conulariids appear to be exceedingly rare, owing perhaps to their periderm having been predominantly organic, palaeontologists might also look for conulariid microfossils (Jerre 1993; Van Iten *et al.* 2006*b*), which have been discovered through acid maceration of Palaeozoic carbonate rock units in which conulariid macrofossils are extremely rare. Such fossils may also be present in Ediacaran shales and phosphorites. More specifically, we recommend that the search for conulariids in Ediacaran marine successions be facies oriented. As demonstrated by several previous studies (Simões *et al.* 2000; Rodrigues *et al.* 2003; John *et al.* 2009; Van Iten *et al.* 2012), the preservation potential of conulariids varies along an onshore–offshore bathymetric gradient, with taphonomically enhanced preservation occurring in sedimentary successions deposited under low rates of sedimentation punctuated by abrupt burial at or below storm wave base. Hence, palaeontologists searching for conulariids should target those portions of transgressive systems tracts (Simões *et al.* 2000; Rodrigues *et al.* 2003) or high-stand systems tracts (Van Iten *et al.* 2012) within which obrution deposits or distal tempestites are likely to occur.
3. Recently published data on the anatomy of putative pentamerous cubozoans from the upper Kuanchuanpu Formation, presently dispersed among several different studies (Dong *et al.* 2013; Han *et al.* 2013; Yasui *et al.* 2013), should be consolidated and integrated. Additionally, a thorough comparative assessment of the homologies between the axes of symmetry of the different cnidarian lineages (extant and fossil) is badly needed to find a common baseline for evolutionary comparisons.
4. Additional taphonomic studies of Ediacaran and Cambrian cnidarians (e.g. Cai *et al.* 2014) are highly desirable to understand their habits and to facilitate the interpretation of their palaeoecology (Brasier *et al.* 2013). Such work is of the utmost importance to understanding the evolution of cnidarians as the group is well known to have benthic and planktonic representatives comprising very complex life histories. The challenges are to understand the ecological role of these different life phases in their respective communities and to homologize the different parts of these life phases to infer their morphological evolution. In this sense, evo-devo and basic life-cycle studies on extant taxa would provide an improved basis for inferring what could have happened at the dawn of Cnidaria.

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CAPÍTULO 2

Afinidades e diversificação de conulários no Ediacarano e Paleozoico

2.1. VAN ITEN, HEYO; LEME, J.M.; PACHECO, M.L.A.F.; SIMÕES, M.; FAIRCHILD, T. R.; RODRIGUES, F.; GALANTE, D.; BOGGIANI, P.C.; MARQUES, A., 2016. Origin and Early Diversification of Phylum Cnidaria: Key Macrofossils from the Ediacaran System of North and South America. In: S. Goffredo, Z. Dubinsky. (Org.). The Cnidaria, Past, Present and Future. 1ed.Cham: Springer International Publishing AG, p. 31-40.

Estudos recentes de relógio molecular colocam a origem do filo Cnidaria dentro do Período Criogeniano (cerca de 850-635 Ma), com a separação entre as duas subfamílias (Anthozoaria e Medusozoa) também ocorrendo durante este intervalo de tempo. No entanto, os macrofósseis cnidários mais antigos, todos os medusozoa, ocorrem em rochas do Período Ediacariano tardio (cerca de 560-541 Ma). *Corumbella werneri*, atualmente conhecida dos estratos ediacaranos tardios do Brasil, Paraguai e Nevada (EUA), foi aliada a conulários, mas também compartilha semelhanças morfológicas com o fóssil *Carinachites spinatus* (Cambriano Estágio 1, China), e pode ser comparado com determinados fósseis tubulares, incluindo *Sinotubulites* e *Wutubus annularis*, da Formação Dengying, Ediacarano, China. A evidência mais forte de afinidade com cifozoários coronados é exibida por *Paraconularia* sp. da Formação Tamengo, Brasil (Mato Grosso do Sul). Finalmente, os quadriformes de *Haootia* das formações ediacaranas Fermeuse e Trepassy (sudeste de Newfoundland, Canadá) exibem intrigantes semelhanças morfológicas com os estaurozoa existentes e podem representar o registro mais antigo da musculatura metazoária. Juntos, *C. werneri* e *Paraconularia* sp. do Ediacarano podem confirmar a divisão entre as classes de medusozoários Cubozoa e Scyphozoa no prazo de aprox. 543 Ma. Se *H. quadriformis* fosse de fato um estaurozoa, então este taxon fóssil confirma a divisão entre a classe Staurozoa e todos os outros cnidários medusozoários no máximo até aproximadamente 560 Ma.

Stefano Goffredo · Zvy Dubinsky *Editors*

The Cnidaria, Past, Present and Future

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3 Origin and Early Diversification of Phylum Cnidaria: Key Macrofossils from the Ediacaran System of North and South America

Heyo Van Iten, Juliana M. Leme, Mírian L.A.F. Pacheco, Marcello G. Simões, Thomas R. Fairchild, Fábio Rodrigues, Douglas Galante, Paulo C. Boggiani, and Antonio C. Marques

Abstract

Recent molecular clock studies place the origin of phylum Cnidaria within the Cryogenian Period (ca. 850–635 Ma), with the split between the two subphyla (Anthozoaria and Medusozoa) likewise occurring during this time interval. However, the oldest cnidarian macrofossils, all medusozoans, occur in rocks of the late Ediacaran Period (ca. 560–541 Ma). Lightly skeletonized *Corumbella werneri*, currently known from late Ediacaran strata of Brazil, Paraguay and Nevada (USA), has been allied with coronate and conulariid scyphozoans, but it also shares gross morphological similarities with *Carinachites spinatus*, a possible conulariid from Cambrian Stage 1 (China), and it may be compared with *Sinotubulites* and *Wutubus annularis* from the late Ediacaran Dengying Formation (China). The strongest evidence of affinity with coronate scyphozoans is exhibited by *Paraconularia* sp. from a *Corumbella*-bearing shale interval in the latest Ediacaran Tamengo Formation of central Brazil. Furthermore, *Paraconularia* sp. from this rock unit establishes conulariids as a cnidarian clade that crossed the Proterozoic-Phanerozoic boundary. Finally, *Haootia quadriformis* from the late Ediacaran lower Fermeuse and Trepassy formations (southeastern Newfoundland, Canada) exhibits intriguing gross morphological similarities to extant

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staurozoans and may represent the earliest record of metazoan musculature. Together, *C. werneri* and latest Ediacaran *Paraconularia* sp. fix the split between the medusozoan classes Cubozoa and Scyphozoa at no later than ca. 543 Ma. If *H. quadriformis* was indeed a staurozoan or stem staurozoan, then this fossil taxon fixes the split between the class Staurozoa and all other medusozoan cnidarians at no later than ca. 560 Ma.

Keywords
Cnidaria • Medusozoa • Conulariids • Cryogeniam • Ediacaran

3.1 Introduction

Students of phylum Cnidaria have long agreed that the origin of this monophyletic group of diploblastic eumetazoans probably lies well within the Neoproterozoic Era (see for example Van Iten et al. 2014a and references cited therein). The phylogenetic relationships of cnidarians to other metazoans, as well as relationships among the major groups within Cnidaria, have been subject to divergent interpretations, but at present the most widely accepted phylogenetic hypothesis for the five cnidarian classes appears to be ((((Cubozoa, Scyphozoa) Hydrozoa) Staurozoa) Anthozoa). Nonetheless, even classical hypotheses (e.g., the traditional concept of Scyphozoa) come to light from time to time, based on new data (e.g., Zapata et al. 2015). Similarly, molecular clock studies have yielded a broad range of age estimates for the origins of major cnidarian groups, yet all agree that at least some cnidarian clades probably are older than suggested by their fossil records, with, for example, Park et al. (2012) estimating that Cnidaria arose 819–686 Ma, Medusozoa 670–671 Ma and Hexacorallia 684–544 Ma.

Until fairly recently it was widely thought that the hypothesis of a Cryogenian-Ediacaran origin for Cnidaria and its major subclades received direct support from the fossil record, in particular from certain iconic, polyp- or medusa-like soft-bodied taxa (e.g., Glaessner and Wade 1966; Wade 1972) of the three classical Ediacaran assemblages (Avalon, ca. 575–560 Ma; White Sea, ca. 560–550 Ma; Nama, ca. 550–541 Ma; sensu Waggoner 2003). However, more recent investigations (e.g., Antcliffe and Brasier 2007; Young and Hagadorn 2010) have demonstrated that similarities between extant cnidarians and cnidarian-like, soft-bodied Ediacaran fossils are not mutually equivalent. Moreover, there are no cnidarian body fossils of Cryogenian age, and no trace fossils from this period can be attributed to this phylum. It should be noted, however, that certain phosphatic microfossils from the middle Ediacaran (ca. 585 Ma) Doushantuo Formation of South China have collectively been interpreted as embryos, larvae and minute adult specimens of anthozoans and hydrozoans (Chen et al. 2002).

In general, estimates of the timing of phylogenetic branching events based on molecular clocks vary substantially, and of course molecular clocks are frequently calibrated using the fossil record. Partly for this reason, we focus in this contribution on the anatomy and phylogenetic affinities of macroscopic Ediacaran body fossils showing the strongest evidence of homology with skeletons or soft bodies of extant cnidarians. To be sure, these fossils continue to present important problems of interpretation, and some of these are reviewed here. Be that as it may, we argue that these fossils can legitimately be used as calibration limits for molecular phylogenetic studies of the early diversification of cnidarians and other metazoan clades.

3.2 *Corumbella werneri*

3.2.1 Background

Conspicuously annulated, possibly weakly mineralized skeletons of *Corumbella werneri* have been described from latest Ediacaran strata in central Brazil, southern Nevada and Paraguay (Hahn et al. 1982; Hagadorn and Waggoner 2000; Babcock et al. 2005; Pacheco et al. 2011, 2015; Fairchild et al. 2012; Warren et al. 2012). Formations hosting *Corumbella* also contain calcareous skeletons of the cosmopolitan genus *Cloudina*, which may have been a cnidarian polyp (Vinn and Zatoń 2012; Cortijo et al. 2015). Examination of specimens showing three-dimensional preservation (Fig. 3.1a–d) revealed that complete skeletons of *Corumbella werneri* consisted of two regions or portions, with the probable aboral portion, approximately circular in transverse cross section, grading into a longer, polyhedral (quadrate) portion having four sub-rounded corners lacking a longitudinal sulcus (Pacheco et al. 2015). No evidence of a terminal holdfast structure has been detected, and indeed the aboral end may have been closed (Fig. 3.1e). The four faces of the quadrate portion are nearly parallel, and at the widest or oral end the skeleton is open, with each face having a straight to gently arcuate apertural margin. The largest skeletons may originally have measured about 100 mm long and up to 5 mm wide. The entire skeleton is transversely corrugated, and in longitudinal cross-sections the corrugations are trochoidal in form, with the crests of the trochoid pointing away

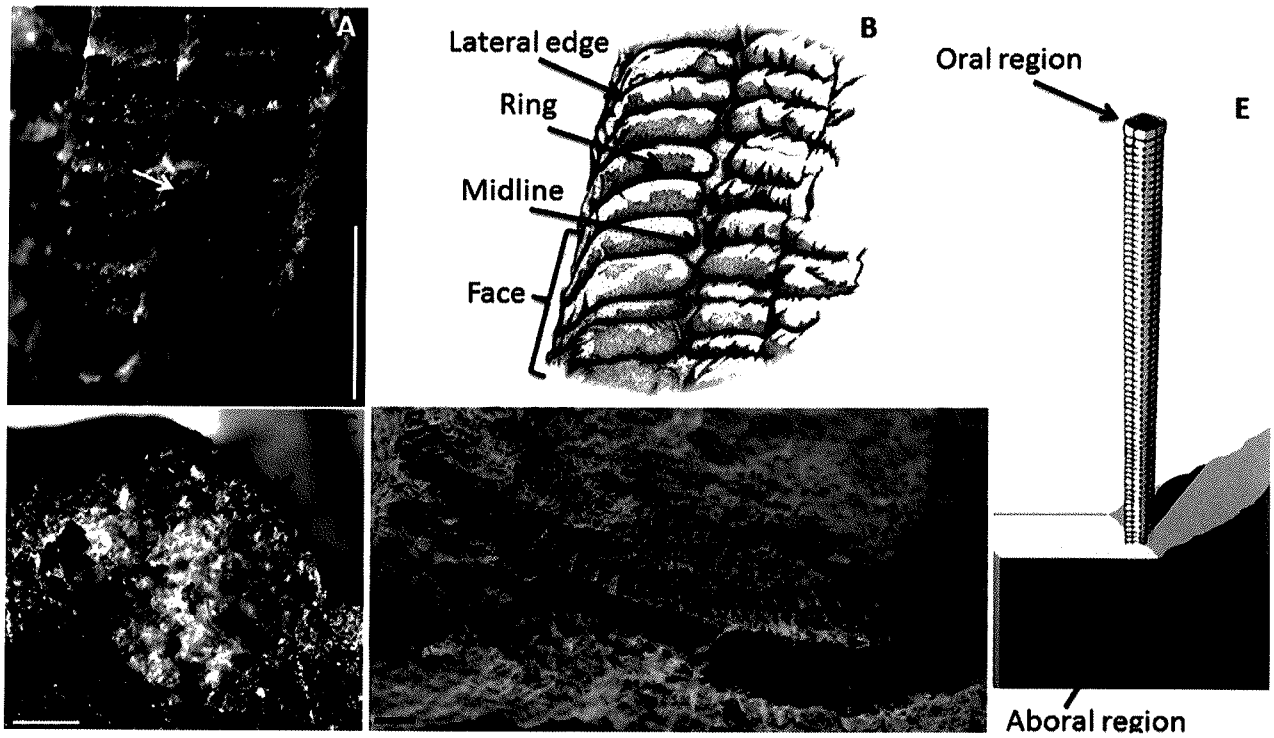

Fig. 3.1 *Corumbella werneri* (latest Ediacaran, Tamengo Formation, Mato Grosso do Sul, Brazil and Wood Canyon Formation, Nevada, USA) (**a**) part of the inner surface of a single face, showing the zigzagged midline sulcus and narrow angular interspaces (specimen number GP1E-4210, Geosciences Institute, University of São Paulo, Brazil) (**b**) drawing of part of GP1E-4210, showing details of a corner, sulcate midline and broadly rounded transverse ridges (rings) (**c**) transverse cross-section through the quadrate portion of another specimen, showing the four faces (*arrows*; specimen number 12802, Los Angeles County Museum of Natural History, California, USA) (**d**) specimen showing the aboral portion of the skeleton (*left*) grading into the polyhedral (quadrate) portion of the skeleton (specimen number DGM-5601-I, Earth Sciences Museum, DNPM, Brazil) (**e**) reconstruction of the complete periderm of a solitary polyp in its original life orientation and with its closed apical region embedded in bottom sediment (All scale bars represent 1 mm)

from the external surface of the skeleton (Fig. 3.1a, b), the thickness of which appears to be less than 0.1 mm. Viewed externally, the skeleton exhibits relatively broad, rounded, ring-like transverse ridges ("rings") that number about 4 per mm (long.) and alternate with narrow angular troughs corresponding to the crests of the aforementioned trochoid. In the short circular portion, the transverse ridges and troughs completely encircle the skeleton, and there is no other ornament. In the quadrate portion, the transverse ridges and troughs are continuous across the corners but are interrupted along the midline of the faces by a narrow, zigzagged angular groove that is expressed on the inner surface of the faces as a corresponding low ridge or carina (Fig. 3.1a). Also along the midline the transverse ridges and troughs are straight to recurved and exhibit slight offset (hence the zigzagged course of the midline sulcus). Results of SEM imaging and elemental analysis (Warren et al. 2012; Pacheco et al. 2015) indicate that the skeleton is finely lamellar, and further that individual lamellae consist of a mosaic of numerous, tightly interlocking polygonal plates measuring approximately 10–120 μm wide and 5 μm thick. The plates exhibit minute (~1 μm in diameter) pores and pillar-like features (papillae) arranged in regular rows. Finally, the trough between adjacent ridges appears to be the site of a single circumferential suture, hence the tendency of *Corumbella* fossils to be incomplete and broken along lines parallel to the annulations.

The hypothesis of a scyphozoan affinity for *Corumbella* is based on a suite of anatomical similarities uniquely shared by this genus with thecate scyphopolyps of the extant order Coronata and the extinct order Conulariida (Van Iten et al. 1996, 2006a, 2014a, b). Like coronates and most conulariids, the quadrate portion of *Corumbella* exhibits tetrameral symmetry, accentuated in all three taxa by the presence of four or eight inwardly projecting, seriated or continuous longitudinal sulci (*Corumbella* and many conulariids) or carinae (many conulariids and some coronates). The four sulcate midlines of *Corumbella* can be interpreted as being homologous to the scyphozoan interradii, which in many living scyphozoans are sites of an endodermal gastric septum, while the four corners can be homologized with the scyphozoan perradii. In many conulariids both the midlines (interradial)

and the corners (perradial) likewise are sulcate, but in several species the corners are rounded, as in *Corumbella*. The transverse ridges and troughs of this genus can be homologized with the transverse ribs and interspaces, respectively, of rib-bearing conulariids and coronates. In sum, then, the skeleton of *Corumbella* can be interpreted as an ectodermally derived, originally non- or weakly mineralized periderm, the open wide end of which was oral (Fig. 3.1e). At this point no detailed alternative hypotheses of homology between *Corumbella* and non-scyphozoan groups such as annelids have been offered.

3.2.2 Additional Comparisons

Corumbella may also be compared with *Carinachites*, a possible conulariid genus from basal Cambrian (ca. 540 Ma) phosphorites of the Yangtze Platform (South China; Conway Morris and Chen 1992; Van Iten et al. 2005a), and with certain annulated body fossils from the late Ediacaran Dengying Formation, also on the Yangtze Platform. Specimens of *Carinachites*, which measure less than 5 mm long, generally are broken at both ends, though recently paleontologists in China have discovered specimens preserving a conulariid-like apertural margin (J. Han, written communication, 2015). Both *Carinachites* and the polyhedral portion of *Corumbella* are square in transverse cross section, and the angle of taper of the skeleton is extremely low (<5° as opposed to ~10–30° in most conulariids; e.g., Babcock and Feldmann 1986). Additionally, the thickness of the skeleton appears to have been less than 0.1 mm. The annulations of *Corumbella* are similar to the rounded, gently arcuate transverse ridges of *Carinachites spinatus* (see Conway Morris and Chen 1992, Fig. 3.5), and these in turn are similar to the smooth, sinusoidal transverse ribs of the conulariid genus *Conularina* (see for example illustrations in Sinclair 1942). Also in these three taxa, the midline of each face is marked by a sulcus (*Corumbella* and *Conularina*) or by a low ridge (*Carinachites spinatus*), and many or all of the transverse ridges are reduced in amplitude and recurved along the midline. Like the rounded transverse ridges of *Corumbella*, the transverse ridges of *Carinachites spinatus* are smooth and more or less rounded, arch gently toward the wide end of the skeleton, and appear to represent corrugations of the thin skeletal wall. The troughs (interspaces) between the transverse ridges likewise are smooth. Unlike *Corumbella*, though, the corners of all species of *Carinachites* are sulcate, in some cases (*C. spinatus*) bearing a transverse ornament that is finer than that crossing the faces (a characteristic shared with conulariids such as *Climacoconus*; see for example Van Iten et al. 1996).

Parsimony-based cladistic analysis of phylogenetic relationships among these taxa lies beyond the scope of the present study. However, two possible hypotheses suggested by the foregoing discussion are (1) that *Corumbella* was more closely related to *Carinachites* than it was to conulariids (based in part on the shared presence of an extremely low rate of skeletal taper; Fig. 3.2a) and (2) that *Corumbella* was more closely related to conulariids than it was to *Carinachites* (based in part on the shared presence of a corner sulcus; Fig. 3.2b).

Finally, the Dengying Formation hosts several taxa, including *Wutubus annularis* and the genus *Sinotubulites*, which consist of an elongate body or tubular skeleton showing conspicuous annulation (Chen et al. 2014; Cai et al. 2015). Like *Corumbella*, the most complete specimens of *W. annularis* (up to 180 mm long) exhibit two regions, one short and narrow and the other long and wide, and its annulations may be ruga-like or broadly rounded (Chen et al. 2014). However, it is not clear whether *W. annularis*, which was more or less cylindrical (transv.) as opposed to quadrate and lacked longitudinal sulci, had a skeleton or even a mouth opening. Skeletons of *Sinotubulites*, broken at both ends and thought to have originally been calcareous (Cai et al. 2015), are laminated and composed of two main layers. In some species, the outer layer is polyhedral, having three, five or six faces, and it exhibits coarse transverse corrugation. However, unlike *Corumbella*, the external ridges of *Sinotubulites* are sharp-crested rather than broadly rounded (being also offset along the corners of the skeleton), and the midline of the faces of *Sinotubulites* appears to lack a sulcus (see Cai et al. 2015, figs. 5, 6b and 8). For these reasons, then, hypotheses of homology between *Corumbella* and other Ediacaran tubular genera appear to be relatively weak, and we do not offer any preliminary phylogenetic hypotheses for these taxa here.

3.3 First Definite Precambrian Conulariid (*Paraconularia* sp.)

3.3.1 Comparisons with Phanerozoic Conulariids

In addition to *Cloudina* and *Corumbella*, the latest Ediacaran Tamengo Formation of central Brazil has also yielded a single specimen of a conulariid (Leme et al. 2013; Van Iten et al. 2014a) (Figs. 3.3 and 3.4). Collected by one of us (TRF) near Corumbá in Mato Grosso do Sul State (Fig. 3.4a), the specimen (Fig. 3.3) is most similar to species in the genus *Paraconularia* and has been assigned to this taxon (Van Iten et al. 2014a), the monophyly of which however has been questioned (Van Iten et al. 2008). Other Ediacaran fossils, including *Conomedusites* (Fedonkin et al. 2007), *Vendoconularia triradiata* (Ivantsov and Fedonkin 2002; Van Iten et al. 2005b) and certain fossils from the Lantian Formation of South China (Van Iten et al. 2013), have been allied or compared with conulariids, but the Tamengo

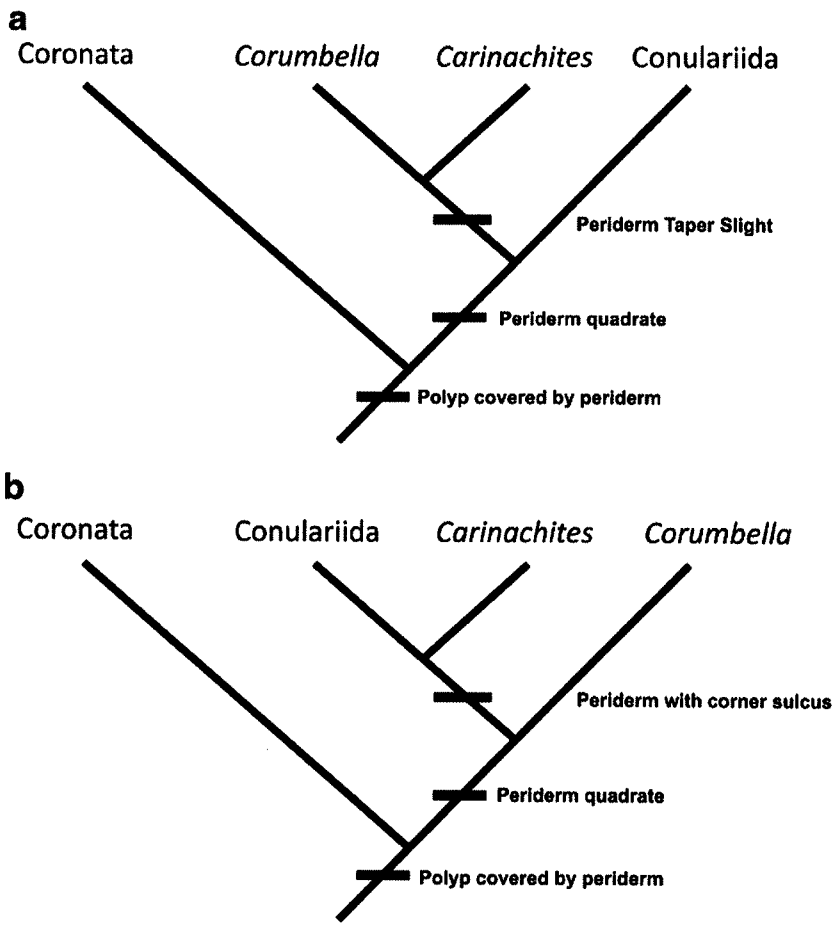

Fig. 3.2 Cladograms showing two alternative interpretations of the phylogenetic relationships among coronate scyphozoans, *Carinachites*, conulariids (order Conulariida) and *Corumbella* (**a**) *Carinachites* and *Corumbella* as sister taxa united by possession of a thin-walled quadrate periderm that tapers very gently (**b**) *Carinachites* and conulariids as sister taxa united by possession of an external sulcus at the corners of the periderm

Formation specimen (Fig. 3.3) is the first such fossil showing compelling evidence of affinity with a particular conulariid genus. The specimen, which has been flattened and is missing the aboral region and apertural margin, measures approximately 26 mm long and 15 mm wide and is oriented parallel to bedding. We estimate that the complete periderm originally measured at least 100 mm long. The conulariid was found in a 1.5-m-thick interval of variegated, *Corumbella*-bearing laminated shale in the middle part of the Tamengo Formation, approximately 35 m below the topmost occurrence of *Cloudina*, a latest Ediacaran index fossil (Gaucher et al. 2003; Cortijo et al. 2015), and approximately 40 m below the topmost occurrence of *Corumbella* (Fig. 3.4b). Zircons from altered volcanic tuffs situated approximately 40 m above the level at which the conulariid was found have yielded a radiometric (U-Pb) age date of 543±3 Ma (see Gaucher et al. 2003 and references cited therein).

Comparisons of this fossil with taxa other than conulariids, including previously described, soft-bodied Ediacaran genera, failed to yield any similarities as detailed as those uniquely shared with *Paraconularia*. Conulariids in general consist of a four-sided (rarely three-, five- or six-sided), gently to strongly tapered lamellar periderm having (in most genera) sulcate corners and a well-defined transverse ornament consisting of transverse ridges (ribs) and/or nodes. The thickness of the periderm ranges from <0.1 mm to several mm, and the corners and/or midlines may be sites of an internal carina (midlines and corners) or pair of carinae (midlines). All *Paraconularia* possess trochoidal (long.), adaperturally arching transverse ribs, thickest beneath their crest, which in most species bears a single row of minute, more or less closely spaced nodes (see Babcock and Feldmann 1986, figs. 23.5, 28.6 and 33.8). Some of the transverse ribs may be offset along the facial midline, and all of the transverse ribs terminate within the corner sulcus, bending towards the aperture on the shoulders of the sulcus and (within the sulcus) alternating with the terminal portion of the transverse ribs of the adjoining face (see Babcock and Feldmann 1986, figs. 22.2, 25.3, 26.1 and 27.5). In most *Paraconularia* possessing nodes, the adapertural half of each node is developed into a short, spine-like ridge (adapertural spine) that extends part way across the interspace (the trough

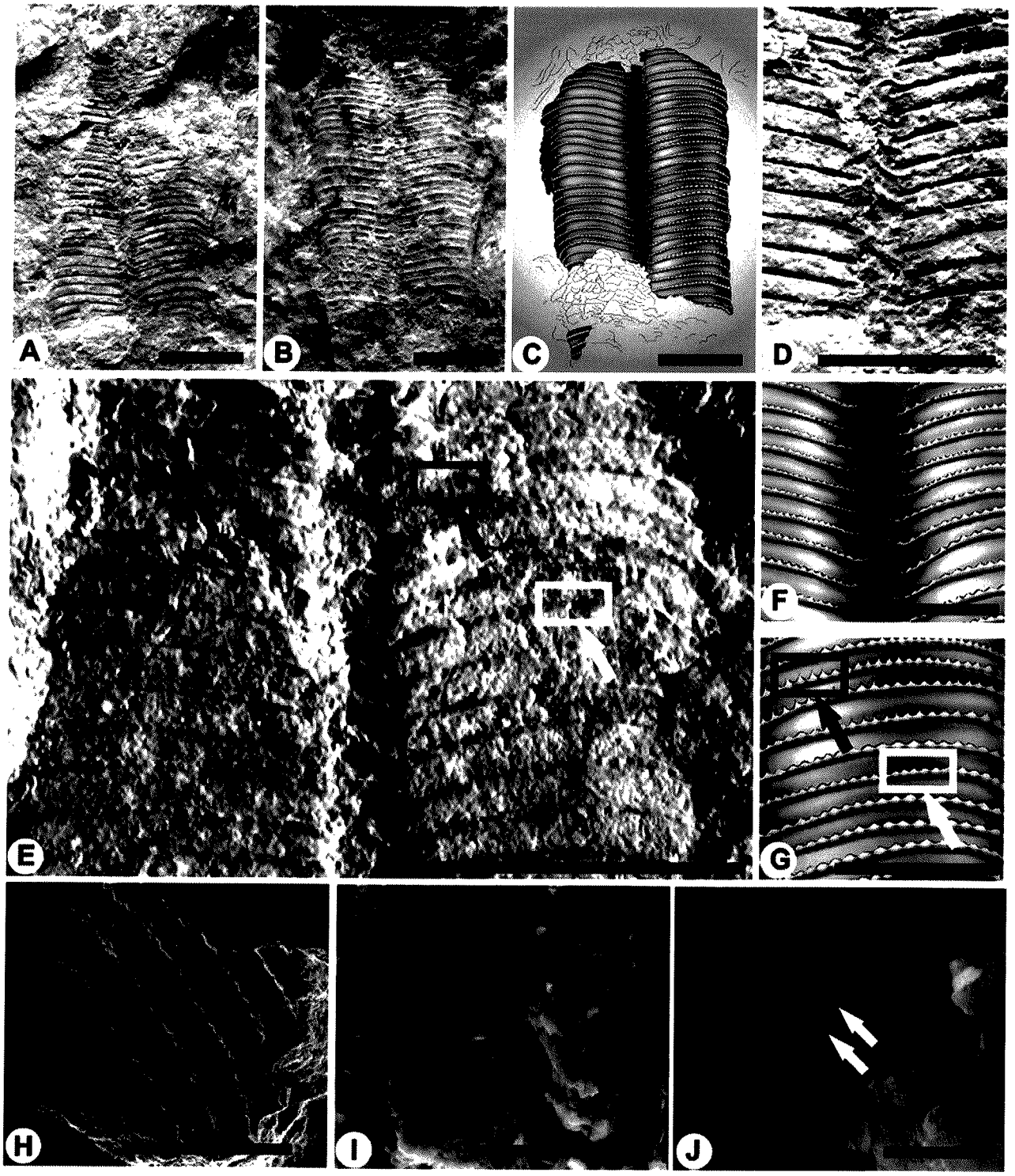

Fig. 3.3 *Paraconularia* sp. (latest Ediacaran, middle Tamengo Formation, Corumbá Group, Mato Grosso do Sul, Brazil; specimen number GP-1T 2301, Geosciences Institute, University of São Paulo, Brazil) (**a**) the counterpart of the specimen (**b**) the part of the specimen, showing the morphology of two faces and the intervening corner sulcus (**c**) schematic drawing of **b**, (**d**) detail of the corner sulcus of the part (**e**) detail of several nodes (*white square* and *arrow*) and adapertural spines (*black square* and *arrow*) (**f**) schematic drawing of the corner sulcus region shown in **e**, (**g**) schematic drawing of the highlighted nodes (*white square* and *arrow*) and adapertural spines (*black square* and *arrow*) shown in **g**, (**h**) scanning electron photomicrograph of a periderm fragment showing transverse ribs and nodes (**i**, **j**) scanning electron photomicrographs of broken and exfoliated periderm showing microscopic lamellae (*white arrows* in **j**) Scale bars: **a**–**c** and **e** = 10 mm; **d** = 7 mm; **f**, **g** = 5 mm; **h** = 3 mm; **i** = 40 μm; **j** = 5 μm

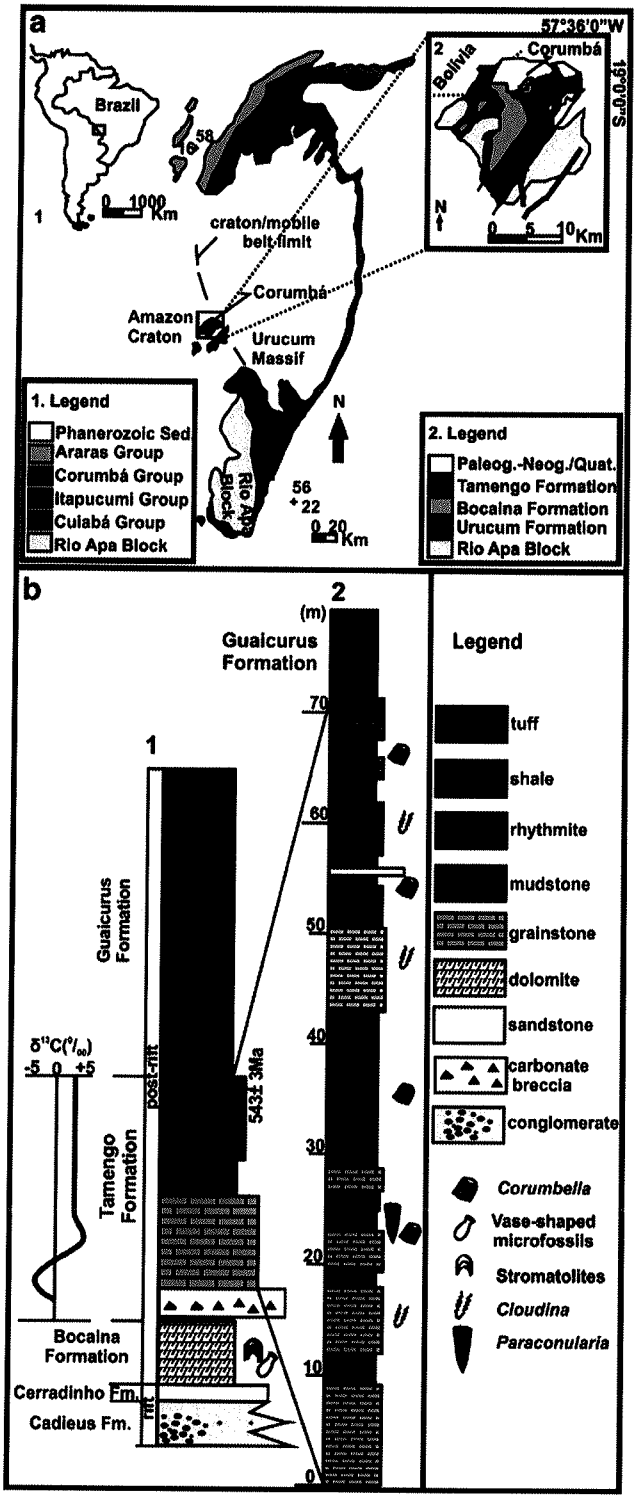

Fig. 3.4 (**a**) Geological map of the Paraguay Belt in South America, showing in (*1*) the location of the Corumbá (Brazil) area and in (*2*) the geology of the Corumbá Group near Corumbá (**b**) measured stratigraphical columns for (*1*) the Corumbá Group and (*2*) the Tamengo Formation, showing in (*2*) the levels of occurrence of *Paraconularia* sp., *Cloudina* and *Corumbella*

between adjacent transverse ribs) (see Babcock and Feldmann 1986, figs. 28.6 and 33.8). Finally, the pattern of arrangement of nodes on the faces is such that the nodes of every other transverse rib are collinear, forming longitudinal series that are approximately parallel to the facial midline or corners.

The relatively thin-walled (~0.2–0.5 mm), gently tapered Tamengo Formation *Paraconularia* exhibits the full suite of gross morphological features uniquely exhibited by conulariids in general, and it is most similar to node-bearing species of *Paraconularia* having adapertural spines. It consists of large portions of all four faces, though because it is flattened only two of the faces and the corner sulcus between them are readily visible (the other two faces, though mostly covered, project slightly beyond the apical edge of the two exposed faces of the part). The two exposed faces (Fig. 3.3a–g) are well-preserved, exhibiting 32 trochoidal, adaperturally arching transverse ribs bearing relatively large, widely spaced nodes with adapertural spines (Fig. 3.3e, h). The midlines and corners lack an internal carina. Next to and within the corner sulcus (Fig. 3.3d–f), the transverse ribs bend and alternate in a manner similar to that of all other *Paraconularia*, and the arrangement of the nodes and adapertural spines on the faces likewise is similar.

Essentially the only difference between the Tamengo Formation *Paraconularia* and Phanerozoic conulariids in general is that whereas the periderm of the latter fossils consists of alternating organic and phosphatic "microlamellae" (Ford et al., in press), the finely lamellar periderm of the Tamengo Formation conulariid (Fig. 3.3i, j) appears to be non-mineralized. Analysis of the periderm using Raman spectrometry yielded multiple bands characteristic of unaltered organic material, but none in the range (900–1100 cm^{-1}) for phosphate (Fig. 3.5). Similarly, phosphate was not detected in the host rock matrix. At present it is unclear whether the Tamengo Formation specimen originally was non-mineralized or whether original skeletal phosphate was removed secondarily, perhaps during diagenesis or weathering (see Muscente and Xiao 2015 and references cited therein). Be that as it may, the detailed gross morphological similarities between the Tamengo Formation specimen and Phanerozoic *Paraconularia*, many shared only by these fossils, constitute compelling evidence of homology.

3.3.2 Implications

The discovery of *Paraconularia* sp. in strata of latest Ediacaran age has important implications for our understanding of the evolution of both conulariids and cnidarians prior to their expansion during the Early Paleozoic. Because soft-bodied Ediacaran fossils originally interpreted as cni-

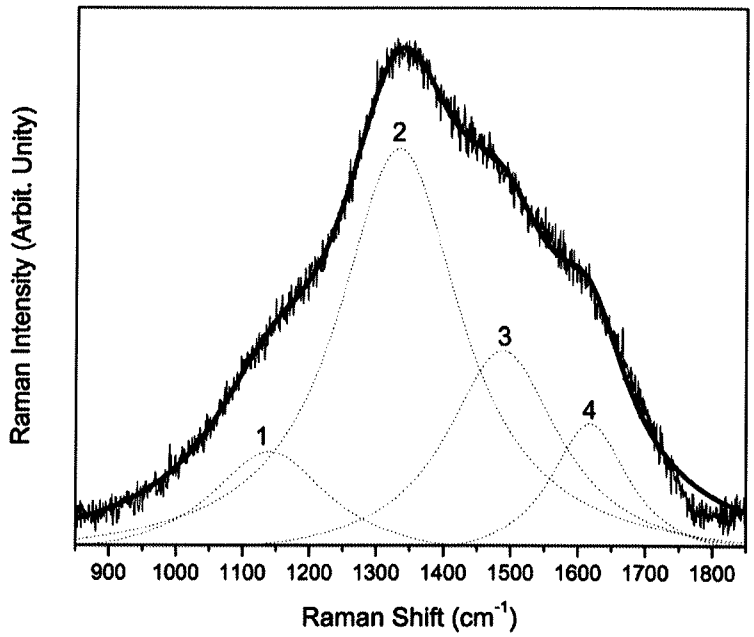

Fig. 3.5 Raman spectra of the periderm of *Paraconularia* sp. (middle Tamengo Formation, Mato Gross do Sul, Brazil)

darians have since been shown to be unrelated to this phylum (see Van Iten et al. 2014a and references cited therein), the Tamengo Formation *Paraconularia* sp. now constitutes the strongest paleontological evidence of the presence of conulariids, scyphozoans or any cnidarians during Neoproterozoic times. Moreover, conulariids survived the end-Proterozoic extinction event (Laflamme et al. 2013), a status currently shared with the probable latest Ediacaran-early Cambrian annelid, *Sabellidites cambriensis* (Moczyłowska et al. 2014). Cladistic analyses of phylogenetic relationships among conulariids (Leme et al. 2008; Van Iten et al. 2014b) show *Paraconularia* to be a relatively apical branch in the conulariid tree. This result implies that conulariids originated even earlier in the Neoproterozoic Era, and it suggests that additional conulariid taxa may occur in rocks of this age (possibly as sub-microscopic fragments; e.g., Van Iten et al. 2006b). Conulariids originated after the medusozoan sister classes Scyphozoa and Cubozoa split from each other, and after these two clades together split from their most recent common ancestor with the class Hydrozoa and, even earlier, after the subphylum Medusozoa split from its most recent common ancestor with the subphylum Anthozoaria (Van Iten et al. 2014a). Therefore the origin of conulariids was preceded by at least three major branching events in the history of phylum Cnidaria. Finally, together with *Corumbella werneri*, the Tamengo Formation *Paraconularia* constitutes a new, internal calibration point for molecular clock studies of early cnidarian evolution, dating the split between Scyphozoa and Cubozoa at no later than ca. 543 Ma.

3.4 *Haootia quadriformis:* The Oldest Fossil Cnidarian?

A new genus and species of (originally) soft-bodied fossil, *Haootia quadriformis*, has recently been described from the late Ediacaran (ca. 560 Ma) lower Fermeuse and Trepassy formations of the Bonavista Peninsula, southeastern Newfoundland (Liu et al. 2014, 2015; Miranda et al. 2015). At present *H. quadriformis* is represented by two specimens, namely the holotype from the Fermeuse Formation and a single incomplete paratype from the slightly older Trepassy Formation. Liu et al. (2014) interpreted *H. quadriformis* as a muscular cnidarian or a muscular metazoan of cnidarian grade. Additionally, these authors proposed that the new species was a sessile benthic animal, originally about 100 mm long, having a circular basal attachment disc connected to a narrow peduncle passing adorally into a broad quadrate calyx bearing four distally bifurcating branches. One of the most salient features of both the holotype and paratype is their unique system of narrow, closely spaced low ridges, interpreted by Liu et al. (2014) as sediment molds of bundled collagenous muscle fibers. These authors stated further that *H. quadriformis* may represent the earliest record of metazoan musculature. More specifically, Liu et al. (2014) posited that ridges in the stalk-like peduncle correspond to longitudinal (retractor) muscles, and that ridges paralleling the upper margin of the calyx correspond to circular coronal muscles. Based in part on these interpretations, Liu et al. (2014) proposed that *H. quadriformis* may have been most

closely related to extant staurozoans, a group of sessile medusae originally placed in the class Scyphozoa.

Still more recently, Miranda et al. (2015) published an alternative interpretation of *H. quadriformis*, supporting the hypothesis of a medusozoan affinity for this taxon but also calling into question certain aspects of Liu et al.'s (2014) reconstruction of the living animal. Specifically, Miranda et al. (2015) noted that the putative muscle impressions appear to overlap each other, possibly owing to post-mortem deformation including superposition of soft-part structures, and thus that it is difficult to interpret how the muscles might have been organized in the living body. Concerning Liu et al.'s (2014) interpretation of narrow ridges paralleling the putative oral margin of the calyx, Miranda et al. (2015) argued that they are less extensive than shown in Liu et al.'s reconstruction (2014, Fig. 3.3b). In the alternative reconstruction offered by Miranda et al. (2015, Fig. 3.3), the muscles are predominantly longitudinal in alignment, extending much closer to the putative oral margin of the calyx than posited by Liu et al. (2014), an interpretation that agrees more closely with the predominantly longitudinal musculature of extant staurozoans. However, Miranda et al. (2015) also stated that if the reconstruction of Liu et al. (2014) is in fact accurate, then perhaps *H. quadriformis* was a benthic form exhibiting vigorous pulsation, possibly to facilitate feeding. This hypothesis has important implications for the evolution of medusozoan life histories, as such a condition could have given rise to a free-living nektonic descendant.

Finally, the possibility that *H. quadriformis* specimens underwent significant taphonomic modification is an important problem meriting further investigation. Assuming that the original host sediment(s) and pore-water chemistry can be duplicated in the laboratory, it might prove worthwhile to conduct controlled taphonomic experiments to determine whether muscles of extant staurozoans or other cnidarians can be replicated under conditions similar to those that existed during final burial of *H. quadriformis*. A positive result would corroborate the hypothesis that the two currently available fossil specimens preserve relic muscle fibers.

3.5 Summary

Crucial to understanding the origin and early diversification of phylum Cnidaria is a thorough understanding of the nature and temporal range of its fossil record. Although recent molecular clock studies place the origins of this clade and its major subgroups within the Neoproterozoic Era, there are no cnidarian body fossils from rocks of Cryogenian age, and no Cryogenian trace fossils can be attributed to cnidarians. The Ediacaran System has yielded numerous genera of macrofossils, but only three of these, *Corumbella*, *Haootia* and *Paraconularia*, are likely to have been cnidarians (medusozoans). *Paraconularia* sp. from the latest Ediacaran Tamengo Formation (Brazil) constitutes the strongest paleontological evidence yet documented of the presence both of cnidarians and scyphozoans below the Proterozoic-Phanerozoic boundary, and it establishes conulariids as a cnidarian clade that survived the terminal Neoproterozoic extinction event. Together with *Corumbella werneri*, a possible close relative of conulariids, *Paraconularia* sp. from the Tamengo Formation serves as a new internal calibration point for molecular clock estimates, fixing the split between the classes Cubozoa and Scyphozoa at no later than ca. 543 Ma. Finally, if *Haootia quadriformis* was indeed a muscular, crown- or stem-group staurozoan, then it fixes the split between the class Staurozoa and all other medusozoans at no later than ca. 560 Ma.

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Os resultados de uma análise cladística da subordem Conulariina Miller e Gurley, um grande grupo extinto de cnidários de cifozoários, são apresentados. A análise procurou testar se as três subfamílias de conulários (Conulariinae Walcott 1886, Paraconulariinae Sinclair 1952 e Ctenoconulariinae Sinclair 1952) reconhecidas no *Treatise on Invertebrate Paleontology* (TIP) são monofiléticas. Um total de 17 caracteres morfológicos foram classificados para 16 taxa de grupo, nomeadamente os gêneros *Archaeoconularia, Baccaconularia, Climacoconus, Conularia, Conulariella, Conularina, Ctenoconularia, Eoconularia, Glyptoconularia, Metaconularia, Notoconularia, Paraconularia, Pseudoconularia, Reticulaconularia, Teresconularia* e *Vendoconularia*. Os táxons medusozoários existentes Cubozoa, Stauromedusae, Coronatae e Semaeostomeae serviram como *outgroups*. A análise não ponderada da matriz de dados gerou 1057 árvores e a análise de ponderação sucessiva resultou em uma das 1057 árvores originais. O ingrupo é monofilético com duas autapomorfias, (a) a geometria quadrada da região oral e (b) a presença de uma periderme mineralizada. Dentro do grupo, o clado (*Vendoconularia, Teresconularia, Conularina, Eoconularia*) é apoiado pela geometria longitudinal sinusoidal dos cristas transversais e o clado maior (*Conulariella, Baccaconularia, Glyptoconularia, Metaconularia, Pseudoconularia, Conularia, Ctenoconularia, Archaeoconularia, Notoconularia , Climacoconus, Paraconularia, Reticulaconularia*) é apoiada pela presença de tubérculos externos, que no entanto foram perdidos no clado (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*). Conforme proposto por Van Iten *et al.* (2000), o clado (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) é suportado por caracteres de terminação e alternância das costelas transversais no sulco da aresta. As subfamílias Conulariina, Paraconulariinae e Ctenoconulariinae previamente reconhecidas não foram recuperadas a partir desta análise. As características diagnósticas de Conulariinae (continuação do ornamento transversal através do sulco da aresta e falta de carina) e Ctenoconulariinae (presença de carina) são simplesiommorfias ou homoplasias, e Paraconulariinae é polifilética. As famílias Conulariellidae Kiderlen 1937 e Conulariopsidae Sugiyama 1942, também reconhecidas no TIP, são monogenéricas, e uma vez que não fornecem informações filogenéticas adicionais, devem ser abandonadas.

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CLADISTIC ANALYSIS OF THE SUBORDER CONULARIINA MILLER AND GURLEY, 1896 (CNIDARIA, SCYPHOZOA; VENDIAN–TRIASSIC)

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Abstract: Results of a cladistic analysis of the suborder Conulariina Miller and Gurley, 1896, a major extinct (Vendian–Triassic) group of scyphozoan cnidarians, are presented. The analysis sought to test whether the three conulariid subfamilies (Conulariinae Walcott, 1886, Paraconulariinae Sinclair, 1952 and Ctenoconulariinae Sinclair, 1952) recognized in the Treatise on Invertebrate Paleontology (TIP) are monophyletic. A total of 17 morphological characters were scored for 16 ingroup taxa, namely the genera *Archaeoconularia, Baccaconularia, Climacoconus, Conularia, Conulariella, Conularina, Ctenoconularia, Eoconularia, Glyptoconularia, Metaconularia, Notoconularia, Paraconularia, Pseudoconularia, Reticulaconularia, Teresconularia* and *Vendoconularia*. The extant medusozoan taxa Cubozoa, Stauromedusae, Coronatae and Semaeostomeae served as outgroups. Unweighted analysisof the data matrix yielded 1057 trees, and successive weighting analysis resulted in one of the 1057 original trees. The ingroup is monophyletic with two autapomorphies: (1) the quadrate geometry of the oral region; and (2) the presence of a mineralized (phosphatic) periderm. Within the ingroup, the clade (*Vendoconularia, Teresconularia, Conularina, Eoconularia*) is supported by the sinusoidal longitudinal geometry of the transverse ridges, and the much larger clade (*Baccaconularia, Glyptoconularia, Metaconularia, Pseudoconularia, Conularia, Ctenoconularia, Archaeoconularia, Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) is supported by the presence of external tubercles, which, however, were lost in the clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*). As proposed by Van Iten *et al.* (2000), the clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) is supported by the termination and alternation of the transverse ribs in the corner sulcus. The previously recognized subfamilies Conulariinae, Paraconulariinae and Ctenoconulariinae were not recovered from this analysis. The diagnostic features of Conulariinae (continuation of the transverse ornament across the corner sulcus and lack of carinae) and Ctenoconulariinae (presence of carinae) are symplesiomorphic or homoplastic, and Paraconulariinae is polyphyletic. The families Conulariellidae Kiderlen, 1937 and Conulariopsidae Sugiyama, 1942, also recognized in the TIP, are monogeneric, and since they provide no additional phylogenetic information, should be abandoned.

Key words: conulariids, phylogeny, systematics, Conulariina, Cnidaria, Medusozoa, Phanerozoic.

CONULARIIDS (subclass Conulata Moore and Harrington, 1956*a*, with single order Conulariida Miller and Gurley, 1896) are an extinct group of marine cnidarians which ranged from the Vendian to the Late Triassic (Van Iten *et al.* 2006). Most genera previously referred to the Conulata, including *Conularia* Miller, *in* Sowerby 1821, are characterized by a steeply pyramidal, four-sided, finely lamellar phosphatic skeleton bearing transverse ridges, transverse rows or longitudinal files of small nodes. In the chapter on conulariids in the Treatise on Invertebrate Paleontology (TIP) (Moore and Harrington 1956*b*), still the most recent and comprehensive published treatment of conulariid taxonomy and systematics, these genera were placed in the suborder Conulariina Miller and Gurley, 1896. The genus *Conchopeltis* Walcott, 1876, assigned to the suborder Conchopeltina Moore and Harrington 1956*b*, has since been removed from the Conulariida (Oliver 1984). This means that the characters of the suborder Conulariina are the same as those of the order Conulariida, which in turn are the same as those of the subclass Conulata (Moore and Harrington 1956*b*).

Since the publication of the TIP, circonulariids (Silurian–Devonian), which differ from pyramidal conulariids in having a conical skeleton (Bischoff 1978; Van Iten

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1992*a*), and certain pyramidal small shelly fossils from the Lower Cambrian (Conway Morris and Chen Menge 1992), have also been classified as conulariids. Most recently, Van Iten *et al.* (2005) proposed a possible rationale, based on cladistic principles, for the inclusion of conulariids, circonulariids and conulariid-like small shelly fossils in a single, putatively monophyletic group that excludes all other taxa.

As argued by a number of authors (e.g. Kiderlen 1937; Moore and Harrington 1956*a*, *b*; Werner 1966, 1967, 1973; Bischoff 1978; Salvini-Plawen 1978; Bouillon 1981; Van Iten 1991*a*, 1992*a*, *b*; Jerre 1994; Bergström 1995; McKinney *et al.* 1995; Van Iten *et al.* 1996, 2000, 2006; Collins *et al.* 2000; Hughes *et al.* 2000; Marques and Collins 2004; Babcock *et al.* 2005), conulariids probably were either scyphozoans (Class Scyphozoa Goette, 1887) or close relatives of this group, which together with hydrozoan and cubozoan cnidarians (classes Hydrozoa Owen, 1843 and Cubozoa Werner, 1975) form the subphylum Medusozoa Petersen, 1979. Although some authors (Kiderlen 1937) interpreted conulariid specimens bearing an apical wall (schott, with a transverse portion, or sleeve, that extends along the inner surface of the faces proper, toward the aperture; Van Iten 1991*b*) as free-swimming medusae, it is now generally thought that conulariid fossils represent benthic polyps that were either sessile (attached) or recumbent (e.g. Van Iten 1991*b*; Simões *et al.* 2000; Van Iten and Vhylasova 2004). Recently, Collins *et al.* (2000) and Marques and Collins (2000, 2004) presented cladistic analyses of the phylogenetic relationships among conulariids and other medusozoans. These authors concluded that conulariids (subclass Conulata Moore and Harrington 1956*b*) are the sister group of Stauromedusae, which are sessile, progenetic medusoid cnidarians traditionally classified within Scyphozoa, and that the clade named Staurozoa (Conulata, Stauromedusae) is equivalent in rank to Scyphozoa. Still more recently, Van Iten *et al.* (2006) reanalyzed the character data of Marques and Collins (2004) by rescoring some of the character states for conulariids and concluded that conulariids are the sister group of the scyphozoan order Coronatae and that they (but not stauromedusans) should also be classified as scyphozoans. The name Staurozoa should, therefore, be kept for the cnidarian class consisting exclusively of the Stauromedusae (Collins *et al.* 2006).

In contrast to these recent efforts to resolve the problem of the phylogenetic affinities of conulariids, the phylogenetic relationships among genera and species currently assigned to this group have received very little attention. Prior to the advent of phylogenetic systematics (Hennig 1950, 1966), and based solely on phenetic criteria, Moore and Harrington (1956*b*) subdivided the suborder Conulariina into three families, Conulariellidae Kiderlen, 1937, Conulariidae Walcott, 1886 and Conulariopsidae Sugiyama, 1942, with the Conulariidae consisting of the subfamilies Conulariinae Walcott, 1886, Paraconulariinae Sinclair, 1952 and Ctenoconulariinae Sinclair, 1952. The families Conulariellidae and Conulariopsidae are monogeneric; therefore, their monophyly cannot be tested under parsimony analysis. Van Iten *et al.* (2000), the first authors to investigate the problem of conulariid systematics using cladistic concepts, proposed, but did not test, the putatively monophyletic, nested grouping (*Notoconularia*, *Paraconularia* (*Climacoconus* (*Changshaconus*, *Reticulaconularia*))) based in part on uniquely shared characteristics of the transverse ornament in the corner sulcus. Later, Leme (2002) presented a cladistic parsimony analysis at the generic level of all of the suprageneric groups presented in Moore and Harrington (1956*b*), using the characters regarded by these authors as diagnostic. Her results indicated that, with the exception of the subfamily Ctenoconulariinae, none of these groups is monophyletic.

The purpose of our study was to investigate the phylogenetic relationships of a still broader array of conulariid genera, using current theories and techniques of cladistics and a larger number of characters than that considered by Moore and Harrington (1956*b*).

MATERIAL AND METHODS

Terminal taxa

A total of 20 taxa, including 16 ingroup genera and four outgroup taxa, were included in our analysis. All published genera in Conulariina are listed in Table 1. The 16 ingroup genera are *Archaeoconularia, Baccaconularia, Climacoconus, Conularia, Conulariella, Conularina, Ctenoconularia, Eoconularia, Glyptoconularia* (monospecific), *Metaconularia, Notoconularia, Paraconularia, Pseudoconularia, Reticulaconularia, Teresconularia* (monospecific) and *Vendoconularia* (monospecific) (see Table 1 for authors' names). These were included in the analyses based upon (1) their preservational state (complete, non-deformed and non-fragmented), (2) abundance (better represented in scientific collections) and (3) the amount and quality of information available in the literature. Following Marques and Collins (2004), Leme (2006) and Van Iten *et al.* (2006), we used the extant medusozoan taxa Cubozoa, Coronatae, Semaeostomeae and Stauromedusae as outgroups. Five of the ingroup genera, namely *Baccaconularia, Notoconularia, Reticulaconularia, Teresconularia* and *Vendoconularia,* were erected after the publication of the TIP. The remaining 11 genera (all included in the TIP) together contain a substantial majority (by our estimate more than 75 per cent) of the conulariid species described

TABLE 1. List of all published conulariid genera (* = ingroup genera of the present study).

GENERA	AUTHOR	TYPE SPECIES	GENERA RANGE
Adesmoconularia	Driscoll, 1963	*A. byblis*	Carboniferous
Anaconularia	Bouček, 1939	*C. anomala*	Ordovician
*Archaeoconularia**	Bouček, 1939	*C. insignis*	Ordovician–Silurian
Arthrochites	Chen Menge, 1982	*A. emeishanensis*	Cambrian
Australoconularia	Bischoff, 1978	*A. borenorensis*	Silurian
*Baccaconularia**	Hughes *et al.*, 2000	*B. robinsoni*	Cambrian
Beijingconularia	Xu Gueiyong and Li Fenglin, 1979	*B. planarea*	Carboniferous
Carinachites	Qian Yi, 1977	*C. spinatus*	Cambrian
Calloconularia	Sinclair, 1952	*C. strimplei*	Carboniferous
Cathayconularia	Xu Gueiyong and Li Fenglin, 1979	*C. qingshuijianensis*	Carboniferous
Changshaconus	Zhu Zhikang, 1985	*C. carinata*	Devonian
Cheliconularia	Waterhouse, 1986	*C. cheliensis*	Permian
Circonularia	Bischoff, 1978	*C. eosilurica*	Silurian–Devonian
*Climacoconus**	Sinclair, 1942	*C. quadrata*	Ordovician
*Conularia**	Miller, *in* Sowerby 1821	*C. quadrisulcata*	Ordovician–Permian
*Conulariella**	Bouček, 1928	*C. robusta*	Cambrian–Ordovician
*Conularina**	Sinclair, 1942	*C. triangulata*	Ordovician
Conulariopsis	Sugiyama, 1942	*C. quadrata*	Triassic
Conulariopsiella	Xu Gueiyong and Li Fenglin, 1979	*C. minima*	Ordovician
*Ctenoconularia**	Sinclair, 1952	*C. obex*	Ordovician
Diconularia	Sinclair, 1952	*C. micronema*	Silurian–Carboniferous
Emeiconularia	Qian Yi *et al.*, 1997	*E. trigemme*	Cambrian
*Eoconularia**	Sinclair, 1943	*C. loculata*	Ordovician–Silurian
Exoconularia	Sinclair, 1952	*C. exquisita*	Ordovician
Flectoconularia	Waterhouse, 1979	*F. abapertura*	Triassic
Garraconularia	Bischoff, 1978	*G. multicostata*	Silurian
*Glyptoconularia**	Sinclair, 1948	*G. gracilis*	Ordovician
Gondaconularia	Waterhouse, 1986	*C. elviniaria*	Permian–Triassic
Hexaconularia	He Yuanxiang and Yang Xianhe, 1986	*H. sichuanensis*	Cambrian
Holoconularia	Hergarten, 1985	*H. hummeli*	Devonian
Hunanoconularia	Xu Gueiyong and Li Fenglin, 1979	*H. hunanensis*	Devonian
Malvinoconularia	Babcock *et al.*, 1987[a]	*M. cahuanotensis*	Devonian
Mesoconularia	Bouček, 1939	*C. fragilis*	Devonian–Carboniferous
*Metaconularia**	Foerste, 1928	*C. aspersa*	Ordovician–Silurian
Neoconularia	Sugiyama, 1942	*N. rectangularis*	Permian
*Notoconularia**	Thomas, 1969	*C. inornata*	Permian
*Paraconularia**	Sinclair, 1940	*C. inaequicostata*	Devonian–Triassic
*Pseudoconularia**	Bouček, 1939	*P. grandissima*	Silurian
Pustuloconularia	Zhu Zhikang, 1985	*P. chinensis*	Permian
*Reticulaconularia**	Babcock and Feldmann, 1986*a*	*C. penouili*	Devonian
Sinusconularia	Hergarten, 1994	*S. blasii*	Devonian
Sphenothallus	Hall, 1847	*S. angustifolius*	Ordovician
Tasmanoconularia	Parfrey, 1982	*T. tuberosa*	Ordovician
*Teresconularia**	Leme *et al.*, 2003	*T. argentinensis*	Ordovician
*Vendoconularia**	Ivantsov and Fedonkin, 2002	*V. triradiata*	Vendian
Yinoconularia	Zhu Zhikang, 1985	*Y. huaqiaoensis*	Devonian

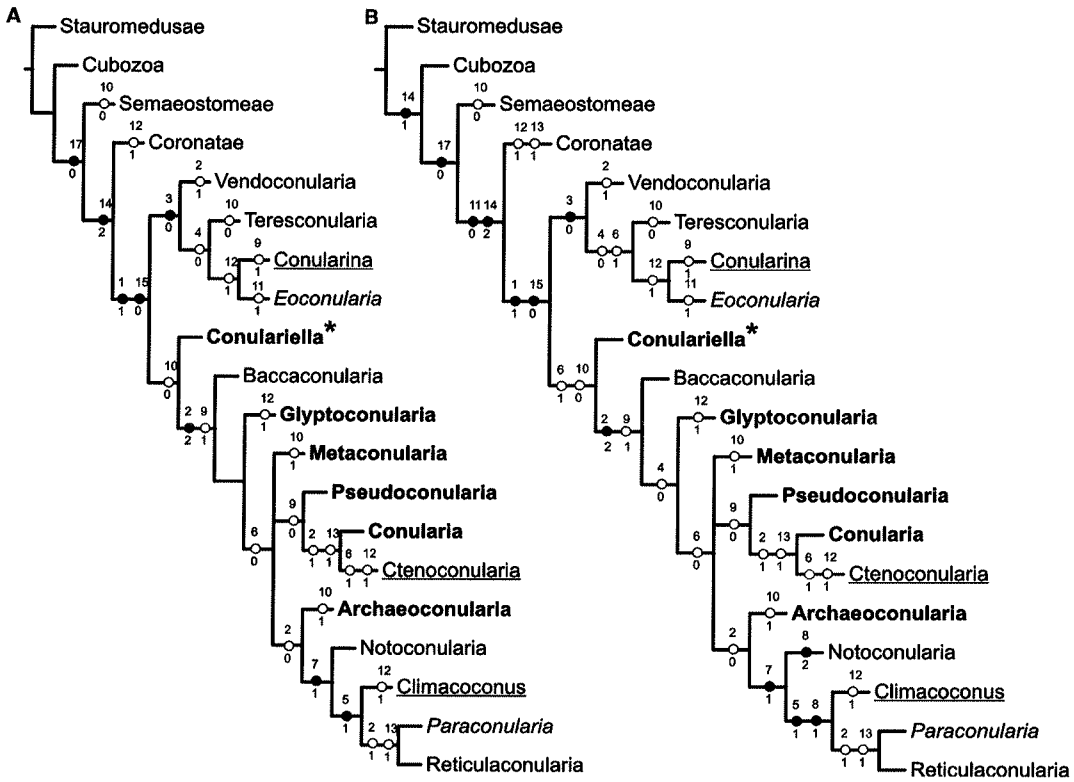
to date. Although the monophyly of the polyspecific ingroup genera has never been tested, we think the assumption that they are monophyletic is reasonable.

Many of the genera listed in Table 1, including most of those erected after the publication of the TIP, were not considered in this analysis. These include all conulariid-like small shelly fossils (*Arthrochites, Carinachites, Emeiconularia* and *Hexaconularia*; Conway Morris and Chen 1992; Qian Yi *et al.* 1997; Van Iten *et al.* 2005) and all genera of circonulariids (*Australoconularia, Circonularia* and *Garraconularia*; Bischoff 1978; Van Iten 1992*a*). Reasons for excluding these taxa include uncertainty

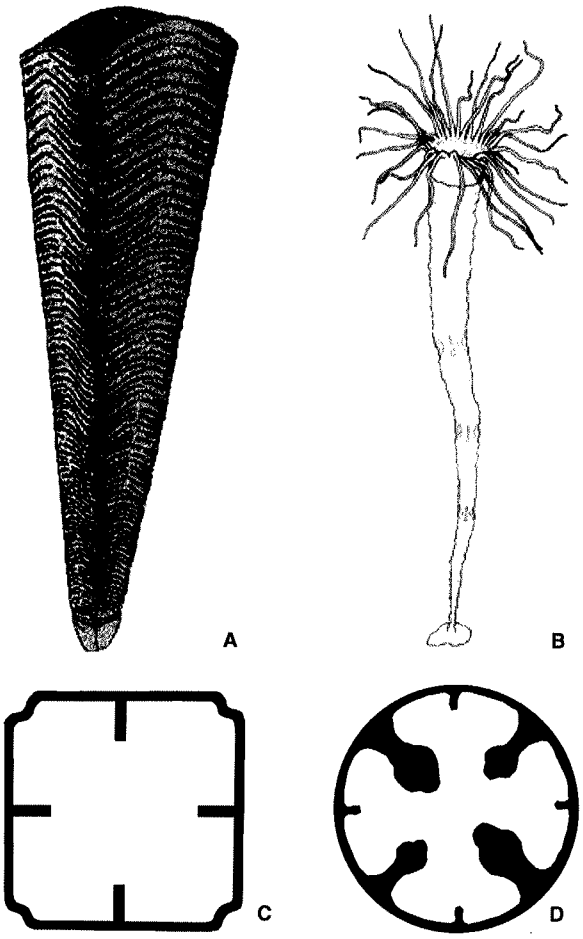
surrounding the phylogenetic affinities of conulariid-like small shelly fossils (Conway Morris and Chen 1992; Van Iten *et al.* 2005) and the generally fragmentary nature of available specimens of circonulariids (Bishoff 1978). At least two other genera have recently been placed in synonymy with *Conularia* (*Diconularia*; Babcock and Feldmann 1986*a*) or with *Paraconularia* (*Adesmoconularia*; Babcock and Feldmann 1986*b*), and *Malvinoconularia* probably is a junior synonym of *Reticulaconularia* (Leme *et al.* 2006). Similarly, when coding our 17 characters (see below) we found that many of the remaining genera (e.g. *Beijingconularia*, *Calloconularia*, *Cathayconularia*, *Cheiloconularia*, *Flectoconularia*, *Gondoconularia*, *Mesoconularia* and *Tasmanoconularia*) were identical to *Conularia* or *Paraconularia*, suggesting that they may not be valid taxa. The genera *Anaconularia* and *Exoconularia* were excluded because of the lack of specimens preserving skeletal material (all specimens previously described or discussed being internal moulds; e.g. see Barrande 1867). The genus *Conulariopsis* Sugiyama, 1942, the sole member of the monogeneric family Conulariopsidae, was also excluded because no specimens were available for examination and published information on this genus (Sugiyama 1942; Moore and Harrington 1956*b*) is scant. Finally, the genus *Sphenothallus* has been removed from the Conulata (Babcock and Feldmann 1986*a*).

Characters

Seventeen morphological characters, including 13 characters of the periderm, were scored for each taxon (see Appendix). Character (char.) state scores were determined through direct examination of specimens (collectively ranging in age from Cambrian to Triassic) and from data presented in recent publications (e.g. Van Iten 1992*a*; Ivantsov and Fedonkin 2002). In most cases, the state of a given character was the same for all published species of a given genus, making its code for the character decisive. In cases where multiple states of a given character occur in the same genus (e.g. presence and absence of carinae in *Climacoconus*; see Van Iten 1992*a*), the state of the type species of the genus was taken in order to preserve nomenclatural stability. Five of the 17 characters (1 and 14–17) are invariable for the ingroup



TEXT-FIG. 1. A, the successive weighting tree (L, 14.65238; CI, 0.7982; RI, 0.8767; RC, 0.6998) with ACCTRAN optimization. B, the successive weighting tree (L, 14.65238; CI, 0.7982; RI, 0.8767; RC, 0.6998) with DELTRAN optimization. Genera in bold face = subfamily Conulariinae; genera in italic font = subfamily Paraconulariinae; genera underlined = subfamily Ctenoconulariinae; * = family Conulariellidae.



TEXT-FIG. 2. Geometry (transverse cross section) of the periderm in oral section. A, C, quadrate (modified from Babcock and Feldmann 1986*a*). B, D, circular (modified from Bischoff 1978 and Van Iten 1992*a*, *b*).

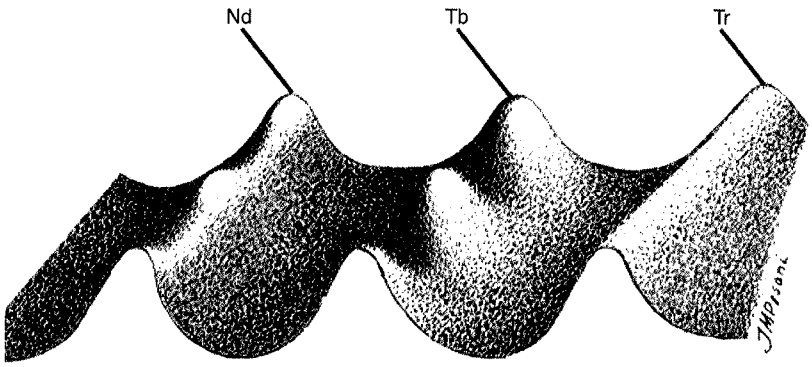
terminals. Ten of the peridermal characters (2, 4–7 and 9–13) were taken directly or with modification from the descriptions of genera and higher level conulariid taxa in Moore and Harrington (1956*a*). The remaining peridermal characters (3 and 14–15) and all other characters (1 and 16–17) are from Marques and Collins or other sources (character 3 is based in part on data in Jerre 1993). All characters were coded as binary or multistate and considered unordered. Non-comparable structures were coded as a hyphen (-). Finally, some characters (e.g. septa/carinae) are dependent upon the quality of preservation of the material (Simões *et al.* 2003) and theca portion available for study. This may weaken some of the interpretations in the discussion section below (e.g. multiple independent derivations or losses of internal characters such as septa/carinae).

Parsimony analysis

Cladistic analyses were carried out using the branch and bound algorithm of PAUP* 4.0.b10 (Swofford 2001). Primary analysis found the most parsimonious trees with unweighted characters. A complementary analysis was performed using successive approximation weighting (Farris 1969; see also Carpenter 1988, 1994) by maximum values of rescaled consistency indices (RC). Both ACCTRAN and DELTRAN optimizations were performed.

RESULTS

Unweighted analysis of the data matrix (Appendix) yielded 1057 trees (length L, 39; consistency index, CI, 0.4872; retention index, RI, 0.6552; re-scaled consistency index, RC, 0.3192), while successive weighting analysis (SW) resulted in 1 tree (L, 14.65238; CI, 0.7982; RI, 0.8767; RC, 0.6998) (Text-fig. 1A–B). This tree represents one of the 1057 trees obtained in the primary analysis. Some of the clades in the SW tree, which was generated using ACCTRAN (Text-fig. 1A) or DELTRAN (Text-fig. 1B) optimization, are supported exclusively by homo-



TEXT-FIG. 3. External ornamentation of the theca: Nd, nodes; Tb, tubercles; Tr, transverse ribs.

plasies. The internal group, which includes most of the genera placed by Moore and Harrington (1956*b*) in the suborder Conulariina, is monophyletic, being supported by two putative autapomorphies, namely the quadrate geometry of the oral region of the polyp and the presence of a mineralized periderm (Text-fig. 2).

Four clades nested within the internal group are supported by non-homoplastic synapomorphies. These are (*Vendoconularia, Teresconularia, Conularina, Eoconularia*), (*Baccaconularia, Glyptoconularia, Metaconularia, Pseudoconularia, Conularia, Ctenoconularia, Archaeoconularia, Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*), (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) and (*Climacoconus, Paraconularia, Reticulaconularia*).

Among the groups justified by non-homoplastic synapomorphies, the clade (*Vendoconularia, Teresconularia, Conularina, Eoconularia*), which contains the oldest conulariid (*Vendoconularia*), is supported by the sinusoidal geometry (as seen in longitudinal cross section) of the transverse facial ridges (char. 3; Pl. 1, fig. 1). The other clade (*Baccaconularia, Glyptoconularia, Metaconularia, Pseudoconularia, Conularia, Ctenoconularia, Archaeoconularia, Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) is supported by the presence of nodes or tubercles (char. 2; Text-fig. 3).

This putative synapomorphy was lost in the clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) (Text-fig. 1). Hence, the absence of nodes or tubercles has at least two distinct evolutionary histories. In the clade (*Vendoconularia, Teresconularia, Conularina, Eoconularia*), the nodes or tubercules were originally absent in the putative ancestors, but in the clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) these characters were secondarily lost (Text-fig. 1).

The clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*) is supported by termination of the transverse ribs and alternation of their ends in the corner sulcus (char. 7; Text-fig. 4B), and by the angular transverse cross section of the corner sulcus (again char. 7; Text-fig. 4B). Finally, the clade (*Climacoconus, Paraconularia, Reticulaconularia*) is united by alternation of the transverse ribs at the midline (char. 5; Text-fig. 4D).

DISCUSSION

The results of our analysis imply that many character states of the conulariid periderm underwent multiple independent derivations or losses. Septa (char. 10; Text-fig. 5), present in *Archaeoconularia, Conularina, Eoconularia, Metaconularia* and *Vendoconularia* (and in some species of several other genera; Van Iten 1992*a*; Van Iten *et al.* 1996), may have been independently derived in these genera. Alternatively, septa originally present in the most recent common ancestors of the two most inclusive subclades may have been lost in the genera (and species) now lacking them. Similar reasoning applies to carinae (char. 12; Text-fig. 5), which are present in all known species of three genera (*Conularina, Eoconularia* and *Glyptoconularia*) and in some species of four other genera, including *Paraconularia* (the type species of which, *P. inaequicostata* DeKoninck, 1883, lacks carinae). Indeed, if the latter four genera are in fact monophyletic, then carinae must have been independently lost or derived at least once in each of them.

In this connection it should be noted that the characterizations of conulariid midline and corner anatomy in Moore and Harrington (1956*b*) are incorrect in certain cases. For example, owing probably to reliance on the descriptions of Sinclair (1942, 1952), the TIP states that septa (internal midline thickenings) are absent in *Climacoconus* and that carinae (internal corner thickenings) are present in all *Ctenoconularia*. Both claims have been refuted by Van Iten (1992*a*) and Van Iten *et al.* (1996), who discovered internal midline structures in species of *Climacoconus* and also found that some specimens of *Ctenoconularia* lack carinae. Regarding the origin of septa and carinae, Jerre (1994) proposed that these structures developed in response to environmental stimuli, specifi-

EXPLANATION OF PLATE 1

Conulariid characters. Figs 1–2, longitudinal geometry (cross section) of the external ornamentation; 3–4, articulation; 5–6, arrangement of the external ornamentation along the facial midline; 7–8, corner sulcus ornamentation.

Fig. 1. *Eoconularia* sp., sinusoidal longitudinal geometry of the transverse ribs; × 50.

Fig. 2. *Climacoconus* sp., trochoidal longitudinal geometry of the transverse ribs; × 40.

Fig. 3. Face of *Conulariella sulca* showing rectilinear transverse ribs; arrow indicates midline region; scale bar represents 0.5 cm.

Fig. 4. Face of *Conularia elegantula* showing transverse ribs inflected at midline; arrow (midline region); × 25.

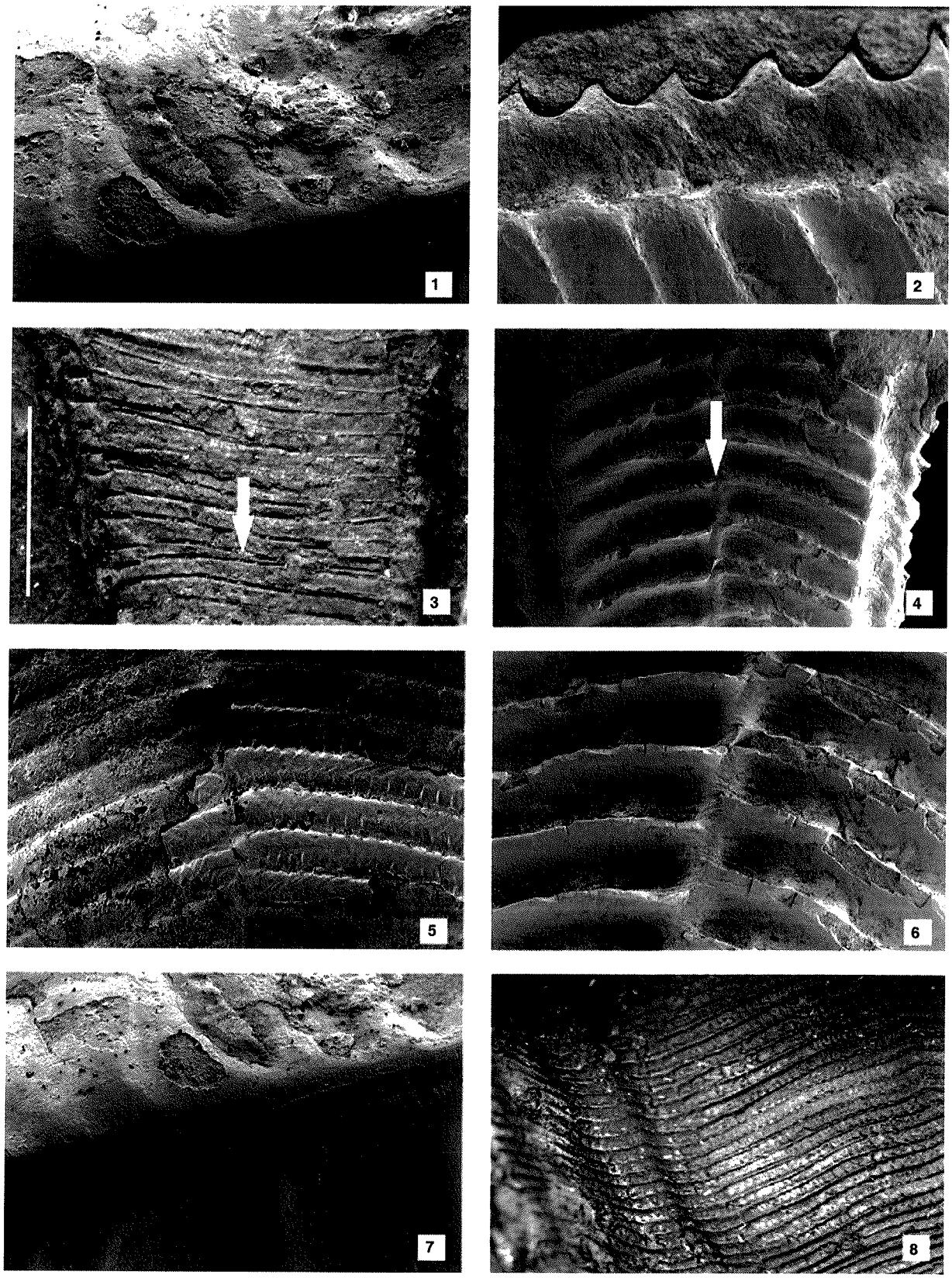
Fig. 5. *Ctenoconularia* with the transverse ribs in opposition along the facial midline; × 30.

Fig. 6. *Climacoconus* with the transverse ribs alternating along the facial midline; × 50.

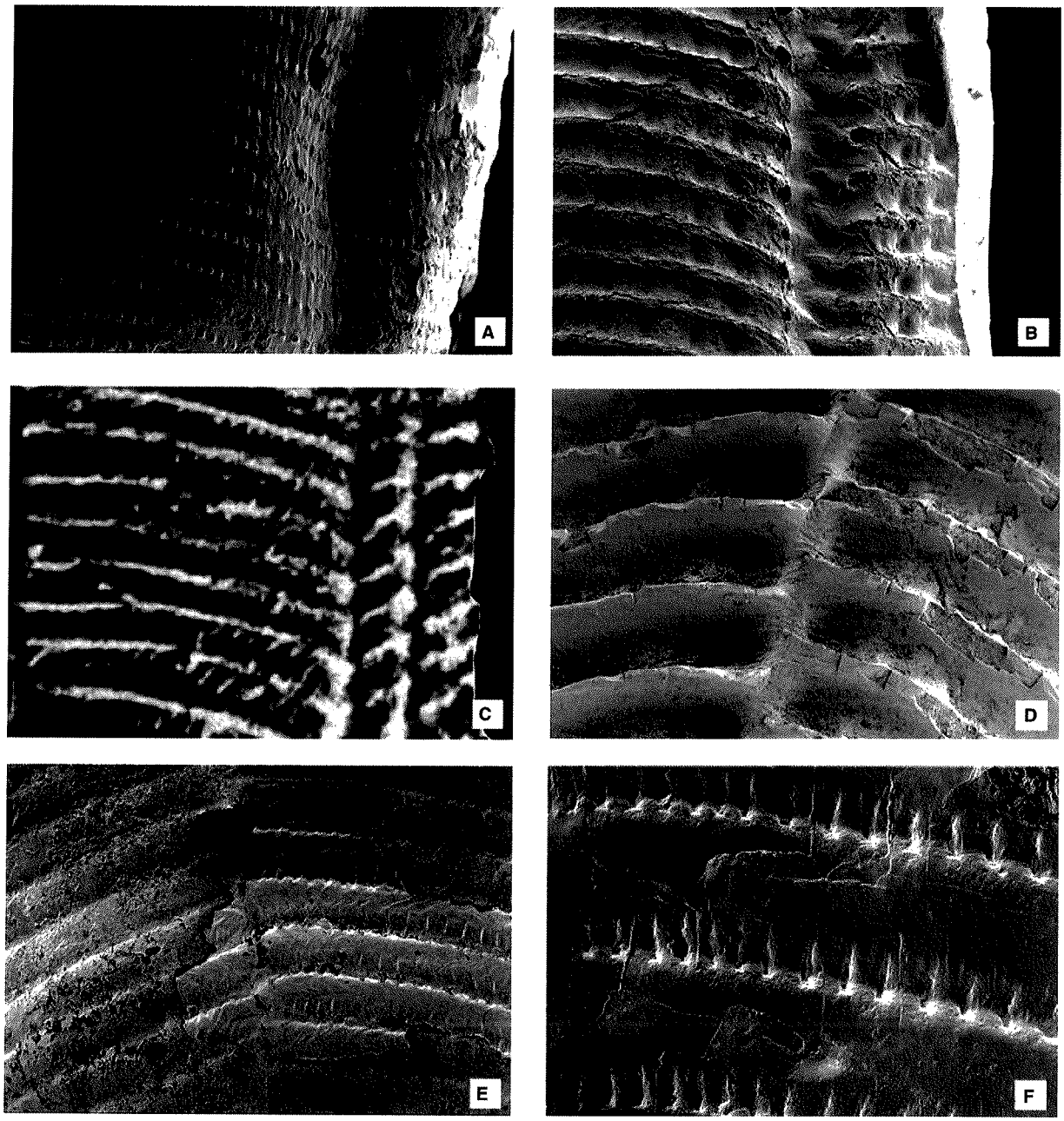
Fig. 7. *Eoconularia* with corner sulcus ornamentation absent; × 50.

Fig. 8. *Conularia quichua* with corner sulcus ornamentation present; × 2.

PLATE 1

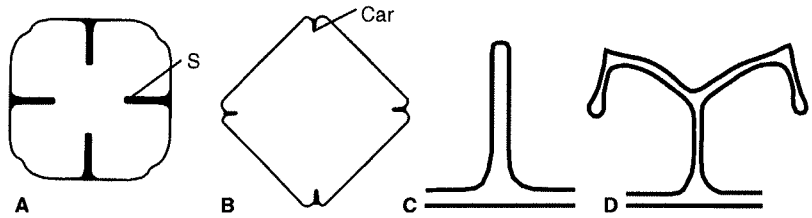


LEME *et al.*, conulariid characters



TEXT-FIG. 4. Conulariid characters. A–C, arrangement of the corner sulcus ornamentation and corner sulcus morphology; D–E, external ornamentation at the midline; F, crests. A, *Metaconularia*, continuous arrangement of the corner sulcus ornamentation and rounded corner sulcus; × 25. B, *Reticulaconularia*, interlaced arrangement of the corner sulcus ornamentation and angulated corner sulcus; × 25. C, *Notoconularia*, interlaced arrangement of the corner sulcus ornamentation and angulated corner sulcus with mesial external fold; reproduced from Thomas (1969, *Journal of Paleontology*, **43**, pl. 149, fig. 4c) × 1. D, *Climacoconus quadratus*, midline with external ridge; × 50. E, *Conularia pyramidalis*, external ornamentation at the midline absent, × 30. F, *Ctenoconularia*, crests present (absent in D); × 120.

cally to conditions of high current energy; however, this hypothesis conflicts with autochthonous occurrences of thin-shelled, carina- or septa-bearing conulariids in strata deposited in low energy environments below storm wave-base (e.g. Simões *et al.* 2000; Rodrigues *et al.* 2003). Finally, multiple independent derivations or losses are



TEXT-FIG. 5. A–B, septa and carina. A, *Eoconularia loculata*. B, *Climacoconus sinclairi*. C–D, septal morphology. C, straight septa. D, bifurcating septa. S, septa; Car, carina.

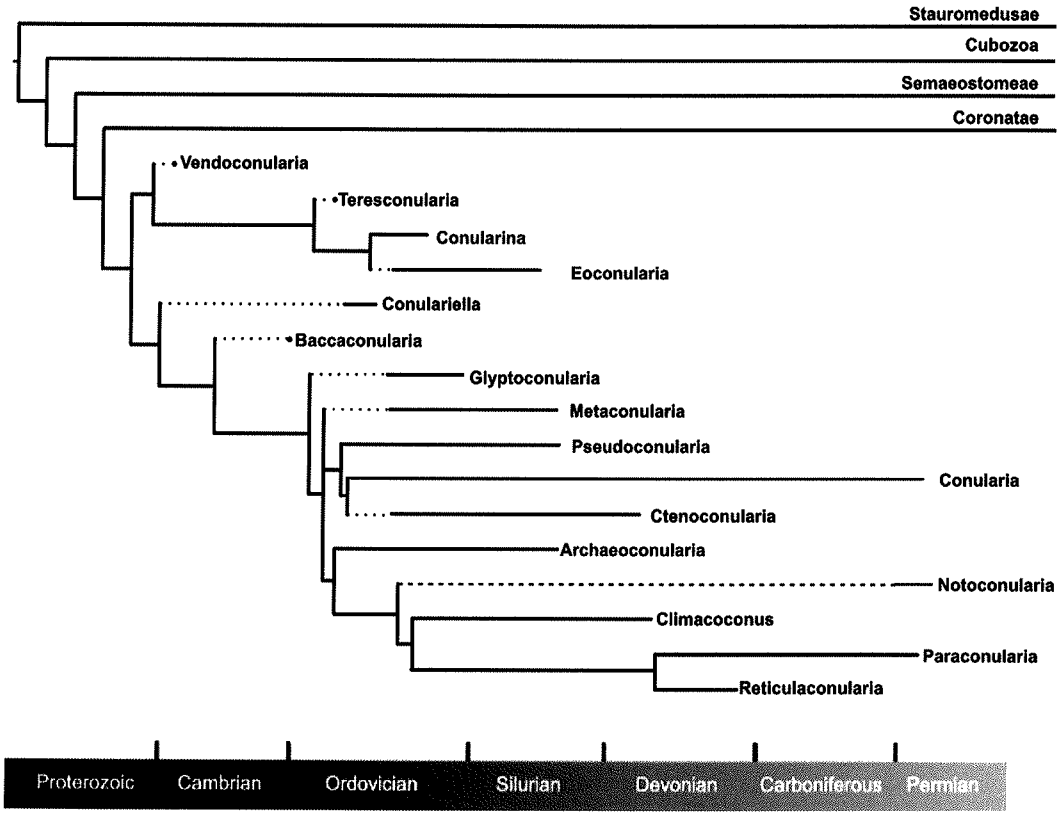
also implied for features of the external ornament (e.g. independent loss of nodes in *Conularina* and *Eoconularia*), the anatomy of the midlines (e.g. independent derivation of an external ridge at the midline in *Climacoconus* and *Pseudoconularia*), and the anatomy of the interspaces (e.g. independent losses of crests or interspace ridges in *Climacoconus* and *Metaconularia*).

As noted above, none of the conulariid subfamilies recognized in the TIP (Moore and Harrington 1956*b*) was recovered in the present analysis. The subfamily Conulariinae, conceived by Moore and Harrington (1956*b*) as consisting of *Anaconularia, Archaeoconularia, Conularia, Diconularia, Exoconularia, Mesoconularia* and *Metaconularia*, forms part of the single polytomy and is probably paraphyletic. Paraconulariinae, conceived by Sinclair (1952) as consisting of *Calloconularia, Eoconularia, Neoconularia* and *Paraconularia*, and Ctenoconulariinae, conceived, again by Sinclair (1952), as consisting of *Climacoconus, Conularina, Ctenoconularia* and *Sphenothallus*, are both polyphyletic. According to Moore and Harrington (1956*b*), the subfamily Conulariinae is characterized by continuation of the transverse ornament (transverse ribs or transverse tubercle rows) across the corner sulcus and by the absence of internal thickening of the periderm at the corners. The subfamily Paraconulariinae is characterized by the presence of an angular (transversely) corner sulcus in which the transverse ribs terminate, with the ends of the ribs from one face alternating and interlocking with the ends of the ribs from the other face. The subfamily Ctenoconulariinae is characterized by the presence of an internal carina or other thickening at the corner sulcus.

Results of our analysis show that the single diagnostic character of Conulariinae (continuation of the transverse ribs or tubercle rows across the corner sulcus) is a symplesiomorphy. As implied above, the single diagnostic character of Paraconulariinae is a synapomorphy of the clade (*Notoconularia, Climacoconus, Paraconularia, Reticulaconularia*), and the single diagnostic character of Ctenoconularinae is probably a non-homologous similarity, having undergone multiple independent derivations, as suggested above. Finally, and not surprisingly, our analysis did not recover the monogeneric family Conulariellidae (type genus *Conulariella*). Erection of this family was clearly based on the philosophy that degree of morphological distinctness is a valid criterion of classification (see Moore and Harrington 1956*b*).

Text-figure 6 incorporates information on the stratigraphic ranges of the ingroup taxa and reveals a number of interesting temporal patterns. For example, the basalmost clade (*Vendoconularia, Teresconularia, Conularina* and *Eoconularia*) contains the oldest conulariid (*Vendoconularia*; Vendian) and the oldest conulariid (*Teresconularia*; Lower Ordovician) from South America. The basalmost genus (*Baccaconularia*) of the most inclusive conulariid subclade is the oldest known conulariid from North America. Three of the genera in the clade (*Notoconularia, Climacoconus, Paraconularia* and *Reticulaconularia*) have the most recent first occurrences (Lower Devonian and Lower Permian) of any conulariids, though according to our cladogram the lineage leading to *Notoconularia*, currently known from the Permian, split from the other members of the clade in the Ordovician. Our cladogram also implies lower range extensions for *Conulariella* (at least into the Upper Cambrian), *Glyptoconularia* (at least into the Lower Ordovician) and *Metaconularia* (at least into the Lower Ordovician).

Finally, although we cannot say where the various lineages of conulariids originated, the data in Table 1 show that the palaeogeographical distribution of conulariids was global throughout most of their history. The earliest conulariids (*Vendoconularia* and *Baccaconularia*; Vendian–Late Cambrian) inhabited siliciclastic environments, but they occurred at both low (*Baccaconularia*) and high (*Vendoconularia*) latitudes. During Middle–Late Ordovician times, when most conulariid genera appear to have originated, conulariids occurred both in low latitude, carbonate-platform settings, mainly in Laurentia and Baltica, and in middle–high latitude, siliciclastic-shelf settings, in Perigondwana and Gondwana. This pattern continued through the Late Carboniferous. For example, Devonian *Conularia* and *Paraconularia* occurred both in low latitude, warm-water carbonate environments (e.g. the Upper Mississippi Valley, Laurentia) and in middle–high latitude, cool-water siliciclastic environments (e.g. the Paraná Basin of Brazil). In addition to tolerating both warm- and cool-water conditions, Ordovician–Permian conulariids inhabited oxic nearshore and dysoxic offshore environments.



TEXT-FIG. 6. The successive weighting tree (L, 14.65238; CI, 0.7982; RI, 0.8767; RC, 0.6998) showing the known stratigraphic distribution of the ingroup genera. Stratigraphic ranges based on data in Sinclair (1948), Thomas (1969), Waterhouse (1979), Ivantsov and Fedonkin (2002) (*Vendoconularia*), Leme *et al.* (2003) (*Teresconularia*) and Van Iten and Vhylasova (2004).

CONCLUSIONS

Cladistic analysis using character weighting shows that an internal group consisting of most of the genera classified by the TIP as conulariids is monophyletic and united by two autapomorphies, namely the presence of a mineralized periderm and the quadrate transverse cross section of the oral region of the periderm. In contrast, many other characters, some of which have been used to diagnose suprageneric groups, are homoplastic. Indeed, none of the suprageneric groups recognized in the TIP, namely the families Conulariidae and Conulariellidae and the subfamilies Conulariinae, Paraconulariinae and Ctenoconulariinae, was recovered in our analysis. All of these groups are based on symplesiomorphies and/or homoplasies. Consequently, the suprageneric taxonomy of the subclass Conulata (Moore and Harrington 1956*b*) must be revised in order to reflect the relative degrees of phylogenetic relatedness of its component genera. In spite of the exclusion of many previously erected genera, and the assumed (untested) monophyly of the included genera, our analysis provides a framework for future research on conulariid taxonomy. At present, conulariid genera may be assigned to the phylum Cnidaria (e.g. Moore and Harrington 1956*a*, *b*; Bischoff 1978; Van Iten 1991*a*, 1992*a*, *b*), class Scyphozoa (Marques and Collins 2004; Van Iten *et al.* 2006) and order Conulariida Miller and Gurley, 1896. Moreover, all of the genera analyzed here must be assigned to the family Conulariidae Walcott, the only valid family of conulariids.

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APPENDIX

Character matrix

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
Stauromedusae	0	-	-	-	-	-	-	-	-	1	1	0	-	0	-	0/1	1
Cubozoa	0	-	-	-	-	-	-	-	-	1	1	0	-	1	1	0/1	1
Semaeostomeae	0	-	-	-	-	-	-	-	-	0	-	-	-	1	1	0	0
Coronatae	0	0	1	1	0	0	0	-	0	1	0	1	1	2	1	0	0
Vendoconularia	1	1	0	1	0	0	0	0	0	1	0	0	0	2	0	0	0
Archaeoconularia	1	0	1	0	0	0	0	0	1	1	0	0	0	2	0	0	0
Baccaconularia	1	2	-	1	0	1	-	-	1	0	-	0	0	2	0	0	0
Climacoconus	1	0	1	0	1	0	1	1	1	0	-	1	0	2	0	0	0
Conularia	1	1	1	0	0	0	0	0	0	0	-	0	1	2	0	0	0
Conulariella	1	0	1	1	0	1	-	0	0	0	-	0	0	2	0	0	0
Conularina	1	0	0	0	0	1	-	0	1	1	0	1	0	2	0	0	0
Ctenoconularia	1	1	1	0	0	1	-	0	0	0	0	1	1	2	0	0	0
Eoconularia	1	0	0	0	0	1	-	0	0	1	1	1	0	2	0	0	0
Glyptoconularia	1	2	-	0	0	1	-	0	1	0	-	1	0	2	0	0	0
Metaconularia	1	2	-	0	0	0	0	0	1	1	0	0	0	2	0	0	0
Notoconularia	1	0	1	0	0	0	1	2	1	0	-	0	0	2	0	0	0
Paraconularia	1	1	1	0	1	0	1	1	1	0	-	0	1	2	0	0	0
Pseudoconularia	1	2	-	0	0	0	0	0	0	0	-	0	0	2	0	0	0
Reticulaconularia	1	1	1	0	1	0	1	1	1	0	-	0	1	2	0	0	0
Teresconularia	1	0	0	0	0	1	-	-	0	0	-	0	0	2	0	0	0

Characters and character states

1. *Transverse cross section of the oral region of the polyp (0: Circular; 1: Quadrate).* The periderm (and, presumably, the soft polyp that made the periderm) of nearly all conulariids exhibits a quadrate geometry, though some rare specimens show a triangular, pentagonal or hexagonal transverse cross section (Babcock *et al.* 1987*b*; Leme 2002; Leme *et al.* 2004; Van Iten *et al.* 2005; Rodrigues *et al.* 2006). Polyps in Cubozoa, Coronatae, Semaeostomeae and Stauromedusae are circular throughout their length (Text-fig. 2).
2. *External ornamentation of the periderm (0: Transverse ribs; 1: Nodes; 2: Tubercles).* In conulariids and coronate polyps, transverse ribs are straight to arcuate ridges. They may be sites of peridermal thickening or they may be unthickened. In conulariids they may be interrupted at the corners (perradii) and/or midlines (interradii). Also in conulariids, nodes are small, discrete thickenings associated with transverse ribs. Nodes that are not associated with transverse ribs are referred to here as tubercles (Text-fig. 3).
3. *Longitudinal cross section of the transverse ribs (0: Sinusoidal; 1: Trochoidal)* (Pl. 1, figs 1–2). In most conulariids showing transverse ribs the crests of the ribs are more or less sharp (trochoidal), but in some conulariids the crests are gently rounded and thus the ribs resemble a sine curve in longitudinal cross sections (sinusoidal).
4. *Inflection (adapertural arching) of the transverse ornament at the interradii (0: Present; 1: Absent).* In conulariids, the interradii may be associated with inflection of the transverse ornament (Pl. 1, figs 3–4).
5. *Offset of the transverse ornament at the interradii (0: Absent; 1: Present).* In conulariids bearing transverse ribs, all or some of the transverse ribs may terminate at the interradii (midlines). In such cases, the ends of the transverse ribs generally are arranged in alternation (Pl. 1, figs 5–6).
6. *Continuation of the transverse facial ornament across the perradii (0: Present; 1: Absent).* In pyramidal conulariids, transverse ornamentation (ribs or tubercle rows) may cross the perradii (corners), with or without disruption and offset, or they may terminate on the margins of the corner sulcus (Pl. 1, figs 7–8). In coronate polyps (and circonulariids), the transverse ornament is continuous around the entire periderm.
7. *Nature of the transverse ornamentation at the perradii (0: Continuous; 1: Disrupted).* In certain conulariids and coronate polyps, the transverse ribs cross the perradii (corners in conulariids), though in conulariids they are slightly deflected toward the oral end (continuous). In other conulariids, the transverse ribs terminate within the corner sulcus (disrupted), where the ends of the ribs from one face alternate and interlock with the ends of the ribs from the other face (Text-fig. 4A–B).
8. *Transverse cross section of the corner sulcus (0: Rounded; 1: Angulated; 2: Angulated with fold).* Viewed in transverse cross sections, the corner sulcus may be rounded, angulated or angulated with an external mesial fold (Text-fig. 4A–C).
9. *External peridermal ornamentation at the interradii (0: Absent; 1: Present).* In certain conulariids the interradii (midlines) are marked by an external ridge that is either straight or zigzagged (Text-fig. 4D–E).
10. *Septa (0: Absent; 1: Present).* In the periderm of conulariids and coronate polyps, septa are single or paired, continuous or seriated internal thickenings or invaginations located at the interradii (midlines in conulariids) (Text-fig. 5). When possible, transverse cross sections were taken in the basal portion of thecae of *Conularia* and *Paraconularia.*
11. *Morphology of the gastric septa (0: Simple; 1: Bifurcated).* These soft part structures, inferred to have been present in conulariids (see in particular, Jerre 1994), may be simple, unbranched infoldings of the gastric cavity or strongly bifurcated (Y-shaped) (Text-fig. 5).
12. *Carina (0: Absent; 1: Present).* In the periderm of conulariids and coronate polyps, carinae are broadly rounded to keel-like, continuous or seriated internal thickenings or invaginations located at the perradii (corners in pyramidal conulariids) (Text-fig. 5).
13. *Crests (0: Absent; 1: Present).* In conulariids having transverse ribs and coronate polyps, the interspaces between the transverse ribs may be corrugated (Text-fig. 4F). The term crests refers to the longitudinal ridges seen when viewing corrugated interspaces from the exterior.
14. *Periderm (0: Absent; 1: Present but limited to the basal area of polyp; 2: Present and covering most of polyp).* The periderm is absent in Stauromedusae, present but limited to the basal area of the polyp in Cubozoa or covers most of the polyp in Coronatae and conulariids (Marques and Collins 2004; Van Iten *et al.* 2006).
15. *Mineralized periderm (0: Present; 1: Absent).* In taxa having a periderm, this structure can be mineralized or non-mineralized.
16. *Symmetry (0: Radial tetramerous; 1: Biradial).* Coronatae, Semaeostomeae and conulariids present radial tetramerous symmetry during the polypoid phase. Cubozoa and Stauromedusae show radial tetramerous and biradial symmetry (scored as polymorphic), having only two primary tentacles early in the ontogeny of the polyps (Salvini-Plawen 1978; Marques and Collins 2004).
17. *Type of medusa formation (0: Strobilation; 1: Metamorphosis without transverse fission).* Strobilation involves transverse fission and occurs only in Coronatae, Semaeostomeae and Rhizostomeae (Werner *et al.* 1971; Kikinger and Salvini-Plawen 1995; Stangl *et al.* 2002; Marques and Collins 2004). In both Cubozoa and Stauromedusae, adult medusae are produced by a metamorphosis which involves the resorption of polyp tentacles and the development of new tentacles without transverse fission. Although the evidence for strobilation in conulariids (Van Iten 1989, 1991*a*) is controversial (Hughes *et al.* 2000), results of the cladistic analysis of Van Iten *et al.* (2006) imply that conulariids are at least descended from ancestors with strobilation and ephyrae.

2.3. LEME, J. M.; GHILARDI, R.; BISSARO JUNIOR, M. C., 2015. Conulários do Devoniano do Brasil: importância paleobiogeográfica. Boletim do Museu Paraense Emílio Goeldi. Ciências Naturais, v. 10, p. 233-236.

Conulários são cnidários, extintos, com teca fosfática. Representantes desse grupo ocorrem em uma variedade de fácies sedimentares do Pré-Cambriano ao Triássico. Conulários são característicos das faunas do Domínio Malvinocáfrico, sendo abundantes nas concentrações fossilíferas do Devoniano. Outras ocorrências são verificadas na Argentina, Peru, Paraguai, Uruguai e África do Sul. No Brasil, ocorrências de conulários são verificadas nas bacias do Amazonas, do Parnaíba e do Paraná. A fauna de conulários do Devoniano do Brasil é pouco diversificada, com três espécies, especialmente quando comparada com a fauna coeva da Bolívia, caracterizada por cinco espécies. *C. quichua* é a espécie dominante no Brasil e na Bolívia. A ampla distribuição paleobiogeográfica das espécies no âmbito do Domínio Malvinocáfrico sugere que essas foram euritérmicas, uma vez que ocorrem em terrenos das províncias Andina, Brasileira e Malvinocáfrica Sul-africana. Essas duas últimas englobam áreas que estiveram situadas nas altas latitudes, próximas do pólo sul devoniano, enquanto a Andina esteve localizada em torno dos 40° a 45° de latitude sul. A presença de *C. quichua* na Bacia do Amazonas reforça o caráter cosmopolita da espécie e demonstra a viabilidade de comunicações paleobiogeográficas entre os diferentes domínios do Devoniano Médio a Superior das bacias intracratônicas da América do Sul.

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Conulários do Devoniano do Brasil: importância paleobiogeográfica

Conulariids of Devonian of Brazil: paleobiogeography importance

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Resumo: Conulários são cnidários extintos, na maioria das vezes com teca fosfática, ocorrendo do Pré-Cambriano ao Triássico. Eles são característicos nas faunas do Domínio Malvinocáfrico, sendo abundantes em concentrações fossilíferas devonianas. Outras ocorrências são verificadas na Argentina, Peru, Paraguai, Uruguai e África do Sul. No Brasil, ocorrem nas bacias do Amazonas, do Parnaíba e do Paraná. A fauna de conulários do Devoniano do Brasil é pouco diversificada, quando comparada com a fauna coeva da Bolívia. *Conularia quichua* é a espécie dominante no Brasil e na Bolívia. A ampla distribuição paleobiogeográfica das espécies no Domínio Malvinocáfrico sugere que essas foram euritérmicas, uma vez que ocorrem em terrenos das províncias Andina, Brasileira e Malvinocáfrica Sul-Africana. Essas duas últimas englobam áreas que estiveram situadas nas altas latitudes, próximas do pólo sul devoniano, enquanto a Andina esteve localizada em torno dos 40° a 45° de latitude sul. A presença de *C. quichua* na Bacia do Amazonas reforça o caráter cosmopolita da espécie e demonstra a viabilidade de comunicações paleobiogeográficas entre os diferentes domínios do Devoniano Médio a Superior das bacias intracratônicas da América do Sul. Aqui são apresentadas informações sobre a discussão das implicações paleobiogeográficas das diferentes ocorrências de conulários no Devoniano do Brasil.

Palavras-chave: Conulatae. Devoniano. Bacia do Paraná. Bacia do Parnaíba. Bacia do Amazonas. Paleobiogeografia.

Abstract: Conulariids are extinct cnidarians, in most cases with phosphate carapace, occurring from Precambrian to Triassic. Conulariids are characteristic of faunas of Malvinokaffric Realm, being abundant in the Devonian fossil assemblages. Other occurrences are observed in Argentina, Peru, Paraguay, Uruguay and South Africa. In Brazil, occurr in the Amazon, Paraná and Parnaíba basins. The Devonian fauna of conulariids in Brazil is undiversified, when compared with the coeval fauna in Bolivia. *Conularia quichua* is the dominant species in Brazil and Bolivia. The wide paleobiogeographic distribution of species in the Malvinokaffric Realm suggests that these were eurythermal, once occurring on lands of Andean, Brazilian and South African Malvinokaffric provinces. These last two areas were located at high latitudes, near the Devonian South Pole, while the Andean was located around 40° to 45° south latitude. The presence of *C. quichua* in the Amazon Basin reinforces the cosmopolitan character of the species and demonstrates the feasibility of paleobigeographical communications between the different areas of the Middle and Upper Devonian of the intracratonic basins of South America. Here we present data about discussion of paleobiogeographical implications of different occurrences of conulariids in the Devonian of Brazil.

Keywords: Conulatae. Devonian. Paraná Basin. Parnaíba Basin. Amazon Basin. Paleobigeography.

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INTRODUÇÃO

Conulários são cnidários extintos, bentônicos, sésseis de epifauna, com teca piramidal, alongada e, na maioria das vezes, fosfática, com quatro faces (Babcock, 1991; Van Iten, 1991a; Leme *et al.*, 2004, 2008, 2010; Van Iten *et al.*, 2013, 2014) (Figura 1). Representantes desse grupo de invertebrados ocorrem em uma ampla variedade de fácies sedimentares, especialmente de águas rasas, plataformais, em ambientes siliciclásticos e carbonáticos do Neoproterozoico ao Triássico (McMenamin, 1987; Jerre, 1994; Van Iten, 1991b; Van Iten *et al.*, 1996, 2005, 2013, 2014; Ivantsov & Fedonkin, 2002; Yuan *et al.*, 2011).

Conulários são característicos nas faunas do Domínio Malvinocáfrico (Richter & Richter, 1942; Clarke, 1913; Kozlowski, 1913, 1923; Babcock *et al.*, 1987; Leme *et al.*, 2004), sendo extremamente abundantes nas concentrações fossilíferas do Devoniano da Bolivía (*e.g.*, Babcock *et al.*, 1987). Outras ocorrências importantes na América do Sul são verificadas também na Argentina (*e.g.*, Thomas, 1905), no Peru (*e.g.*, Steinmann, 1930), no Paraguai (Babcock *et al.*, 1990), no Uruguai (*e.g.*, Mendéz-Alzola & Sprechmann, 1973) e na África do Sul (*e.g.*, Schwarz, 1906). No Brasil, conulários são abundantes nas bacias paleozoicas (Bacia do Paraná, Bacia do Parnaíba e Bacia do Amazonas), sendo a principal ocorrência no Devoniano (Clarke, 1899, 1913; Kozlowski, 1913, 1923; Kegel, 1953; Babcock *et al.*, 1987; Melo, 1988; Siviero, 2002; Leme *et al.*, 2004). Também ocorrem no Ediacarano, Grupo Corumbá, Formação Tamengo (Van Iten *et al.*, 2014).

Na Bacia do Paraná, ocorrências espetaculares de conulários, dada sua abundância, qualidade e modo de preservação, são verificadas na Formação Ponta Grossa (Clarke, 1913; Kozlowski, 1913; Simões *et al.*, 2003; Rodrigues *et al.*, 2003; Leme *et al.*, 2004). Clarke (1913) identificou as espécies *Paraconularia africana*, *P. ulrichana* e *C. quichua* (Figuras 2A-2C) nos sedimentitos da Formação Ponta Grossa, nas regiões de Tibagi, Jaguariaíva e Ponta Grossa (Paraná). Leme *et al.* (2004) identificou que os conulários da Formação Ponta Grossa são fortemente

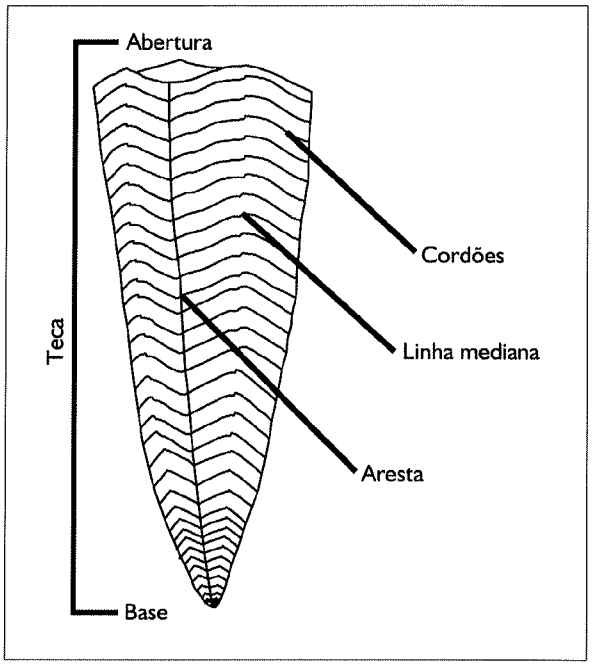

Figura 1. Morfologia geral dos conulários, com as principais feições e termos morfológicos utilizados nas descrições anatômicas.

representados pelas espécies cosmopolitas *C. quichua* e *P. africana*, porém a fauna de conulários é dominada por *C. quichua*. A morfologia de *C. quichua* e *P. africana* foi redescrita por Leme *et al.* (2004), sendo mais detalhada do que a descrita por Clarke (1913) e Babcock *et al.* (1987). A fauna de conulários da Formação Ponta Grossa do Paraná é, portanto, pouco diversificada, especialmente se comparada com faunas coevas da Bolívia (Leme *et al.*, 2004).

Em relação à tafonomia, Rodrigues *et al.* (2003) reforçou a ideia de que conulários presentes nos depósitos da Formação Ponta Grossa são animais bentônicos de epifauna preservados em diferentes classes tafonômicas, cujos processos de preservação são bastante complexos. Na seção de Jaguariaíva foi observado que a distribuição vertical dos conulários não é aleatória, já que os mesmos ocorrem em dois intervalos estratigráficos onde depósitos de sufocamento associados às tempestades estão amalgamados. Desta forma, os dados tafonômicos apresentados por Rodrigues *et al.* (2003) contribuíram para

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o melhor entendimento da paleobiologia desse enigmático grupo de cnidários extintos.

Adicionalmente, Simões *et al.* (2003) verificaram que, dependendo do modo de preservação de conulários no Devoniano da Bacia do Paraná, podem ocorrer alterações morfológicas dos espécimes. Foram descritos exemplares de uma mesma espécie, preservados tanto de modo inflado na matriz quanto fortemente comprimidos. Nesse sentido, torna-se problemática a comparação de caracteres morfométricos (*e.g.*, ângulo apical, ângulo do cordão, espaçamento relativo entre os cordões) entre exemplares tafonomicamente distintos, como até então havia sido feito na literatura (Babcock & Feldmann, 1986a, 1986b; Babcock *et al.*, 1987). Essas feições, especialmente as características biométricas, são passíveis de alterações, dependendo do grau de achatamento e da direção dos esforços tensionais, se horizontais ou verticais.

Contrariamente à frequência de publicações voltadas aos conulários da Bacia do Paraná, seu estudo nas demais bacias paleozoicas brasileiras é esparso. Na Bacia do Parnaíba, Kegel (1953) apresentou um dos trabalhos pioneiros sobre a fauna de invertebrados marinhos fósseis do Devoniano. Siviero (2002) desenvolveu uma dissertação de mestrado acerca dos conulários da Bacia do Parnaíba, identificando que a fauna de conulários desta unidade geológica também é dominada por *C. quichua*.

Na Bacia do Amazonas, Clarke (1899) descreve conulários que ocorrem no Grupo Trombetas (Siluriano Superior), identificados como *Conularia amazonica* (Figura 2D). Na porção devoniana da Formação Manacapuru (Lochkoviano Inferior), *C. quichua* foi identificada por Ramos *et al.* (2003) (Figura 2E). Recentemente, foi encontrada uma amostra fóssil de conulário na Formação Maecuru, no estado do Pará, identificada como *C. quichua* (Figura 2F). Este fóssil foi encontrado, mais precisamente, na margem direita do rio Jari, na fronteira entre os estados do Pará e do Amapá, durante os trabalhos de resgate e salvamento paleontológico realizado na área de influência direta da Usina Hidrelétrica Santo Antônio do Jari (coordenadas UTM 9.934.456 N/319.654 E, datum WGS 84). Essas novas ocorrências na Bacia do Amazonas reforçam a ideia de que *C. quichua* é cosmopolita e representa a espécie dominante no Domínio Malvinocáfrico. Portanto, são aqui apresentados os dados bibliográficos disponíveis para discussão das implicações paleobiogeográficas das diferentes ocorrências de conulários no Devoniano do Brasil.

PALEOBIOGEOGRAFIA DA FAUNA DE CONULÁRIOS DO DEVONIANO DO BRASIL

O Devoniano é caracterizado pela existência de três domínios paleobiogeográficos, denominados de Américas Orientais, Velho Mundo e Malvinocáfrico, os quais são bem caracterizados por suas faunas de braquiópodes (*e.g.*, Spiriferida) e trilobitas (*e.g.*, Calmoniidae) (Boucot, 1974, 1985). O Domínio Malvinocáfrico foi inicialmente proposto por Richter & Richter (1942) para definir uma província englobando localidades austrais, caracterizada pelo alto grau de endemismo da fauna de trilobitas (Eldredge & Ormiston, 1979). De fato, o Domínio Malvinocáfrico é bem definido na porção ocidental do Gondwana, havendo, ao norte do supercontinente, áreas transicionais entre os três domínios.

O provincialismo exibido pelas faunas de trilobitas e braquiópodes que caracterizam o Domínio Malvinocáfrico é mais pronunciado durante o Praguiano, Emsiano e Eifeliano, englobando amplas áreas marinhas rasas nas altas latitudes do hemisfério Sul. O domínio abrangeria, portanto, terrenos devonianos do Peru, da Bolívia, do Chile, do Paraguai, da Argentina, do Brasil, do Uruguai, da Antártica e da África do Sul (Boucot *et al.*, 1969; Boucot, 1971; Eldredge & Ormiston, 1979; Melo, 1988).

Fundamentados nas ocorrências de trilobitas da América do Sul, Eldredge & Ormiston (1979) propuseram subdividir o Domínio Malvinocáfrico em três províncias, denominadas de Província Andina, Província Brasileira e Província Malvinocáfrica sul-africana (Figura 3). No Brasil, a Bacia do Paraná constitui a principal área de abrangência da Província Brasileira, no âmbito do Domínio Malvinocáfrico, cujos táxons mais característicos, isto é, os braquiópodes (*Australocoelia*, *Australospirifer*)

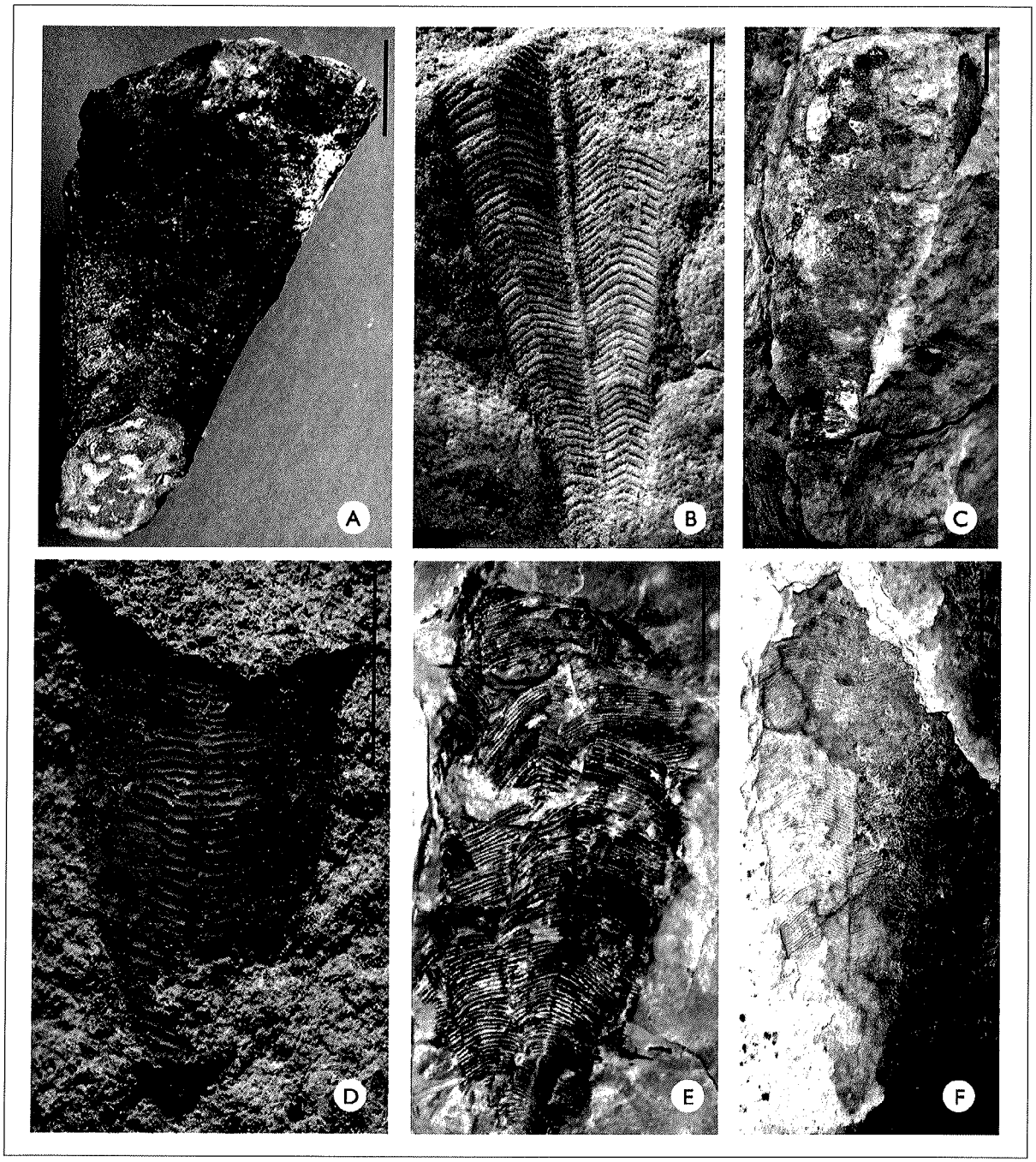

Figura 2. A) *P. africana*, Formação Ponta Grossa (IGc/USP GP/1E2300), Bacia do Paraná, modificado de Leme *et al.* (2004); B) *P. ulrichana*, Formação Ponta Grossa, Bacia do Paraná (DNPM-3656-1), modificado de Lima (1989); C) *C. quichua*, Formação Ponta Grossa, Bacia do Paraná (IGc/USP 2444); D) *C. amazonica*, Grupo Trombetas, Bacia do Amazonas (MN- 2698-1), modificado de Lima (1989); E) *C. quichua*, Formação Manacapuru, Bacia do Amazonas (U/MS 184), foto de Marcelo Vieira; F) *C. quichua*, Formação Maecuru, Bacia do Amazonas (CCLP- 757). Escalas = Figuras 2A-2C, 2E, 2F: 1 cm; Figura 2D: 0,5 cm.

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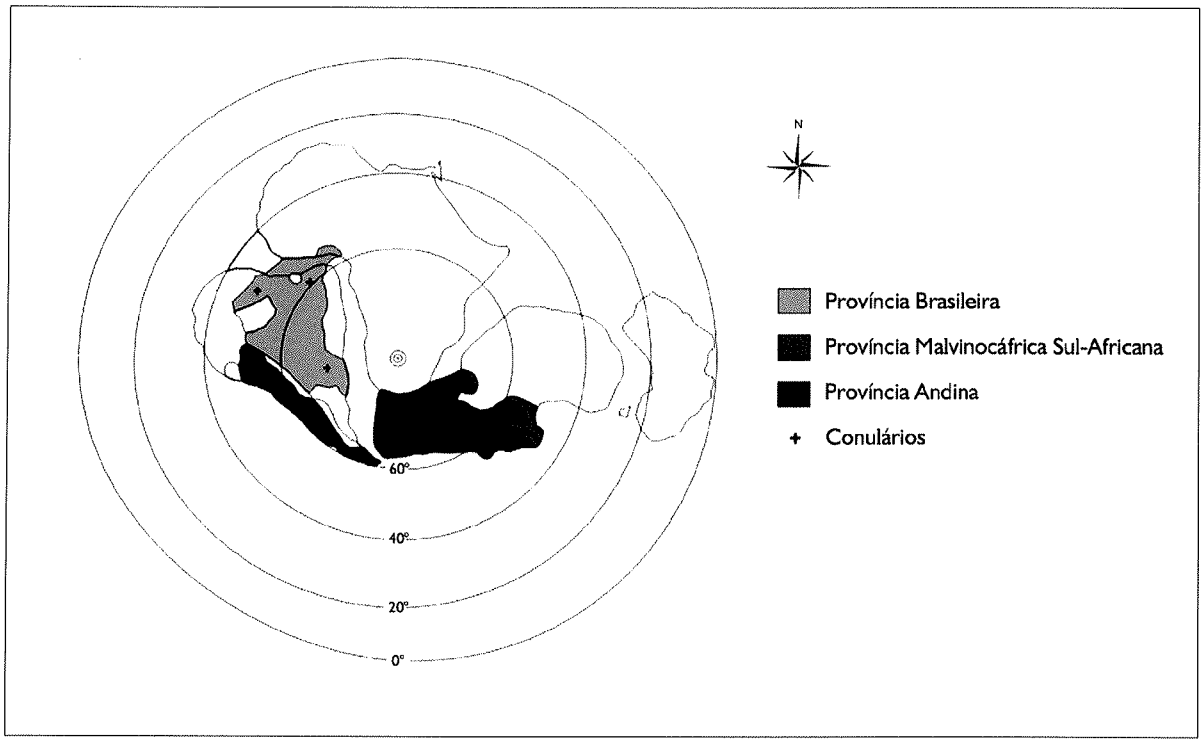

Figura 3. Mapa paleogeográfico representando as Províncias do Domínio Malvinocáfrico e as ocorrências dos conulários no Devoniano das bacias paleozoicas brasileiras. Modificado de Eldredge & Ormiston (1979).

e os trilobitas (*Calmonia*) ocorrem na Formação Ponta Grossa. Diversos autores (*e.g.*, Cooper, 1977; Eldredge & Ormiston, 1979) notaram, entretanto, que as faunas de braquiópodes e trilobitas da Formação Ponta Grossa são menos diversificadas do que as coevas encontradas em outras partes do Domínio Malvinocáfrico, por exemplo, na Bolívia e na Argentina. Os dados indicam claramente que a fauna de conulários da Província Brasileira é uma versão menos diversificada daquela presente na Província Andina, especialmente da Bolívia. Enquanto a fauna boliviana é caracterizada por cinco espécies (*C. quichua*, *C. albertensis* *P. africana*, *P. ulrichana* e *Reticulaconularia baini*), a fauna das bacias paleozoicas brasileiras é constituída por *C. quichua* (predominantemente), *P. africana* e *P. ulrichana*, todas pertencentes a gêneros e espécies cosmopolitas.

A presença de *C. quichua* na Formação Maecuru, da Bacia do Amazonas, reforça o caráter cosmopolita da espécie e demonstra a viabilidade da existência de comunicações paleobiogeográficas entre os diferentes domínios do Devoniano Médio a Superior das bacias intracratônicas da América do Sul. De fato, já no Neo-Mesodevoniano, mais precisamente no Givetiano, ocorrem alterações profundas na fauna do Domínio Malvinocáfrico, devido ao evento de extinção KAČÁK (Horodyski, 2010; Bosetti *et al.*, 2010, 2011, 2012; Horodyski *et al.*, 2014). Tais alterações evidenciaram a entrada, principalmente a partir do Mesodevoniano (Ghilardi *et al.*, 2011; Scheffler *et al.*, 2011a, 2011b), de elementos exógenos de águas mais quentes, oriundos das bacias do Amazonas e do Parnaíba, ou até mesmo do Velho Mundo, na Bacia do Paraná.

A ampla distribuição paleobiogeográfica apresentada por *C. quichua*, *P. africana* e *P. ulrichana* não é facilmente entendida à luz da paleobiologia dos conulários. Admitindo-se relação de parentesco dos conulários com cifozoários, é

notável que a distribuição zoogeográfica desse grupo de cnidários, nos mares do Presente, seja controlada pela temperatura da água (Arai, 1997, p. 201).

Diversos autores (*e.g.*, Boucot, 1974; Cooper, 1977; Eldredge & Ormiston, 1979) postularam que a distribuição e a diversidade dos invertebrados marinhos no Domínio Malvinocáfrico está relacionada, em parte, a barreiras climáticas. Considerando-se as paleolatitudes do intervalo de ocorrência dos conulários da Bolívia e da Bacia do Paraná, por exemplo, verifica-se que sua distribuição latitudinal é apreciável. Durante o Devoniano, os conulários bolivianos viveram em águas entre 45° e 50° de latitude sul, e as da Bacia do Paraná próximas aos 70° sul. Portanto, as espécies que colonizaram a Bacia do Paraná estavam submetidas a condições ambientais de águas muito frias, em decorrência da proximidade ao pólo da época. Não pode ser esquecido ainda que os gêneros *Conularia* e *Paraconularia* ocorrem em terrenos do Domínio das Américas Orientais e do Velho Mundo, portanto em zonas tropicais durante o Devoniano. As espécies *C. quichua*, *P. africana* e *P. ulrichana* devem ter sido, desse modo, euritérmicas. Curiosamente, espécies de cifozoários viventes, que são cosmopolitas, são também euritérmicas, suportando amplas variações de temperatura quando em águas de mares subtropicais e tropicais, o que não ocorre com aqueles das águas das regiões polares (Arai, 1997).

Durante o Devoniano, a Bacia do Paraná não esteve apenas em posição latitudinal mais alta do que os mares da região andina, especialmente da Bolívia. Para alguns autores (Cooper, 1977; Eldredge & Ormiston, 1979), o alto grau de endemismo da fauna de trilobitas da Província Brasileira, em comparação com a da Província Andina, sugere algum isolamento físico da Bacia do Paraná durante o Devoniano. Autores como Eldredge & Ormiston (1979), fundamentados nos padrões de correntes oceânicas do Devoniano, postularam migração das espécies andinas de trilobitas para a Bacia do Paraná. Curiosamente, as faunas de trilobitas da Província Brasileira apresentam maior grau de endemismo do que a Andina, mesmo considerando se tratar de um grupo com formas adultas com capacidade de locomoção (Cooper, 1977). Admitindo-se que o mesmo tenha ocorrido com as faunas de conulários, isso é, migração da área andina para a Bacia do Paraná, a comparação desse padrão com o observado para os cifozoários viventes também não é fácil de ser compreendida. A ampla distribuição de algumas espécies de conulários no Domínio Malvinocáfrico sugere a presença de formas larvais planctônicas teleplânicas (*sensu* Scheltelma, 1989), isto é, com capacidade para sobreviver nas correntes oceânicas por prolongados períodos de tempo. A distribuição de larvas teleplânicas sugere que essas são capazes de uma dispersão transoceânica, pois são encontradas tanto no oceano Atlântico como no Pacífico (Ventura & Pires, 2002). Nos cifozoários viventes, no entanto, as medusas são responsáveis pela maior dispersão das espécies, enquanto as plânulas, por apresentarem um tempo de vida mais curto, são importantes na seleção de condições ambientais favoráveis para o assentamento e desenvolvimento da fase bentônica (Arai, 1997, p. 139).

CONCLUSÕES

A fauna de conulários do Devoniano do Brasil é pouco diversificada, especialmente se comparada com a fauna boliviana. Do ponto de vista paleobiogeográfico, há afinidades com as faunas de conulários do Domínio Malvinocáfrico, conforme indicado pela ocorrência comum de *Conularia quichua* e *Paraconularia africana* nos sedimentitos devonianos da Bolívia, Argentina, Peru e África do Sul.

A ampla distribuição paleobiogeográfica das espécies no âmbito do Domínio Malvinocáfrico sugere fortemente que essas foram euritérmicas, uma vez que ocorrem em terrenos das províncias Andina, Brasileira e Malvinocáfrica sul-africana. Especialmente, essas duas últimas províncias englobam áreas que estiveram situadas nas altas latitudes, próximas do pólo sul devoniano, enquanto a Província Andina esteve localizada em torno dos 40° a 45° de latitude sul. A presença de *C. quichua* na Formação Maecuru, da Bacia do Amazonas, reforça o caráter cosmopolita da espécie e demonstra a viabilidade da existência de comunicações paleobiogeográficas entre os diferentes domínios do Devoniano Médio a Superior das bacias intracratônicas da América do Sul.

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CAPÍTULO 3

Corumbella werneri: morfologia, paleoecologia e afinidades filogenéticas

3.1. PACHECO, M.L.A.F.; GALANTE, D.; RODRIGUES, F.; LEME, J. M.; PIDASSA, B.; HAGADORN, W.; STOCKMAR, M.; HERZEN, J.; PFEIFFER, F.; MARQUES, A. 2015. Insights into the Skeletonization, Lifestyle, and Affinity of the Unusual Ediacaran Fossil Corumbella. Plos One, v. 10, p. e0114219.

O fóssil de Ediacarano *Corumbella* é considerado um cnidário cifizoário, portanto, pode ser um dos raros exemplos de animais Neoproterozoicos. Infelizmente, o modo de vida, o estilo de esqueletização e a afinidade taxonômica têm sido muito controversos na literatura. Aqui, usamos micro-CT, SEM e análise de raios-X para comparar os modos de preservação de *Corumbella*, a fim de melhor compreender a simetria, modo de construção, estilo conservacional e taxonomia desse grupo. Os resultados sugerem que os espécimes articulados e desarticulados de *Corumbella* do Ediacarano do Brasil, Paraguai e os Estados Unidos, embora às vezes preservados de forma muito diferente, representam o mesmo táxon: *Corumbella werneri*. Corumbellídeos tinham uma teca flexível e provavelmente viviam com a sua parte basal ancorada no sedimento, bem como *Conotubus*. Quando considerados juntos, esses resultados sugerem que *Corumbella* foi um dos primeiros animais a construir um exoesqueleto, empregando uma microfama lamelar semelhante aos conulários.

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RESEARCH ARTICLE

Insights into the Skeletonization, Lifestyle, and Affinity of the Unusual Ediacaran Fossil *Corumbella*

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Abstract

The Ediacaran fossil *Corumbella* is important because it is hypothesized to be a scyphozoan cnidarian, and thus might be one of the rare examples of bona fide Neoproterozoic animals. Unfortunately, its mode of life, style of skeletonization, and taxonomic affinity have been very controversial. Here, we use X-ray micro-CT, SEM, and taphonomic analysis to compare preservational modes of *Corumbella*, in order to better understand the symmetry, mode of construction, preservational style, and taxonomy of this group. Results suggest that articulated and disarticulated specimens of *Corumbella* from the Ediacaran of Brazil, Paraguay, and the United States, although sometimes preserved very differently, represent the same taxon—*Corumbella werneri*. Corumbellids had a thick but flexible theca and probably lived with their basalmost part anchored in the sediment, much like *Conotubus*. When considered together, these results suggest that *Corumbella* was one of the first animals to build a skeleton, employing a lamellar microfabric similar to conulariids.

Introduction

The Corumbá Group of Mato Grosso do Sul, southwest Brazil (Fig. 1), has the most diverse assemblage of Neoproterozoic fossils in South America [1, 2]. These include vase-shaped microfossils, algae (*Tyrasotaenia* sp.), and metazoans (*Corumbella werneri*, *Cloudina lucianoi*) [3–8].

Perhaps the most enigmatic of these taxa is *Corumbella werneri*, a polyhedral multi-segmented flexible organism. It has been associated with scyphozoan cnidarians or other extinct cnidarian clades, such as the conulariids [4–6, 9]. This fossil is abundant in the limestone mines located in Corumbá and Ladário, Brazil, where it occurs in the Ediacaran Tamengo

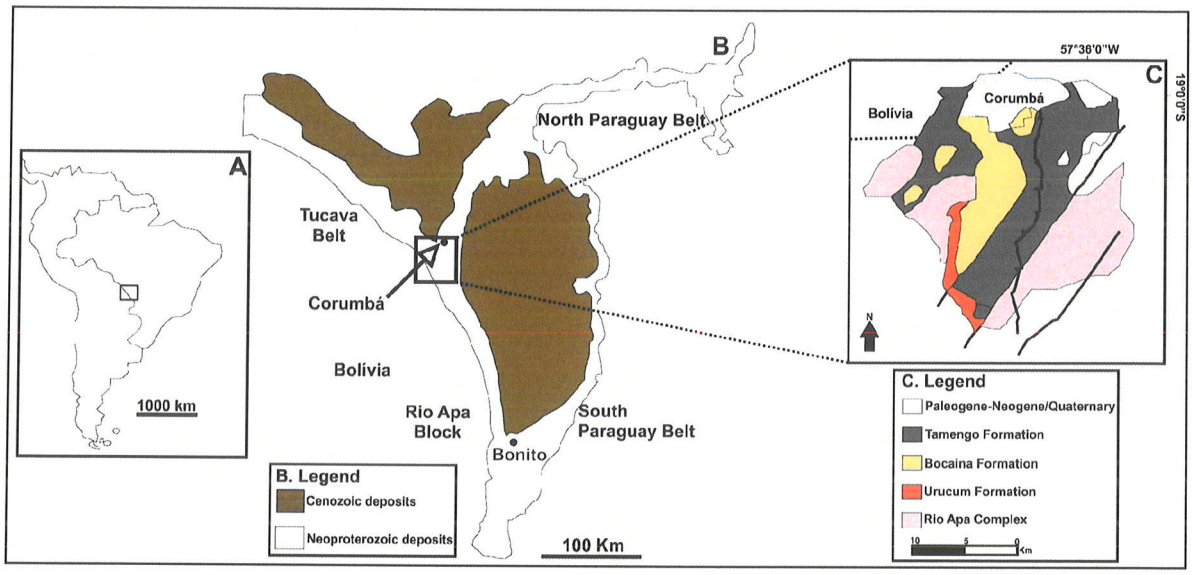

Fig 1. Simplified map of South America (A) with detail of the geological map of the Paraguay Belt (B), and Corumbá Group (C) Modified from Oliveira, 2010, [48].

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Formation (Fig. 2). Co-occurrence of *C. werneri* with the Ediacaran index fossil *Cloudina* suggests that the Tamengo Formation fossils are part of the Ediacara biota [2, 8, 10–12].

Although the Tamengo Formation lacks other biomineralized Ediacaran fossils, such as *Namacalathus* [13, 14] and *Namapoikia* [15], its shales and marls show a range of preservational style of fossils. *Corumbella* also occurs in the grainstones and shales of the coeval Itapucumi Group of Paraguay [16, 17], as well as in the sandstones of the Wood Canyon Formation of the USA [9]. In these three deposits, *Corumbella* occurs as casts, molds, and body-fossils, in bed-parallel or bed-perpendicular orientations, and as single specimens or as clasts within pavements.

This diversity of preservational styles, together with an abundance of new corumbellid specimens, allows reassessment of the ecology, biology, and taxonomy of this organism, and places it among the novel evolutionary changes that occurred during the end of the Ediacaran period, such as the rise of skeletonized animals and carnivores predators [15, 17]. New specimens of *Corumbella* were collected from the Corumbá and Ladário exposures in Brazil, which were analyzed and compared to previously described specimens from Brazil, Paraguay and the USA, aiming to better understand its taxonomy and paleobiology.

Historical Taxonomy and Morphology

The first taxonomic description and paleoecologic and paleobiogeographic interpretations of *Corumbella werneri* were based on material from marls and shales of the Saladeiro quarry (Fig. 2), located in Ladário, adjacent to Corumbá. Originally, this material was assigned to a new subclass Corumbellata, and placed among the Cnidaria Scyphozoa [4]. Two distinct body regions were recognized in *Corumbella werneri* (Fig. 3A). The first is the proximal region, consisting of a curved, elongate, unbranched tubular periderm (or stalk), designated as the "primary polypar", which is made up of isolated, and hypothesized, chitinous rings, externally and internally reinforced on the sides with four small, short internal sclerosepta. The second is a distal region, consisting of a biseriate arrangement of secondary, contiguous polypars, each

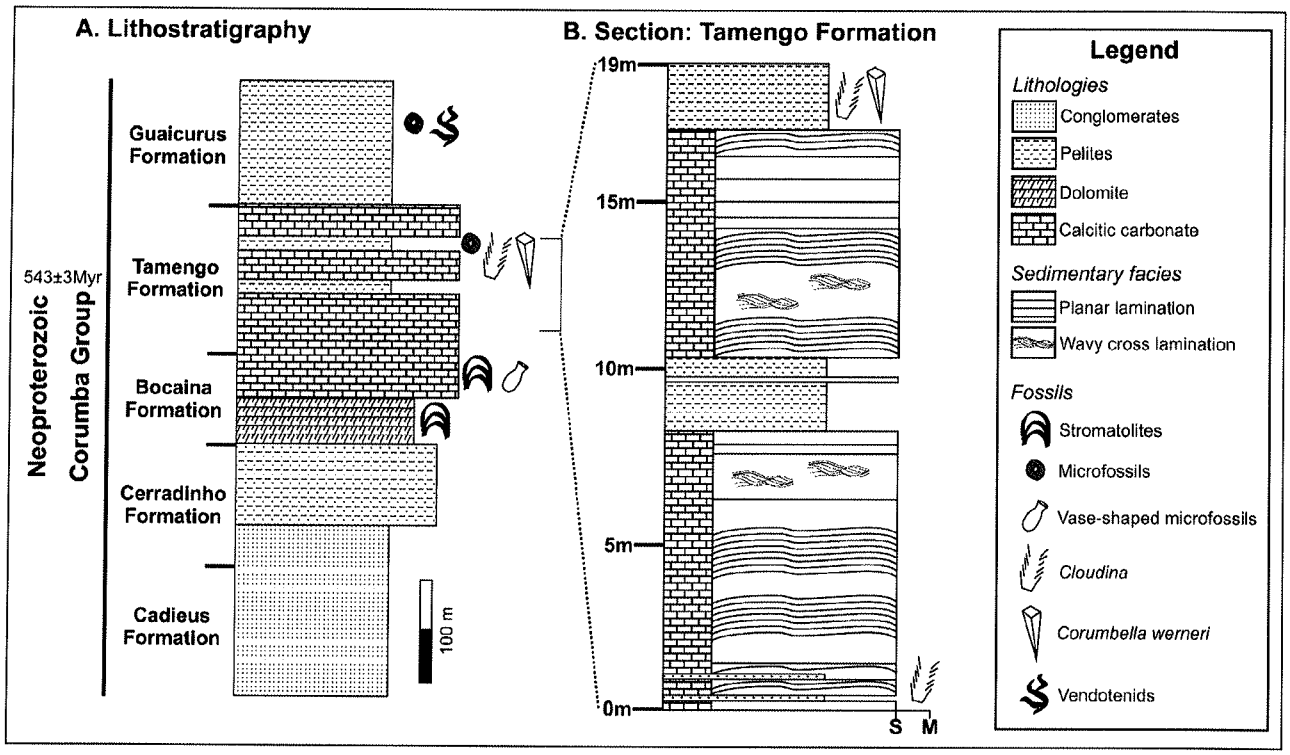

Fig 2. Lithostratigraphic column for Corumbá Group and section for the upper part of Tamengo Formation (Neoproterozoic) at the Saladeiro quarry. Detail of the position where *Corumbella werneri* and other fossils occur. M—mud; S—sand. Modified from Warren *et al.*, 2012, [17]; and Morais, 2013, [49].

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formed by a small, distinct chitinous periderm tube, with no clear ring formation or visible sclerosepta. Secondary polypars are merged to each other at the adaxial surface. The set of two secondary polypars has a morphology similar to the primary polypar, differing only in the diameter. The biseriate portion is slightly wider and shorter (8–10 cm) than the uniseriate one. An apical part (here named attachment portion) in the primary polypar was not recognized (though basalmost oriented).

In the first description [4], it was also highlighted the internal four-fold radial symmetry of *C. werneri*, which was implied by the arrangement of sclerosepta in cross-sections of the primary polypar. This character was considered to be similar to the internal arrangement found in the polyps of the recent scyphozoan genus *Stephanoscyphistoma* Jarms, 1990 (Coronatae; former *Stephanoscyphus* Allman, 1874), which was used to classify *Corumbella* as a Scyphozoa (phylum Cnidaria). However, they considered the transition from the proximal uniseriate primary polypar to the distal biseriate secondary polypars of *Corumbella werneri* to be a distinct character and, on the basis of this hypothesis, the authors erected the family Corumbellidae, order Corumbellida, subclass Corumbellata [4, 10].

It was described [9] from the Ediacaran portion of the lower member of the Wood Canyon Formation (USA), but not named, "*Corumbella* n. sp.", remarking that the two specimens they had found had a single longitudinal groove along the midline and were spirally twisted (Fig. 4A, B). Authors motivate the comparisons between *C. werneri* and USA specimens [9] by the original description [4], now considered outdated by the more recent studies [5, 6]. They do not consider *Corumbella* n. sp. conspecific with *C. werneri*, which in original description [4]

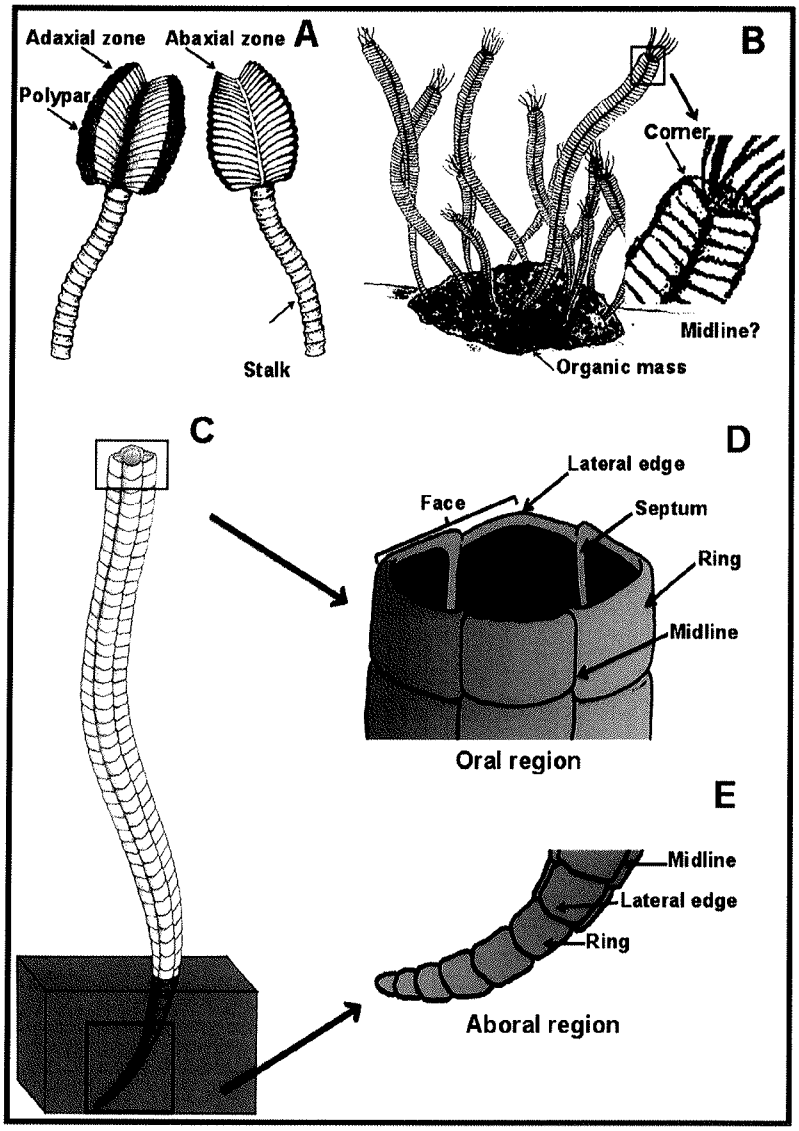

Fig 3. Models for Corumbella werneri. (A) Reconstruction of *Corumbella werneri* proposed by Hahn *et al.* (1982) [4], showing a stalk and polypars (modified by Wilson Soares Jr). (B) Reconstruction of *Corumbella werneri* as a colonial sessile organism, as interpreted by Babcock *et al.* (2005) [5] (modified by Abner Santos). Detail of the square symmetry. (C) Reconstruction of *Corumbella werneri* proposed by Pacheco *et al.* (2011) [6] and improved in this work (draw by Abner Santos). (D) Detail of the oral region, lateral edges, faces, septa and midline. (E) Aboral region with unisseriated rings on the attachment portion.

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lacks a helical twist and has transverse ornamentation, secondary polypars and circular geometry in cross sections (Fig. 4 E, F) [4]. Therefore these specimens were not assigned to *Corumbella werneri* (Brazil). *Corumbella* n. sp. was assigned to the Cnidaria [9] because the specimens were similar in symmetry and external ornamentation with conulariids, a group previously allied with Scyphozoa, Cnidaria [18–26].

Then, a new morphological and taxonomic interpretation for *C. werneri* [5] was presented, in which a tetramerous elongated narrow tube would be secreted from an "apical attachment

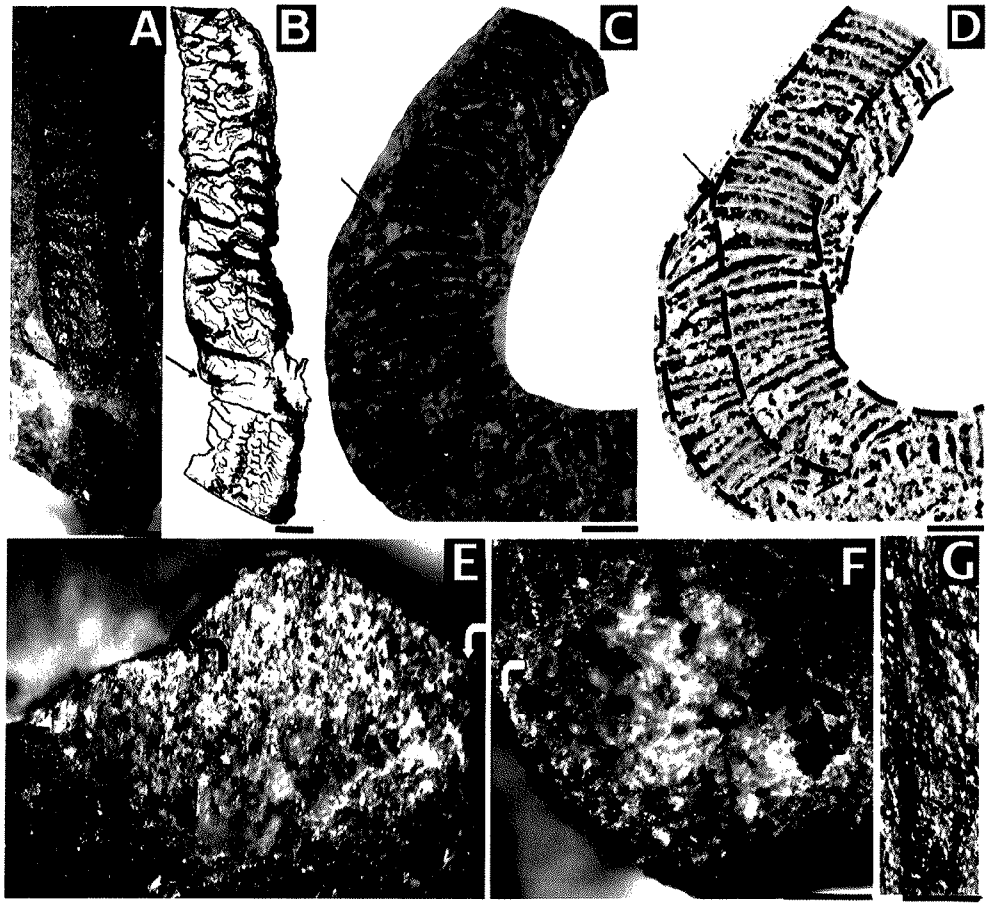

Fig 4. Corumbella werneri, Wood Canyon (USA) and Tamengo Formation (Brazil). Morphology. (A) LACMNH 12802 (Wood Canyon Formation). Polyhedral specimen, covered with desert varnish. Observe rings (black dashed arrow) alternately converging on the midline (marked with an "X" in the draw), in continuity with the lateral edges. Detail of the helical twist (black arrow). (B) Draw representing (A) with detail of the rings (black dashed arrow); midline (marked with an "X" in the encounter of two rings in the face) and torsion (black arrow). (C) and (D) GP1E-5808b (Tamengo Formation). Note torsion in the two-dimensional tube (black arrow) (C) and detail of the helical twist represented in (D) (black dashed lines). (E) LACMIP loc. 17130 (Wood Canyon Formation). End section quadrangular pressed torsional in (A). Observe lateral edges (white curved arrow) and septa (black curved arrow). (F) LACMNH 12802. Quadrangular section untwisted end in (A). See lateral edge (white curved arrow) (G) LACMNH loc. 17130. Aboral region. Detail for lateral continuity of the rings (black dotted arrow). Scale: 1 mm.

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region" (referred as the apex, though basalmost oriented) (Fig. 3B). The animals were hypothesized to be benthic colonial predators fixed to the substrate by an "organic mass". The reinterpretation of *C. werneri* as tubular and its budding reproduction strengthen their similarity with the modern *Stephanoscyphistoma*, and possibly with the extinct conulariids [5]. However, key morphological features essential for testing this paleoecological and taxonomic interpretation were described but not indicated in the described material [5], including midline thickening, attachment structures, oral region, the "organic mass", and rectangular sections showing fourfold symmetry.

Other researchers [16] described *Corumbella werneri* from Itapucumi Group, Paraguay, as long and flattened fragments made up of articulated, apparently organic, narrow, annular elements, possibly corresponding to transverse rod-like skeletal elements that occur in conulariid scyphozoan cnidarians.

Recently, geometric modelling and taphonomic analysis were used to refine the understanding of the original specimens of *Corumbella werneri* and to carry out a more detailed taxonomic analysis of the group [6]. It was hypothesized that *Corumbella* would have a uniseriate aboral region that graded to a polyhedral geometry bearing lateral edges (Fig. 3C-E). The theca was constructed of polygonal rings merged into each other at a midline, the central region of the faces, as apothem of a pyramid, the side height of a lateral face—see ref. [6], (Fig. 7, pg. 278); (Fig. 3D).

However, there are still aspects of the morphology of *C. werneri* that are unknown, such as the nature of inner structures, its aboral region and skeletal micro and ultrastructure. For example, important questions are: Did corumbellids have septa? What was the microfabric or mineralogy of their theca? And did they lay on or attach to the seafloor? In the past, it was difficult to answer these questions because the fossil's attachment region or internal features are usually obscured by sediment or flattening during compaction, or because specimens previously studied were not well enough preserved to show primary microstructural details. Using microfocus X-ray computed tomography (microCT) in tandem with SEM and ultrastructural analysis of newly collected material, it is possible to fill some of these knowledge gaps and gain insights into the paleobiology, paleoecology, and phylogenetic affinity of these fossils.

Geological Background

The Corumbá Basin outcrops in the southern part of the Paraguay Belt, Brazil (Fig. 1). In this region, the base of the sequence consists of the Cadiueus and Cerradinho formations, which were deposited in an initial continental rift basin, before the widespread of carbonate deposition [2]. Overlying these strata are the Bocaina, Tamengo and Guaicurus formations, which were deposited in a stable marginal basin [27–29]. The Bocaina Formation comprises stromatolitic dolostones and subordinate phosphorites that grade to black limestones, marls and shales of the Tamengo Formation. The Guaicurus Formation, which is the youngest unit of the Corumbá Group, is comprised of thick siltstones and shales overlying the Tamengo Formation (Fig. 2) [28, 32].

The Bocaina, Tamengo, and Guaicurus formations represent the evolution to open shelf sedimentation in a post-rift to drift stage, as indicated by the occurrence of phosphorite at the top of the Bocaina Formation and the presence of the fossil *Cloudina* in the Tamengo Formation [2, 28], similar to other late marine Ediacaran environments, such as Namibia and Canada [13, 14, 32].

The *Corumbella*-bearing portion of the Tamengo Formation was dated about 543±3 Ma [30, 31] by U-Pb SHRIMP zircon form an ash bed interbedded in the upper Tamengo Formation (Fig. 2B). This age collaborates the correlation with records of Precambrian-Cambrian boundary in previous age constrains from Siberia and Namibia around 543Ma [33]. Also in Ara Group of Oman, the anomaly negative carbon excursion and abrupt last appearance of *Cloudina* and *Namacalanthus*, are dated by U-Pb zircon age in ash interbedded, directly define these event to be at 542±3Ma [34]. This parameters allow confirm that the *Corumbella* record and the age in Tamengo Formation agree very well with Precambrian-Cambrian boundary showed in previous work in distinct records.

The widespread carbonate deposition of the Tamengo Formation is related to a transgression event also observed in the calcareous grainstones of the Tagatiya Guazu Formation (Itapucumi Group, Paraguay). This unit is thought to be a wave- and tide-dominated depositional environment that represents a shallow tidally-influenced setting on a rimmed carbonate ramp [16], where the association of *Cloudina* fossils with thrombolites together with remains of *Corumbella* [17] were found.

The presence of the *Cloudina* and *Corumbella* in the Itapucumi Group and Tamengo Formation confirms that these two units are correlated [16]. In Corumbá, *Cloudina* occurred in a shallow, protected carbonate setting [16], whereas *Corumbella* lived in a calm terrigenous environment, indicated by its abundance in marls. In Paraguay, these animals probably co-occurred in environments with similar conditions of water temperature, depth, and salinity [17]. The siltstones and very fine-grained sandstones of the lower member of the Wood Canyon Formation in Nevada, USA, also bear *Corumbella* and *Cloudina*. Based on chemostratigraphic and biostratigraphic correlation with other radiometrically dated units, it was proposed that the fossil-bearing strata of the Wood Canyon Formation were probably deposited in the latest Ediacaran time, in shallow subtidal nearshore marine environments [9].

Material and Methods

Examined collections

419 samples were analyzed: 401 from Brazil, deposited at the Scientific Collection of the Geoscience Institute of the University of Sao Paulo (IGc/USP) ("GP/1E"), 2 from the Collection of the Laboratory of Paleobiology (IGc/USP), 12 from the Collection of the Department of Paleontology of the National Department of Mineral Production (DNPM), Rio de Janeiro ("DGM"), and 2 from the United States, deposited at the Los Angeles County Natural History Museum ("LACMNH" and "LACMIP"). Regarding the specimens from Paraguay, published data were used [9].

X-ray Microtomography

X-ray imaging can help the visualization of inner structures of fossils because X-rays penetrate opaque minerals and matrices without destructive sectioning of specimens [35]. The contrast between two features of X-ray imaging is based on differences in the attenuation of X-rays, as they pass through materials of different densities and elemental compositions. Computed tomography allows the use of multiple projected images recorded while the sample is rotated around an axis to assess the three-dimensional geometry and internal structures of fossils.

Specimens from the Brazilian and USA collections were examined using a "V|tome|x" (Phoenix X-Ray/General Electric) micro-CT scanner, at 90 kV and 130 μA. Tomographic reconstructions were based on 2000 single projection images equally spaced through 360°. Projection images were captured using a 2000 x 990 pixel coupled scintillator-CCD with 2 s exposure time. The resulting effective voxel size due to geometrical magnification was 12.3 μm^3.

Scanning electron microscopy and Energy Dispersive Spectroscopy (SEM/EDS)

The microstructural analyses of fossils were also performed by the means of SEM/EDS at Brazilian Nanotechnology National Laboratory (LNNano). Fossils were examined using a SEM FEI Quanta 650 FE in secondary electrons detection mode, with acceleration voltages of 10 and 20 kV. EDS was performed using an X-Max detector in mapping mode, in order to detect the distribution of calcium in exoskeleton and rock matrix.

Morphological description and systematic analysis of specimens

Morphological and microstructural features are described using the published terminology [4–6, 9, 12, 20, 22]. Whenever possible, we followed the recommendations of other authors [36, 37], *viz.* (a) the taxonomic study of invertebrate fossils is based on the highest number of samples available, aiming to collect a broad spectrum of morphological and taphonomic data;

(b) the study prioritizes the examination of specimens with different types of preservation; (c) comparison is based on morphometric characters of specimens with similar preservation.

New Data on Structure and Morphology

The first reconstructions of *C. werneri* [4] were based on some specimens that were three-dimensionally preserved. The type-specimens, as well as types, paratypes, and comparable specimens from Paraguay and the USA, were carefully re-examined. In this regard, microCT images and some additional data on SEM/EDS proved to be essential in showing some new aspects of the morphology and taphonomical implications, such as deformation of morphologic features, that could result in wrong taxonomic descriptions. In this sense, it was possible to observe in *C. werneri* specimens: the morphology and arrangement of the aboral portion or anchor in the substrate, aspects of geometry and construction (Fig. 5), internal exoskeletal, mineralogy, lamellar microfabric, compression and fragmentation (Fig. 6, 7).

Structural and morphological attributes were considered here in order to compare specimens from South and North America.

Morphology

The bipartite region of *C. werneri* body (Fig. 3A) may have originally been attributed to fragments of three-dimensional or two-dimensional uniseriate tubes. These tubes were interpreted as part of a primary polyp or stalk (DGM-5601-I, Fig. 8C), and the biseriate region was interpreted as polypars (DGM-5601-I, 5606-DGM-I, Fig. 8C, F). In previously analyzed samples, these parts were often arranged separately. In this paper, they are interpreted as fragments, sometimes from the same individual. Based on this study, it appears that *Corumbella werneri* is a polyhedral tube (Fig. 5D, E) with oral and aboral regions, and that the aboral region has a conical attachment (Figs. 3C-E and 5A-C) see ref. [6], pg. 277.

Three-dimensional modeling of *Corumbella* specimens from the Wood Canyon Formation indicates that their structure and anatomy are strikingly similar to the Tamengo Formation specimens. They have an elongated tubular polyhedral (Fig. 4A) appearance and are formed by four faces and four lateral edges, showing an almost quadrangular cross-section (Fig. 4F). The rings are inconspicuous, but it is possible to see they are polygonal, and merge with each other across midline (Fig. 4A, B). There are lateral edges (Fig. 4E, F) and faces with no clear demarcation of midlines, but with internal septa (Fig. 4E). These specimens were stretched, and fossilized in sandstone, and the fragments of the theca are partly obscured by desert varnish. Unlike the Tamengo Formation's specimens, the Wood Canyon Formation's specimens have a thinner theca without longitudinal striations, and there is no evidence of the oral region in these specimens. One specimen has an aboral region (Fig. 4G), but not a clear attachment portion.

Structure and ultrastructure

Unlike completely biomineralized integuments of other metazoans, biomineralized Ediacara fossils often have weak or unusually flexible integuments (*e.g. Cloudina*). Thecae of *C. werneri* are similar—they show twisting and stretching in response to deformation, which suggests they had some plasticity. For example, both specimens from the USA and Brazil show torsions along the tube (Fig. 4A-D). In Brazilian specimens, the basalmost part ends directly in the substrate (Fig. 5A-C), just as described for *Conotubus* [38], suggesting that adults might be benthic. *Corumbella werneri* from the USA also has an aboral region, recognized as a basalmost ending attachment portion. In this sense, the presence of helical twisted regions suggests that these torsions result from mechanical processes acting on the pyramidal structure of the tube. When twisting a polyhedron, this usually happens due to its asymmetric geometry and/or due to

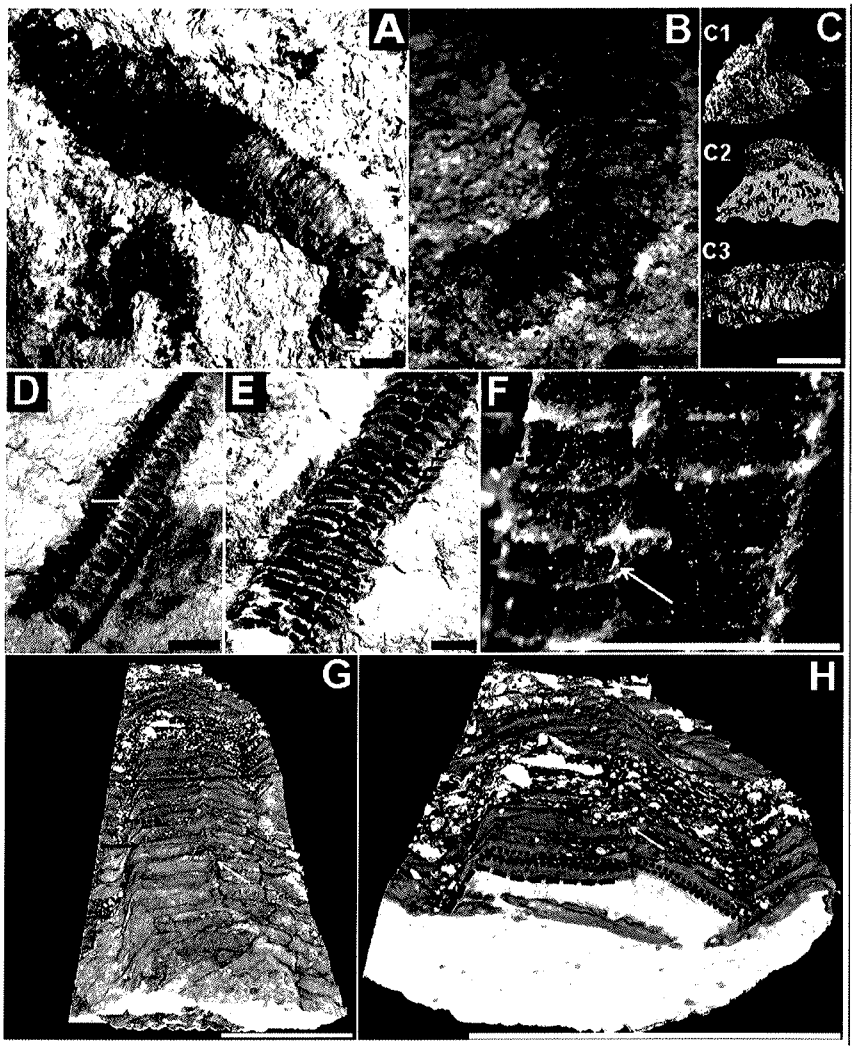

Fig 5. Corumbella werneri: morphology and modes of life. (A) GP1E-4216: *Corumbella werneri* and (B) attachment region evidenced by (C) 3D-rendered microCT. (C1) shows a transverse-lateral section of (B). In (C1), it is possible to observe the conical morphology of the final attachment region, obliterated by the rock matrix in (B) (black arrow). (C2) is a detail of the attachment region in transversal section. (C3) is a lateral view of the final attachment region. (D) GP1E-4109: external mold of (E), GP1E-4210: internal mold with prismatic geometry and almost square in cross section. Note lateral edge (black arrow), midline (white arrow) and the alternate disposition of rings (black dashed arrow) across midline, on the face. (F) Zoom of specimen (E) to observe the "u" alternate disposition of rings across midline (white arrow), rings (black dashed arrow) and the continuity of rings on the lateral edges (black arrow). (G) and (H) MicroCT of (E). (G) Transversal section (black dashed line) showing a folded polyhedral tube in (H). Details of the rings (black dotted line), lateral edges (black dashed line) and open folded lateral edge (black line). Scale: 1mm. (A), (B) and (E): reprinted from Pacheco *et al.* (2011) [6] under a CC BY license, with permission from Luis Alcalá, original copyright 2011.

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mechanic *torques* (Fig. 9). In the case of *Corumbella*, helical twisting could have happened if the animal was partially buried when it was subjected to an external twisting force (such as a current or turbid flow that might also bury the organism). Hence, the response of tube to external forces depends not only on the rigidity of the theca, but also on their internal filling. Wood

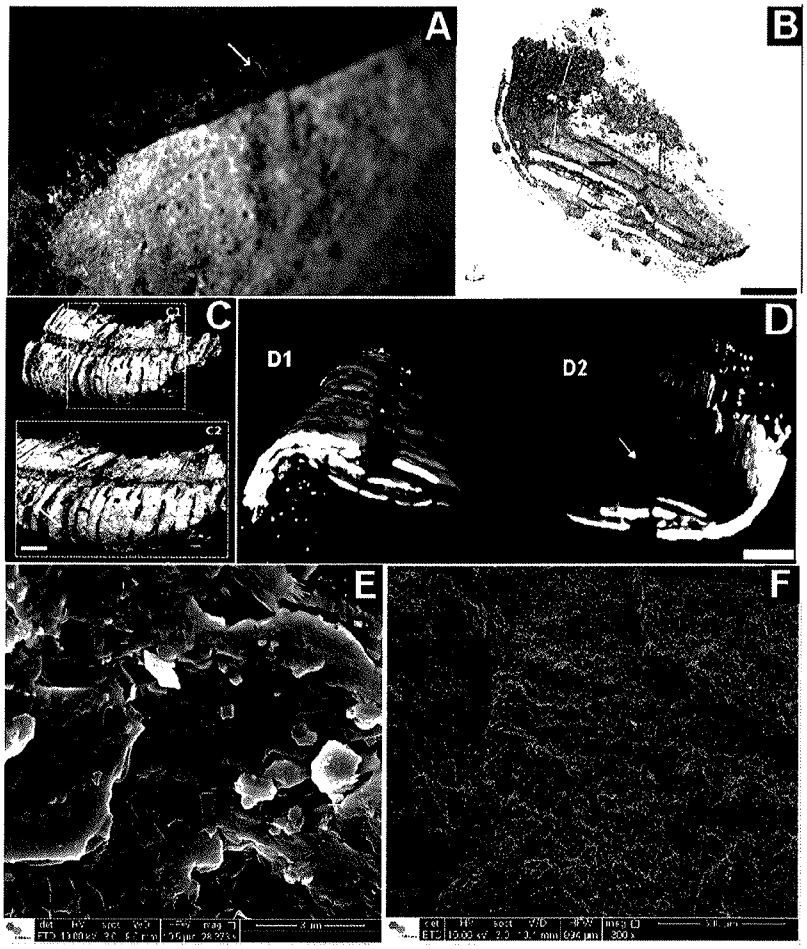

Fig 6. Corumbella werneri: ultrastructure of theca. (A) GP1E-574a: three-dimensional specimen with theca. (B) 3D-rendered microCT of *Corumbella* theca,flipped by 180° compared to (A): interior view and detail for lamellae microfabric and plates (black arrow). (C) 3D-rendered microCT of *Corumbella* theca (A) without flipping in C1 and C2, with details of rings (white arrow). (D) compression and fragmentation along theca. D1 shows a transversal section in the fossil structure. Flipped by 180° of it produces D2, with details of small breakages (white arrow). (E) Details of lamellar plates by SEM (black arrow) and (F) pores in plates (black dashed arrow). Scale: 1mm.

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Canyon specimens are commonly filed with sediments coarser than the surrounding matrix, which causes a differential mechanical response to external *torques*, such as those produced on the burial process. Torsions can result from this transfer of forces from the matrix sediments to the structure, which can be more pronounced depending on the grain size of the sediment.

Since the structure of the tube was not entirely rigid, but fairly flexible in some twisted specimens, only a restricted area of the animal's body was twisted. If the skeleton was completely hard (*e.g.* strongly mineralized), it could not be twisted. A simplified version of this scenario is presented (Fig. 9) in order to explain the observed deformation and twisting of some *Corumbella* specimens.

Although the theca of *Corumbella* was flexible, its tube-like body and its segments were not elastic, which is supported by the evidence that its structure was susceptible to breakage. For example, in the Tamengo Formation, *Corumbella* fossils are highly fragmented and fractured

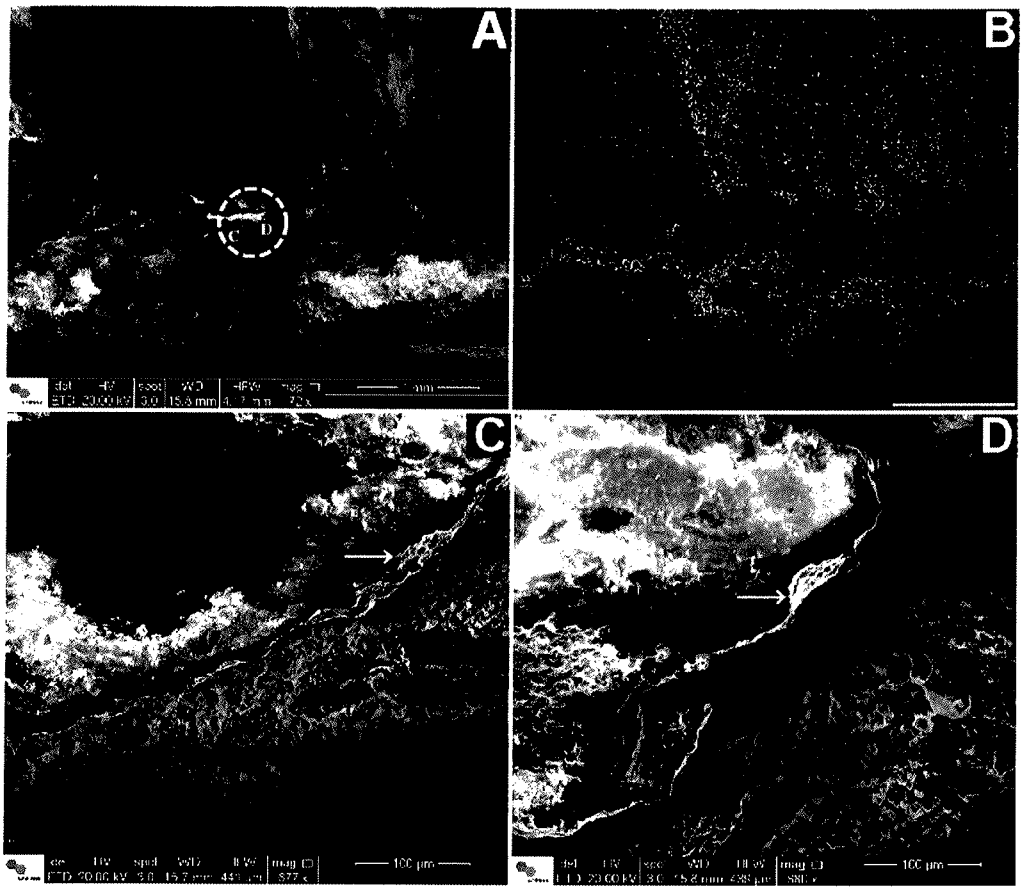

Fig 7. Corumbella werneri: ultrastructure of theca. (A) SEM of a longitudinal section of a *Corumbella* theca. Dashed circle marks a detail of a sectioned ring. (B) EDS mapping of (A). Here it is possible to observe higher concentration o calcium in fragments of theca (represented by white dots) in comparison to the rock matrix and molds of fossil without fragments. (C) and (D) are details of the white dashed circle in (A), showing micro layers in *Corumbella* theca (white arrow). Scale for B: 1mm.

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(Fig. 6C, D), including specimens that show evidence of syndepositional and/or pre-burial fragmentation and cracking. For instance, some fragments were broken prior to deposition, or are oriented inconsistently with the vertical compaction processes attributable to burial compaction. Similarly, abundant intricate specimens are sometimes concentrated in a single horizon, forming a pavement of *Corumbella* remains.

Considering these characteristics, thecae of *C. werneri* (Corumbá Group) may have been as flexible but not as functionally elastic as the periderm of modern coronates [39] and of some cnidarian fossils, like *Byronia* [40] or *Olivooides* [41] for example.

The coronate periderm is composed of thin lamellar layers of chitin [42] in a smooth microtexture arrangement [39, 43], functionally resulting in a soft tube that can be compressed and return to its original shape without damage or injury [39]. Morphologically, thecae of *C. werneri* also consist of a lamellar microfabric but made of polygonal plates (Figs. 6B, E and 7D, E); see ref. [17], like the Ordovician scyphozoan *Sphenothallus* that have integuments quite similar to some chitino-mineralized thecae of conulariids [17, 44, 45], and linguliids [46]. However, the theca of *Corumbella* is morphologically unique, because its polygonal plates sometimes have pores and papillae (Fig. 6F); see ref. [17].

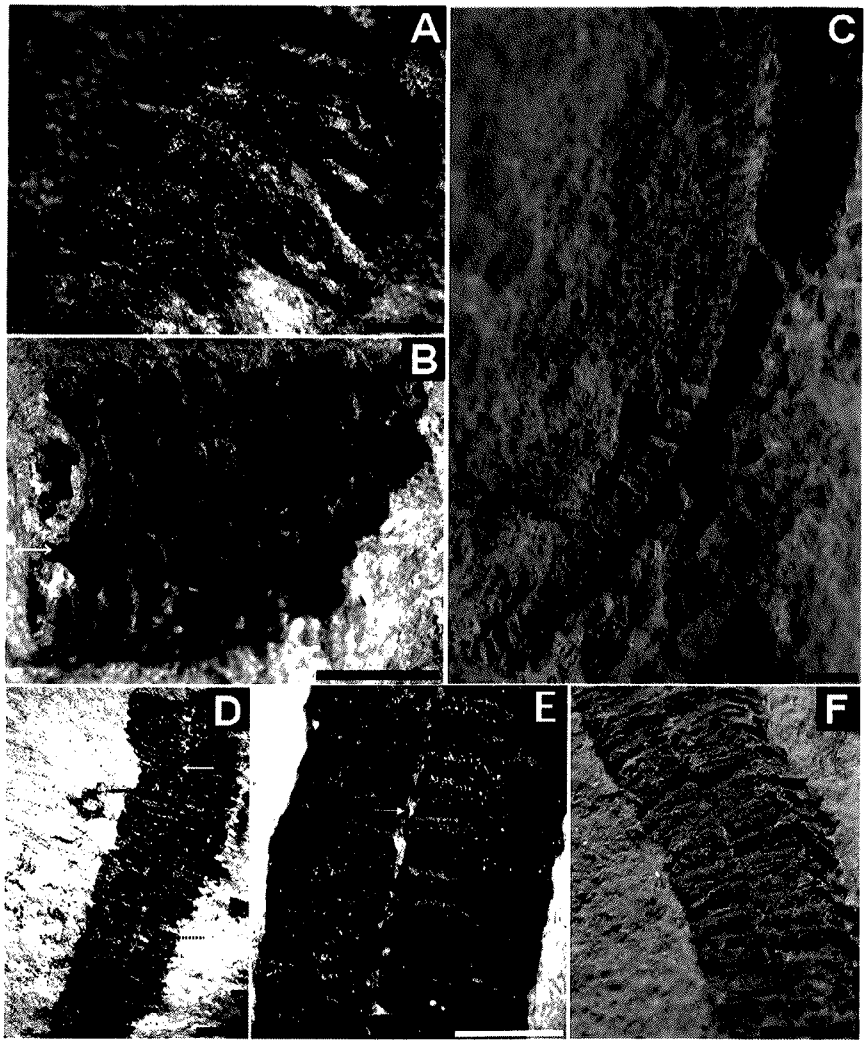

Fig 8. Corumbella werneri: morphology and modes of life. (A) GP1E-4089: oral region. (B) GP1E-4077: Inflated tube. Detail of a face with septum (white arrow), midline (black dashed arrow), rings (black dotted arrow) and lateral edge (black arrow) relatively compressed. (C) DGM-5601-I: specimen used in the original description by Hahn *et al.* (1982). Internal mold, recurved. It is observed the aboral region, uniseriate, without evidente midline in the (incomplete) attachment region. These rings (black dotted arrow) grade to an approximately polyhedral portion, with midline (on the face) (black dashed arrow) and lateral edge (black arrow). Notice a break in the longitudinal mid-distal portion of the fossil. (D) GP1E-4204: tube with longitudinal breakage, where it is evident the septum (white arrow), lateral edge (black arrow) and rings (black dotted arrow). (E) GP1E-3093: internal portion of folded tube, thick exoskeleton, where it is possible to see the septum (white arrow) formed by the inner part of the alternate rings (black dashed arrow). (F) DGM-5606-I: internal mold, three-dimensional, with midline (black dashed arrow), rings (black dotted arrow) and fragments of theca on the lateral edge (black arrow). Scale: 1mm. (A), (B), (C) and (D): reprinted from Pacheco *et al.* (2011) [6] under a CC BY license, with permission from Luis Alcalá, original copyright 2011.

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The EDS mapping detected a higher concentration of calcium in remains of *Corumbella* thecae in comparison to the rock matrix (Fig. 7B). It suggests a biomineralized theca. But we have not ruled out the possibility that the calcium concentrations may be the result of diagenetic mineralization of organic tissue, rather than original biomineralization.

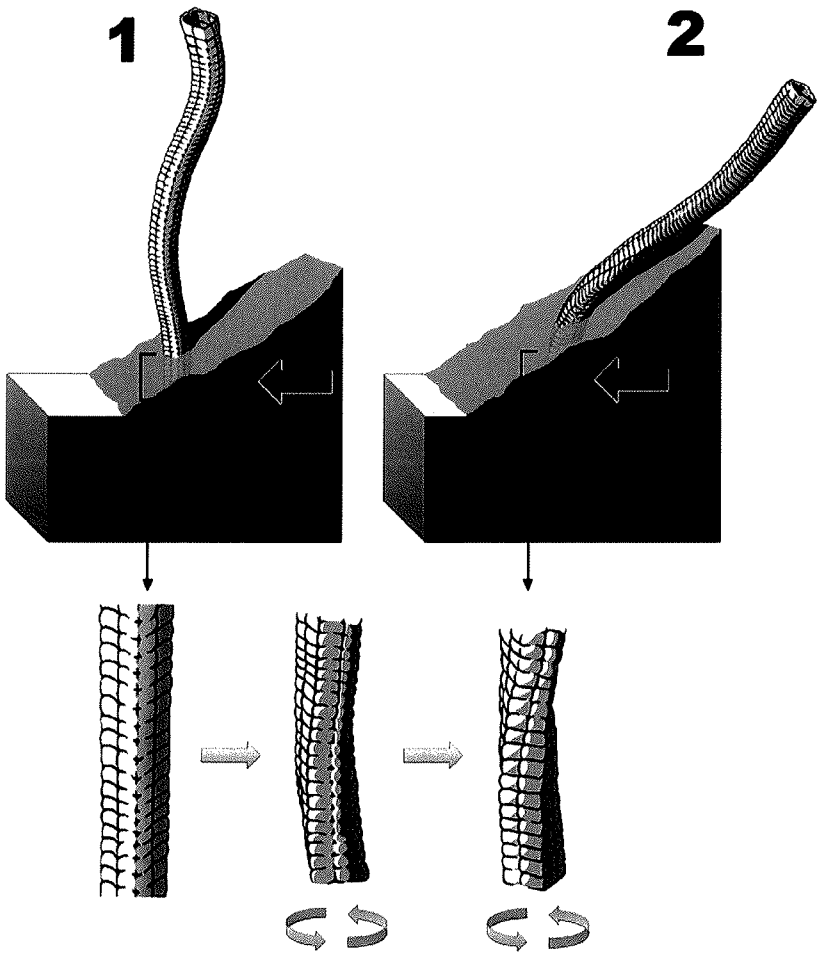

Fig 9. Simplified model for the mechanical origin of the torsion observed on the Corumbella specimen from USA (LACMNH 12802), which is dependent of the physical conditions of the animal and/or of the external forces. Subfigures 2 to 1 correspond to different stages: black arrows show a reconstitution from helical twisting happening when a *Corumbella* tube becomes partially buried (stage 2) until a possibility of *Corumbella* life mode (stage 1). Gray arrows point details of twisting until stage 2. Gray circular arrows show possibilities of twisting degrees in tubes.

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Nevertheless, skeletogenesis is the process of synthesizing skeletons and not necessarily involves biomineralization (which is the process that organisms precipitate solid materials to the formation of skeletal structures). Many animals synthesize completely organic skeletons, like insects, for example. Because our main issue is to investigate elements related to skeletogenesys process (including biomineralization as well), we also consider other elements related to cnidarian biomineralization, such as phosphate for example. However, we have not detected yet phosphate and other important elements related to this process besides calcium. We even had tried the chemical test for phosphate (1 dg of ammonium molybdate in reaction with 1:1 HNO3) [17] and it was not detected.

The ultrastructure of *Corumbella* also lacks the standard parabolic design characteristic of chitin-protein complexes, common to the former chitinous integuments exclusive from the Cambrian, such as the scyphozoan *Byronia robusta* [40, 47]. Moreover, unlike *Corumbella* and

other current cnidarians, *Byronia* integuments are thinner, exclusively organic, and almost always preserved as carbonaceous films that are flattened but not fragmented [40, 47].

In summary, the plastic deformation of *C. werneri* suggests that its theca was flexible, organic, or even weakly mineralized. Furthermore, we hypothesize that the lamellar nature, thickness (and mineralization?) of its integument (Figs. 6B, E and 8E) may have contributed to its vulnerability to fragmentation (Fig. 6C, D). These characteristics suggest that the theca may have been originally thicker and less elastic than the periderms of modern coronates and *Byronia*, and that it was originally flexible but inelastic.

Systematic Paleontology

The systematic review proposed here takes into account the approaches established for Brazilian specimens of *Corumbella werneri* [4–6, 12], which are applied to better constrain the systematic affinities of the incompletely described corumbellids from the lower member of the Wood Canyon Formation [9]. In order to facilitate this study and a comparison between Brazilian and USA specimens, we summarized data on the Brazilian specimens in a synoptic treatment, presented in Table 1.

Kingdom METAZOA Linnaeus 1758

Phylum CNIDARIA Verrill 1865

Class SCYPHOZOA Goette 1887

Family CORUMBELLIDAE Hahn, Hahn, Leonardos, Pflug e Walde 1982

Genus *Corumbella* Hahn, Hahn, Leonardos, Pflug and Walde 1982

Type species. *Corumbella werneri* Hahn, Hahn, Leonardos, Pflug and Walde 1982, by monotypy.

Emended diagnosis. Polyhedral, elongated tube, with internal septa formed by junction of alternate rings at midlines.

Corumbella werneri Hahn, Hahn, Leonardos, Pflug and Walde 1982

(Figs. 4–6 and 8)

Corumbella werneri Hahn et al., 1982: p. 4–9, Tables 1–3, Figs. 3–5, 9, 11.

Corumbella n. sp. Hagadorn and Waggoner 2000: Fig. 5 p. 356.

Emended diagnosis. Elongated polyhedral pyramidal exoskeleton (theca), thick, diameter along tube slightly variable; cross section circular at basal part, otherwise quadratic distalwards; external midline groove formed by junction of polygonal rings at apothem, continuous along the polyhedral tube; internal septa located internally to midline, when present; rings continuous over lateral edges, absence of carinae.

Description. Sample DGM-5601-I (Fig. 8C): three-dimensional internal mold, slightly compressed; tube "J"-shaped, 34 mm in height; aboral region of tube polyhedral, elongated, 9 mm in height; midline and lateral edges present. Sample GP/1E 4210a (Fig. 5E, F): internal mold of part of a three-dimensional polyhedral tube, quadrangular geometry, lateral edges visible; rings continuous at lateral edges; midline demarcated by merging of polygonal rings, in "U" conformation, with fragments of theca, alternately on face apothem (Fig. 5F); maximum length 9 mm, width 2 mm, maximum width of ring 1 mm, maximum length of ring 0.3mm. Sample DGM-5606-I (Fig. 8F): internal mold of part of a three-dimensional polyhedral compressed tube; lateral edges; rings continuous at lateral edges; midline demarcated by merging of rings alternately in face apothem, maximum length 19 mm, width 2.4 mm. Sample GP/1E 3093 (Fig. 8E) internal view of fragment compressed theca, thick; rings continuous at lateral edges; septa formed by merging of rings internally; thickness 0.05–0.2 mm, maximum length 9 mm. Sample GP/1E 4089 (Fig. 8A): oral region compressed at lateral edges, rings and lateral edges present; oral opening characterized by well marked hole. Sample GP/1E 4077 (Fig. 8B): tube

Table 1. Revision of morphological terminology and taxonomic affinities of *Corumbella werneri*.

Description	Hahn *et al.* (1982)	Zaine (1991)	Babcock *et al.* (2005)	This study
Body Organization	Growth polarity	Growth polarity not evident	Growth polarity	Growth polarity
	Bipartite organization: composed of primary and secondary polyps	No bipartite organization	Description of oral region and observation of an apical attachment region	Observation of oral-aboral organization
			No secondary polyps	No secondary polyps
				Articulation and cross continuity of rings
Geometry	Uni- and biseriate cylindrical parts, circular in section	One to four longitudinal series of hollow flat, nearly cylindrical compartments	Elongate tube, square in cross-section	Elongated polyhedral tube (pyramidal), approximately quadrangular in cross-section
Symmetry and internal thickening	Sclerosepta only in primary polyp (tetraseptation)	Not observed	Carinae (attributed to the midline)	Presence of septa
				Carinae not observed
	Tetramery		Tetramery	Tetramery
External structures	No external structures (*e.g.* midlines and corners) corresponding to internal septations	Absent	Midline and corner	Midline, lateral edges and faces
Covering	Isolated rings in the proximal part	Isolated chitinous rings	Isolated rings	Rings are alternate across midline and continued at the lateral edges
	No rings in polypar			Thick carapace, sometimes with longitudinal striations
	Chitinous periderm		Possible chitinous periderm	Composition of carapace probably organic (chitinous?) or weakly mineralized
Attachment structures	Not observed	Not observed	Apical region attached to an organic mass	Apical region attached to the substrate
Paleoecological considerations	Colonial	Reproductive modes not evident	Reproduction by budding	Inferred gregarious and/or colonial habit
Taxonomy	Subclass Corumbellata, Order Corumbellida, Family Corumbellidae	Vendozoa, Vendobiont	Cnidaria, Scyphozoa, Conulata	Metazoa, Cnidaria, Scyphozoa,
Phylogenetic relationships	Cnidaria: *Stephanoscyphus*	Giant protists related to an extinct order (or subclass) of rhizopods	Cnidaria: Modern *Stephanoscyphus* and fossil conulariid	Cnidaria: fossil conulariid
	Pennatulacea, Charniidae			

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inflated with three-dimensional rings, midline and septum present, lateral edges relatively compressed. Sample GP/1E 4204 (Fig. 8D): part of a three-dimensional polyhedral tube broken at the face and lateral edges; presence of polygonal rings; lateral edges and septa at midline visible in some parts of tube, absence of carinae. Sample LACMNH 12802 (Fig. 4A): three-dimensional polyhedral tube, presence of septa at midline and lateral edges; rings alternately converging at midline, apothem of face, twisting; specimen square in cross section; carinae absent.

Type series. DGM-5601I, DGM-5604I, DGM-5605I, DGM-5606I, DGM-5608I, DGM-5609I, DGM-5610I, DGM-5611I, DGM-5612I, DGM-5613I (Hahn et al., 1982, p. 4–9,Tables 1–3, Figs. 3–5, 9, 11), LACMNH 12802, LACMNH loc. 17130, LACMIP loc. 17130 (Hagadorn and Waggoner, 2000, p. 356, Fig. 5).

Examined Material. DNPM-RJ (DGM), 10 specimens; GSA/IGc-USP (GP/1E), 6 specimens; NHMLA (USA) (LACMNH, LACMIP), 2 specimens.

Discussion. All specimens studied here have similar morphology, and are summarized under the diagnosis of the genus *Corumbella*. The specimens from USA, which were previously assigned to "*Corumbella* n. sp.", show longitudinal grooves at the midline and the alternated rings at the center of the polygonal faces. In the USA fossils, the midline is also indicated by the presence of its respective internal thickening (septum), which is visible in cross section. Septa are not always visible in all specimens, even in the Brazilian ones, a pattern that may be attributed to decay prior to burial. Comparisons between USA and Brazilian specimens showed that they can be considered the same species, *Corumbella werneri*, as evidenced by the presence of an external midline, formed by the alternation of polygonal rings at the apothem (Figs. 4A and 5F, H). This midline is continuous throughout the polyhedral tube, showing an unbroken continuity of the rings at the lateral edges (Figs. 4A and 5F-H). In considering these specimens, it is possible that the tube was occasionally expanded. Such expansion might have occurred since the flexible integument was susceptible to sediment infilling (maybe during life as in the case of some modern coronates) [50], or movement of the tube (Fig. 9). Hence, there is not a diagnostic and unique characteristic that justifies the assignment of a new species to the *Corumbella* from USA [9]; after comparisons based on [4]. Re-examination of these three-dimensional molds showed spaces between the molds and the rock matrix (Fig. 4A, G), which indicates the previous existence of a relatively thick theca—one that would be similar in thickness to the skeletal integument of the specimens from the Tamengo Formation of Brazil and the Tagatiya Guazu Formation of Paraguay. The quadrangular cross-section along the length of the tube (Figs. 4A, F and 5D, H) reinforces our interpretation that the skeletal structure of *Corumbella* was more resistant than many fossils that are always found flattened or compressed but never fragments or with breaks (such as *Byronia*).

Conclusions and Future Directions

Our data not only confirms previously published observations [5, 9], but also add new information about morphology (*e.g.* attachment portion, oral region, rings disposition and midline) and ultrastructure (*e.g.* lamellae microfabric) that contributes an important complement to the interpretation and a new description of *C. werneri*.

This study is consistent with the idea that *Corumbella* is a scyphozoan cnidarian and that specimens from Brazil, Paraguay, and the USA are part of a similar taxonomic and benthic assemblage. The occurrence of specimens with the tip of *Corumbella*'s tube-like skeleton embedded in the sediment suggests that their mode of life was possibly similar to that of helicoplacoids, in which the animal was attached to or rooted in the substrate. *Corumbella* also had a relatively thick and sturdy theca that showed complex growth and flexure.

The taphonomic aspects considered here are only those essential to better perform morphological studies (*e.g.* distortion, compression) refusing bias in taxonomic descriptions. As the flexible exoskeleton of *Corumbella* may be susceptible to molding processes and/or sediments filling, we performed some insights into the importance of some deformations (*e.g.* twisting) to the interpretation of how some taphonomic classes, such as three-dimensional, can be preserved and incur in important specimens for taxonomic descriptions. Here we only offer a model that justifies the twists observed in *Corumbella* are not intrinsic to the organism (morphological) but an artifact of deformation related to external forces on its polyhedral structure during burial (see Fig. 9).

In this sense, some causes of the preservational style of its theca still remain enigmatic. The distribution of *Corumbella* remains among the marls and shales of Tamengo Formation lacks satisfactory paleoenvironmental explanation and taphonomic models. Detailed taphonomic

studies (involving the compilation of a deep sedimentological database) are still crucial to reveal fundamental aspects of fossilization process in *Corumbella* specimens.

In addition, further research about the possible mineralized nature (phosphatic or calcitic) of specimens may shed light on the corumbellids's role in the development of metazoan biomineralization.

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Author Contributions

Conceived and designed the experiments: MLAFP ACM. Performed the experiments: MLAFP PB MS JH FP JML. Analyzed the data: MLAFP PB MS JH DG. Contributed reagents/materials/analysis tools: PB MS JH FR JML. Wrote the paper: MLAFP ACM WH DG FR PB IDR.

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Corumbella werneri Hahn *et al.*, 1982 é um fóssil ediacarano originalmente documentado do Grupo Corumbá, Brasil. *Corumbella* é um dos primeiros fósseis de animais conhecidos com a capacidade de construir carapaça, tornando-se importante para a nossa compreensão da evolução da esqueletogênese animal. Embora já tenha sido sugerido como um cnidário, ainda não existe uma análise formal que avalie a posição filogenética de *Corumbella* dentro do Scyphozoa. Novos dados sobre a morfologia de *Corumbella* obtidos usando técnicas não-destrutivas revelam uma série de novos dados e interpretações sobre ultraestrutura, estrutura externa, estrutura interna e modo de vida. O objetivo deste estudo foi incorporar esses novos dados em uma análise filogenética formal para reavaliar a posição filogenética de *Corumbella* dentro da Cnidaria. Consideramos que, juntamente com os conulários, *Corumbella* fazia parte de um novo subgrupo dentro do Scyphozoa que chamamos o Paleoscyphozoa, um grupo irmão para Coronatae. Nesse sentido, os paleocifozoários seriam os primeiros representantes conhecidos de Scyphozoa a partir do registro fóssil.

Phylogenetic position of the Ediacaran paleoscyphozoan fossil *Corumbella* (Corumbá Group, Brazil) among cnidarians

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Abstract

Corumbella werneri Hahn *et al.*, 1982 is an enigmatic Ediacaran fossil originally documented from the Corumbá Group (ca 543 Ma) of Brazil. It is hypothesized to be a sessile scyphozoan cnidarian characterized by an elongated polyhedral tube. *Corumbella* is one of the first known animal fossils with the capacity for building hard parts, making it important for our understanding of the evolution of animal skeletogenesis. Although already suggested to be a cnidarian, there is as yet no formal analysis assessing the phylogenetic position of *Corumbella* within the Scyphozoa. New data on the morphology of *Corumbella* obtained by us using non-destructive techniques reveals a series of new characters and interpretations regarding ultrastructure, external structure, internal structure, and mode of life. The goal of this study is to incorporate these new data into a formal phylogenetic analysis in order to reassess the phylogenetic position of *Corumbella* within the Cnidaria. We consider that, together with fossil conulates, *Corumbella* formed part of a new subgroup within the Scyphozoa that we here call the Paleoscyphozoa, a sister group to living Coronatae. In this sense, paleoschyphozoans provide the earliest known representatives of the Scyphozoa known from the fossil record.

Key words: phylogeny, systematics, cladistics, *Corumbella*, Ediacaran, morphology, Cnidaria, Medusozoa, conulates.

Introduction

While some ancient fossils have been regarded as the polyps of Scyphozoa, all can currently be regarded as having uncertain affinities within the class. Examples include those Ediacaran-Cambrian boundary specimens of *Olivooides* from South China (Bengston and Zhao, 1999; Chen and Dong, 2008; Dong *et al.*, 2013; but see a contrary perspective in Yasui *et al.*, 2013), some late Cambrian fossils from the USA (Hughes *et al.*, 2000), putative Ediacaran conulates from the Lantian biota of China (Van Iten *et al.*, 2013), late Ediacaran *Vendoconularia* from the White Sea of Russia (Ivantsov and Fedonkin, 2002; Van Iten *et al.*, 2005a; Leme, 2006; Leme *et al.*, 2008a, b), and the late Ediacaran fossil *Corumbella* from Brazil (Hahn *et al.*, 1982; Hagadorn and Waggoner, 2000; Pacheco *et al.*, 2011; Warren *et al.*, 2012).

The initial diagnosis for the genus *Corumbella* Hahn et al. 1982 and species *C. werneri* Hahn *et al.*, 1982, came from abundant material obtained from the Tamengo Formation (Ediacaran, Corumbá Group, Brazil, ca. 543 Ma), found within the marls and shales of Saladeiro quarry, at Ladário town, Mato Grosso do Sul (Hahn *et al.*, 1982). The co-occurrence between *Corumbella* and conical shells of *Cloudina* provide clear evidence that the Tamengo Formation was deposited during to the last evolutionary and ecological phase of the Ediacara Biota (*e.g.* Hagadorn and Waggoner, 2000; Babcock *et al.*, 2005; Pacheco *et al.*, 2011; Warren *et al.*, 2012).

The original description of Hahn *et al.* (1982) regarded *Corumbella* as having a tetramerous bipartite structure, comprising a proximal primary polyp or stalk, without an anchoring base region, and a distal portion called the 'polypar', characterised by an arrangement of small, secondary and biseriate polyps (Hahn *et al.*, 1982). Other specimens have since been recorded from sandstones of the Great Basin in the USA (Lower Member of the Wood Canyon Formation, USA, Hagadorn and Waggoner, 2000), and from grainstones and mudstones of the Itapucumi Group in Paraguay (Warren *et al.*, 2011, 2012 – see Pacheco *et al.*, subm.). These North American records of *Corumbella* are currently regarded as conspecific with the South American ones (Pacheco *et al.*, subm.).

While a cnidarian affinity for *Corumbella* has already been postulated, there has as yet been no formal analysis of its possible phylogenetic position with the class Scyphozoa. Previous work has suggested relationships with either the living Coronatae (Hahn *et al.*, 1982; Leslie *et al.*, 2001; Babcock *et al.*, 2005) or the fossil Conulatae (Collins *et al.*, 2000; Hagadorn and Waggoner, 2000; Babcock *et al.*, 2005). On one hand, the elongated, ringlet and narrow tubes of *Corumbella* appear similar to those of the coronate *Stephanoscyphistoma*, but on the other hand they share similarities with fossil conulates such as pyramidal geometry, square cross section, midlines, septa, lateral edges (called corners in conulates) and polygonal rings arranged on faces in a way similar to conulate (called transverse ribs) (Fig. 1 and 2; *see* also Pacheco *et al.*, 2011).

New data on the morphology of *Corumbella* obtained using non-destructive techniques reveals a series of new characters, leading towards new interpretations regarding ultrastructure (*e.g.* polygonal

plates and lamellae microfabric; Warren *et al.*, 2012; Pacheco *et al.*, subm.; Fig. 3A-D), external structures (*e.g.* arrangement of rings along the midline) and internal structures (*e.g.* septa; Fig. 1D and 2C), and modes of life (Pacheco *et al.*, 2011, subm.; Fig. 1F, G). The goal of this study is to incorporate these new data into a formal phylogenetic analysis so as to allow a reassessment of the phylogenetic position of *Corumbella* among the cnidarians, and the testing of previous proposals (Hahn *et al.*, 1982, Hagadorn and Waggoner, 2000, Babcock *et al.*, 2005).

Material and Methods

The phylogenetic position of *Corumbella* based on previous analyses.

Our analysis is primarily based on previous phylogenetic inferences for the cnidarians. We have updated the matrix put forward by Van Iten *et al.* (2006a), coding four characters for *Corumbella* (17, 18, 39, and 43), and reassigning one for the Conulatae (42). The coding adopted by Marques and Collins (2004) and Van Iten *et al.* (2006a), supported by mitogenomic data (Kayal *et al.*, 2013), for extant cnidarians were maintained, except for our exclusion of Laingiomedusae, suggested to be a lineage of "Anthoathecata" (Cartwright *et al.*, 2008). We have also added six new characters related to both the Conulatae and to *Corumbella* (88 to 93). These character states are listed in Tables A1 and A2 below.

Our cladistic analysis (Fig. 4) follows the procedures of Marques and Collins (2004) and Van Iten *et al.* (2006a) in using branch-and-bound algorithm of PAUP* 4.0 (Swofford 2001), except that we did not carry out successive weighting analysis.

Remarks about some characters from Van Iten *et al.* (2006a).

Character 17. Life habit. One *Corumbella* specimen from Tamengo Formation (GP1E - 4216) has its basalmost region preserved and attached to the substrate (Fig. 1F, G), suggesting that adults had a benthic life habit.

Character 18. Symmetry. On the external surface, *Corumbella* is pyramidal at its distal (widest, oral) end and circular at its basal (smallest, aboral) end. Cross section of distal parts, including the septal arrangement, reveals a radial tetramerous symmetry. Septal arrangement runs throughout the inside of the tube (Pacheco *et al.*, 2011), implying an internally tetramerous arrangement as well (Fig. 2C). *Corumbella* supposedly grows by distal addition, and the ontogenetic development would therefore change from circular to pyramidal.

Character 39. Periderm. The exoskeleton of *Corumbella* is herein homologized with the periderm of Conulatae and other cnidarians on the basis of its ultrastructure. *Corumbella* displays multiple polygonal plates with pores (Warren *et al.*, 2012), and a exoskeleton with a lamellar microfabric (Fig. 3 B, C, D), which are both distinctive features shared with fossil conulates.

Character 42. Number of tentacular whorls. The character state for Conulatae is here updated on the basis of recent work by Van Iten *et al.* (2013).

Character 43. Septa in polyp. The midline feature of *Corumbella* is similar to that seen in fossil Conulatae. They are formed by alternating polygonal rings inserted as lateral apothems that divide each face of the pyramidal structure (Pacheco *et al.*, 2011, subm.; Fig 1A, B and Fig. 2).

Characters added to the matrix.

Character 88. Midline on polyp: 0- absent; 1-present.

Character 89. Transverse cross section of the polyp: 0- circular;, 1- quadratic.

Cnidarian polyps typically have a circular cross section to their bodies. This contrasts with the periderm, and presumably also the unpreserved soft parts of the polyp in nearly all fossil conulates, which have a quadrate cross section, although some rare specimens show a triangular, pentagonal or hexagonal transverse cross section (Babcock *et al.*, 1987b; Leme *et al.*, 2004, 2008, 2010; Van Iten *et al.*, 2005a; Rodrigues *et al.*, 2006). Polyps of *Corumbella* show a unique morphology in having a aboral uniseriate region with a circular cross section, grading to an elongated form with a tetraseriate or polyhedral cross section in the oral region (Fig. 2; Pacheco *et al.*, 2011, subm).

Character 90. Mineralized periderm: 0- absent; 1- present.

When present, the periderm can be either mineralized or non-mineralized. Some examples of mineralized periderm are known to be apormophic within a given lineage, as found within the "Anthoathecata" forms of Milleporidae and also the Stylasteridae (*e.g.*, Cartwright *et al.*, 2008). Nevertheless, neither the chemical composition nor the exoskeleton constitution of *Corumbella* have yet been fully elucidated. It may have been either wholly organic or weakly mineralized.

Character 91. Corner sulcus: 0- absent; 1- present.

Cross sections show that the quadrate exoskeletons of different conulate taxa can have corners that are either grooved or not grooved. This character is inferred to change from the former to the latter in *Anaconularia* and *Baccaconularia* (Sinclair, 1948; Moore & Harington, 1956; Hughes *et al.* 2000) The 'lateral edges' of *Corumbella* (Fig. 2 C; Pacheco *et al.*, 2011) are here regarded as homologous to the 'corners' of conulates.

Character 92. Pores and papillae alternating on polygonal plates: 0- absent; 1- present.

The pores of *Corumbella* occur in closely spaced rows, with some degree of organization (Warren *et al.*, 2012), unlike those pores found within the thecae of Paleozoic conulates (Kozlowski, 1968; Bischoff, 1978; Van Iten *et al.*, 2005b, 2006b). The papillae of *Corumbella* are similar in shape (although differing in patterns of organization) to structures observed on rods of some Phanerozoic conulates (Van Iten *et al.*, 2006a; John *et al.*, 2010). *Corumbella* pores may correspond to papillae on opposite sides of plates (Warren *et al.*, 2012).

Character 93. Polypoid hardened septa: 0- formed by the thickened theca; 1- formed by the insertion of alternate rings in the midline.

The septa of *Corumbella* are defined by an internal thickening resulting from the insertion of alternating rings along the midline on each face (Fig. 1A, B and Fig. 2 C: Pacheco *et al.*, 2011). Septa in *Corumbella* are therefore related to the insertion of alternate rings along the midline. The septal formation of fossil conulates (Conulatae) is different, however, since they were formed by an internal thickening of the theca. The septa of living coronates are not thought to compare with these patterns.

Phylogenetic Patterns and Discussion

Our analysis of the revised data set results in a single tree (Fig. 4 length=125 steps, consistency index=0.77, retention index=0.74). In comparison with the previous hypotheses of Van Iten *et al.* (2006a), the framework remains essentially the same, except for slight differences in the relationships among the Trachylina.

Corumbella can be regarded as the sister group to the conulates, making a grouping that we here propose to call the Paleoscyphozoa, an extinct group of conulate-like scyphozoans, which are themselves taken to be the sister-group of Coronatae (Fig. 4). Features shared between paleoscyphozoans and coronates include tough external coverings of the soft tissues (theca or exoskeleton in paleoscyphozoans, periderm in coronates), and an external morphology that gives some expression to the internal structures (Chapman and Werner 1972; Wurmbach and; Siewing 1985; Fig. 1 A, B). In these two groups, the external coverings may both be ornamented.

Unlike the conulate paleoscyphozoans, however, we note that *Corumbella* also shares features with the coronate *Stephanoscyphistoma*. Notable here is its elongate and somewhat flexible exoskeleton (Fig. 1 and 2), which could be taken to constitute indirect evidence in *Corumbella* for retractable muscles (cf. Seipel and Schmid 2006), and even for a well-developed muscle epithelium. Unlike *Corumbella,* however, the coronate *Stephanoscyphistoma* is conical-cylindrical, rounded in section, and shows no continuous septation along its tube interior (Werner 1967, 1971, 1973, 1979). These characteristics do not support sister-group relationships between *Corumbella* and *Stephanoscyphistoma* (*contra* Hahn *et al.*, 1982).

Although *Corumbella* tubes are conspicuously narrower, and have a lower rate of taper than those of conulates of comparable length, a striking similarity is their pyramid-shaped body (Pacheco *et al.*, 2011), with four faces and four lateral edges (Babcock and Feldmann 1986a; Babcock *et al.* 1987b; Van Iten, 1991; Leme *et al*, 2008a,b, 2010). The architecture of the faces in *Corumbella* is morphologically comparable with the midline of conulates, consisting of an external longitudinal groove which reflects the position of a continuous internal septum along the inside of the exoskeleton (Fig. 1 A, B, D and Fig. 2 C).

The rings (Fig. 1A, B) in *Corumbella* are similar to, maybe homologous with (cf. Babcock *et al.*, 2005), the ribs of conulate thecae. Indeed, conulates, *Corumbella* and coronates all have laterally arranged rings around the exoskeleton (Fig. 1 A, B), though there are differences too. In coronates and

Corumbella, the rings are pivotable, allowing some flexibility to the tube, whereas the ribs of conulates were thickened by chitinous-phosphatic layers and were dependent upon a flexible, although not pivotable tegument (Van Iten 1992b).

Interestingly, as with some species of *Conularia*, *Corumbella* presents a midline marked by overlapping rings that encounter each other alternately, with possibility of absence of internal thickenings on the lateral edges (cf. conulate corners) and midlines (Sinclair 1940; Moore and Harrington 1956b; Babcock and Feldmann 1986a; Van Iten, 1992a; Hagadorn and Waggoner 2000; Babcock *et al.*, 2005; Leme *et al*, 2008, 2010).

According to our data, and much like the periderm of the coronate *Stephanoscyphistoma* (Dunn 1982), *Corumbella* had a thick, organic or possibly poorly mineralized tegument, perhaps comparable with that of some putative Ediacaran conulates (e.g. *Vendoconularia*, Ivantsov and Fedonkin 2002) and maybe even with some Ordovician conulates (Van Iten *et al.* 2005b), whose exoskeleton is darkened and shows no obvious sign of significant mineralization.

The ultrastructure of the exoskeleton of *Corumbella* therefore supports homology with the periderm of Conulatae and other scyphozoans such as *Sphenothallus* (Van Iten *et al.*, 2005b). The multiple polygonal plates with pores (Warren *et al.*, 2012), as well as the lamellar microfabric of the exoskeleton, are additional characteristics shared with conulates. *Corumbella* appears to have been constructed from a thick, but flexible exoskeleton having a lamellar microfabric, as in extinct conulates, and lived with its basal part anchored in the sediment, much like living coronate scyphozoan *Conotubus* (Cai *et al.*, 2011), with its most distal part containing an opening and the oral region.

Many of these aspects of the internal morphology, ultrastructure and mode of life of *Corumbella* remained unknown until the application of microfocus X-ray tomography (microCT) and SEM techniques, which have here been used for the first time to reassess the phylogenetic position of *Corumbella* among the cnidarians. Together with conulates, *Corumbella* formed an extinct group we called the Paleoscyphozoa, which is here argued to have been a sister group to the coronate scyphozoans. In this sense, paleoschyphozoans arguably comprise the earliest representatives of not only the Class Scyphozoa but also the Phylum Cnidaria yet known from the fossil record.

SUMMARY AND CONCLUSIONS

Together with some data about basic external morphology, and thanks to microCT and SEM analysis, some aspects of internal morphology, ultrastructure and mode(s) of life helped to apply cladistics for better understanding of *Corumbella* affinities among scyphozoans. *Corumbella* is hypothesized to be a sessile cnidarian scyphozoan characterized by an elongated polyhedral tube and may have been one of the first known animals capable of building a mineralized skeleton, making it important in our understanding of the evolution of animal skeletogenesis. These specimens appear to

have originally been constructed of a thick, but flexible carapace, with lamellar microfabric, similar to extinct conulariids. According our analysis, *Corumbella* can be considered as a sister group to the extinct conulates, making a grouping that we here propose to call the Paleoscyphozoa.

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Appendix

A 1. List of characters and states.

Cellular and microstructural characters
1 – Cnidocil (0 – mobile; 1 – immobile).
2 – Mitochondrial DNA (0 – circular; 1 – linear).
3 – Gap junction plaques (0 – absent; 1 – present).
4 – Mesoglea (0 – non-cellular; 1 – cellular).
5 – Collagen structure (0 – homotrimerous; 1 – heterotrimerous).
Cnidome characters
6 – Cnidae (0 – absent; 1 – present).
7 – Stenoteles (0 – absent; 1 – present).
8 – Euryteles (0 – absent; 1 – present).
9 – Desmonemes (0 – absent; 1 – present).
10 – Mastigophores (0 – absent; 1 – present).
11 – Basitrichous isorhizas (0 – absent; 1 – present).
12 – Apotrichous isorhizas (0 – absent; 1 – present).
13 – Isorhizas (holotrichous or atrichous) (0 – absent; 1 – present).
14 – Heterotrichous anisorhizas (0 – absent; 1 – present).
15 – Birhopaloids (0 – absent; 1 – present).
16 – Rhopalonemes (0 – absent; 1 – present).
Life habit and symmetry characters
17 – Life habit (0 – benthic adults; 1 – planktonic adults).
18 – Symmetry (0 – radial; 1 – radial tetramerous; 2 – biradial).
Characters of reproduction
19 – Sexual condition (0 – hermaphroditic; 1 – gonochoric).
20 – Location of medusa formation (0 – lateral, budding from an entocodon; 1 – oral; 2 – direct development without polyp stage).
21 – Type of apical medusa formation (0 – strobilation; 1 – metamorphosis without transverse fission).
22 – Strobilation type (0 – polydisk; 1 – monodisk).
23 – Oocyte development (0 – oocytes develop without accessory cells; 1 – oocytes develop with accessory cells; 2 – oocytes develop within follicles; 3 – oocytes develop from uptake of somatic or other germ line cells).
24 – Spermatophore (0 – absent; 1 – present).
25 – Location of gonads (0 – gastrodermis; 1 – epidermis).
Characters of body organization
26 – Nectosome (0 – absent; 1 – present).
27 – Pneumatophore (0 – absent; 1 – present).
Characters of the planula
28 – Planula larva in the life cycle (0 – present; 1 – absent).
29 – Planula ciliation (0 – ciliated; 1 – non-ciliated).
30 – Number of endodermal cells of the planula (0 – varied number; 1 – constant, n = 16).
31 – Glandular cells in the planula (0 – absent; 1 – present).
32 – Nervous cells in the planula (0 – absent; 1 – present).
33 – Relationship between axes of planula and adult (0 – oral-aboral axis in the adult derived from the longitudinal axis of the planula; 1 – oral-aboral axis in the adult derived from the transverse axis of the planula).
Post planula characters
34 – Ephyrae (0 – absent; 1 – present).

35 – Actinula (0 – absent; 1 – present).
36 – Polypoid phase (0 – absent; 1 – present).
37 – Polymorphic polyps (0 – absent; 1 – present).
38 – Desmocytes (0 – present; 1 – absent).
39 – Periderm (0 – absent; 1 – limited to the basal area of body or to podocysts; 2 – present).
40 – Podocysts (0 – absent; 1 – present).
41 – Structure of polyp tentacles (0 – hollow; 1 – solid).
42 – Number of tentacular whorls (0 – one; 1 – 2 or more).
43 – Septa in polyp (0 – absent; 1 – gastrodermic folds present; 2 – present).
44 – Hydrotheca / gonotheca (0 – absent; 1 – present).
45 – Stomodeum (0 – absent; 1 – present).
46 – Organization of the nervous system (0 – in 1 or 2 nets; 1 – with nerve rings).
47 – Canal system (0 – absent; 1 – present).
48 – Gastrodermic musculature (0 – not organized in bunches; 1 – organized in bunches of gastrodermic origin; 2 – organized in bunches of ectodermic origin).

Medusoid characters

These characters apply to an adult life phase that typically follows an intermediate polyp stage. While homology between cnidarian medusoid phases has long been debated, the strong similarity in morphology of different medusae leads us to score these characters across the medusozoan groups. Anthozoa has no comparable life history phase and is scored accordingly throughout.

49 – Medusoid phase (0 – absent; 1 – present).
50 – Pedalium of coronate type (0 – absent; 1 – present).
51 – Rhopalia / rhopalioids (0 – absent; 1 – present).
52 – Complexity of rhopalium / rhopalioids (0 – simple hollow structures; 2 – rhopalia; 3 – rhopalia with complex eyes).
53 – Nerve ring(s) (0 – absent; 1 – one; 2 – two).
54 – Gastric filaments (0 – absent; 1 – present).
55 – Coronal muscle (0 – well developed; 1 – marginal and tiny).
56 – Pedalium of the cubozoan type (0 – absent; 1 – present).
57 – Velum (0 – absent; 1 – present).
58 – Umbrellar margin (0 – smooth and continuous; 1 – lobed).
59 – Tentacles (0 – absent; 1 – present).
60 – Tentacular bulbs (0 – absent; 1 – present).
61 – Statolith composition (0 – MgCaPO4; 1 – CaSO4).
62 – Septa (0 – absent; 1 – present).
63 – Septal shape (0 – straight; 1 – Y-shaped).
64 – Radial canals (0 – absent; 1 – present; 2 – present in the form of complex structures).
65 – Circular canal (0 – absent; 1 – partially present; 2 – fully present).
66 – Velarium (0 – absent; 1 – present).
67 – Coronal furrow (0 – absent; 1 – present).
68 – Gonadal location (0 – manubrium; 1 – radial canals).
69 – Statocysts (0 – absent; 1 – endodermic; 2 – ectodermic).
70 – Perradial "mesenteries" (0 – absent, 1 – present).
71 – Adult medusoid shape (0 – bell; 1 – pyramidal; 2 – cubic; 3 – actinuloid).
72 – Shape of horizontal cross-section (0 – circular; 1 – quadrate, i.e., with 4-parted symmetry).
73 – Urticant rings (0 – absent; 1 – present).
74 – Oral arms with suctorial mouths (0 – absent; 1 – present).
75 – Tentacular insertion (0 – umbrellar margin; 1 – away from the umbrellar margin).

76 – Manubrium (0 – absent; 1 – present).
77 – Nervous system organization (0 – GFNN absent; 1 – GFNN present).
78 – Structure of medusa tentacles (0 – hollow; 1 – solid).
79 – Tentacular morphology (0 – straight tentacles in their whole extension; 1 – tentacles with an angular inflection).
80 – Peronia (0 – absent; 1 – present).
81 – Ocelli (0 – absent; 1 – present).
82 – Peripheral system (0 – absent; 1 – present).
83 – Umbrellar furrow (0 – absent; 1 – present).
84 – Development of the umbrella (0 – fully developed; 1 – aboral cone).
85 – Number of tentacular whorls (0 – 1 whorl; 1 – 2 whorls).
86 – Velar canals (0 – absent; 1 – present).
87 – Frenulae (0 – absent; 1 – present).
88. Midline on polyp (0- absent; 1-present).
89. Transverse cross section of the polyp (0- circular; 1- quadratic).
90. Mineralized periderm(0- absent; 1- present).
91. Corner sulcus (0- absent; 1- present).
92. Pores and papillae alternating on polygonal plates (0- absent; 1- present).
93. Polypoid hardened septa (0- formed by the thickened theca; 1- formed by the insertion of alternate rings in the midline).

A 2. Re-coded data matrix of characters. ?: unknown state; N: non-comparable; x/y: polymorphic.

TAXA	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
Anthozoa	0	0	0	1	0	1	0	0	0	1	1	0	1	0	0	0	0	21	1	N	N	N	1	0	0	0	0	1	1	0
Stauromedusae	?	1	0	0	?	1	0	1	0	0	0	0	1	0	0	0	0	21	1	1	1	N	2	0	0	0	0	1	0	1
Conulatae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	11	?	?	?	?	1	?0	?	0	0	?	?	?
Cubozoa	1	1	0	0	?	1	1	1	0	1	0	0	1	0	0	0	1	21	1	1	1	N	?	1	0	0	0	1	1	0
Coronatae	?	?	0	1	?	1	0	1	0	0	0	0	1	0	0	0	1	11	1	1	0	0	0	0	0	0	0	1	1	0
Semaeostomeae	1	1	0	1	1	1	0	1	0	0	0	0	1	1	0	0	1	21	1	1	0	0	1	0	0	0	0	1	1	0
Rhizostomeae	?	1	0	1	?	1	0	1	0	0	0	0	1	1	0	0	1	20	1	1	0	1	1	0	0	0	0	1	1	0
Limnomedusae	1	1	?	0	?	1	0	10	0	1	0	0	1	0	0	0	1	2	1	0	N	N	3	0	1	0	0	1	1	0
Actinulida	?	?	?	0	?	1	1	1	?	0	0	0	1	0	0	0	1	N	1	2	N	N	?	0	1	0	0	0	N	N
Trachymedusae	?	1	1	0	?	1	1	1	0	0	0	0	1	0	0	0	1	N	1	2	N	N	3	0	1	0	0	1	1	0
Narcomedusae	?	?	?	0	?	1	0	0	0	0	0	1	1	0	0	0	1	N	1	2	N	N	3	0	1	0	0	1	1	0
Laingiomedusae	?	?	?	0	?	1	0	0	0	1	0	0	1	0	0	0	1	N	?	?	N	N	?	0	1	0	0	?	?	?
Leptothecata	1	1	?	0	?	1	0	0	0	1	1	0	1	0	0	0	1	2	1	0	N	N	3	0	1	0	0	1	1	0
Siphonophorae	1	1	1	0	?	1	1	1	1	1	0	0	1	0	1	1	1	2	1	0	N	N	?	0	1	0	0	1	1	0
Anthoathecata	1	1	1	0	?	1	1	1	1	1	1	0	1	1	0	0	1	2	1	0	N	N	3	0	1	0	0	1	1	0
Corumbella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	0	1	?	?	?	?	?	?	?	?	?	?	?	?

TAXA	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60
Anthozoa	1	1	0	0	0	1	10	0	0	0	0	0	2	0	1	0	0	1	0	N	N	N	N	N	N	N	N	N	N	N
Stauromedusae	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	2	1	0	1	0	0	1	1	0	0	0	0	1
Conulatae	?	?	?	?	?	1	0	?	2	?	?	0	2	0	?	?	?	2	?	?	?	?	?	?	?	?	?	?	?	?
Cubozoa	1	2	1	0	1	0	1	1	1	0	1	0	1	0	0	1	1	2	1	0	1	2	1	1	0	1	0	0	1	0
Coronatae	1	1	0	1	0	1	0	1	2	0	1	0	2	0	0	0	1	2	1	1	1	1	0	1	0	0	0	1	1	0
Semaeostomeae	1	1	0	1	0	1	0	0	1	1	1	0	2	0	0	0	1	2	1	0	1	1	0	1	0	0	0	1	1	0
Rhizostomeae	0	0	0	1	0	1	0	1	1	1	1	0	2	0	0	0	1	2	1	0	1	1	0	1	0	0	0	1	0	N
Limnomedusae	0	1	0	0	0	1	10	0	1	0	0	0	0	0	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	0
Actinulida	N	N	N	0	0	0	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	?	0	?	0	N	0	1	0
Trachymedusae	0	0	0	0	1	0	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	2	0	0	0	1	0	1	0
Narcomedusae	0	0	1	0	1	0	N	N	N	N	N	N	N	N	N	N	N	N	1	0	0	N	?	0	0	0	1	1	1	0
Laingiomedusae	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0	0	N	?	0	?	0	1	1	1	1
Leptothecata	1	1	0	0	0	1	1	0	20	0	1	0	0	0	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	1
Siphonophorae	1	1	0	0	0	1	1	0	2	0	0	?	0	0	0	?	0	0	1	0	0	N	2	0	0	0	1	0	0	1
Anthoathecata	1	1	0	0	0	1	1	0	2	0	0	0	1	1	0	0	0	0	0	1	0	0	N	2	0	0	0	1	0	1	1
Corumbella	?	?	?	?	?	1	0	?	2	?	?	?	2	0	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?

TAXA	61	62	63	64	65	66	67	68	69	70	71	72	73	74	75	76	77	78	79	80	81	82	83	84	85	86	87	88	89	90
Anthozoa	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	N	0	0			
Stauromedusae	N	1	1	0	0	0	0	1	0	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0			
Conulatae	?	1	1	?0	?	?	?	?	?	?	1	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?			
Cubozoa	1	1	1	1	0	1	0	1	1	0	2	1	0	0	0	1	1	0	0	0	1	0	0	0	0	1	1			
Coronatae	1	1	0	1	0	0	1	1	1	0	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0			
Semaeostomeae	1	0	N	2	1	0	0	1	1	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0			
Rhizostomeae	1	0	N	2	1	0	0	1	1	0	0	0	0	1	N	1	1	N	N	0	1	0	0	0	N0	0	0			
Limnomedusae	?	0	N	1	2	0	0	1	1	0	0	0	1	0	0	1	1	0	0	0	0	0	0	0	1	0	0			
Actinulida	?	0	N	0	0	0	0	0	1	0	3	0	0	0	0	1	?	1	0	0	0	0	0	1	1	0	0			
Trachymedusae	0	0	N	1	2	0	0	1	1	0	0	0	1	0	0	1	1	1	0	0	0	0	0	0	0	0	0			
Narcomedusae	?	0	N	0	2	0	0	0	1	0	0	0	0	0	1	0	?	1	0	1	0	1	0	0	0	0	0			
Laingiomedusae	N	0	N	1	2	0	0	0	0	0	0	0	0	0	1	1	?	1	1	1	0	1	1	0	0	0	0			
Leptothecata	0	0	N	1	2	0	0	1	2	0	0	0	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0			
Siphonophorae	N	0	N	1	2	0	0	0	0	0	0	0	0	0	N	1	1	N0	N	0	0	0	0	0	N	0	0			
Anthoathecata	N	0	N	1	2	0	0	0	0	1	0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0			
Corumbella	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	0 1	?

TAXA	91	92	93
Anthozoa	1	1	0
Stauromedusae	0	0	0
Conulatae	?	?	?
Cubozoa	?	?	0
Coronatae	?	?	0
Semaeostomeae	1	1	0
Rhizostomeae	0	0	0
Limnomedusae	0	1	0
Actinulida	N	N	N
Trachymedusae	0	0	0
Narcomedusae	0	0	1

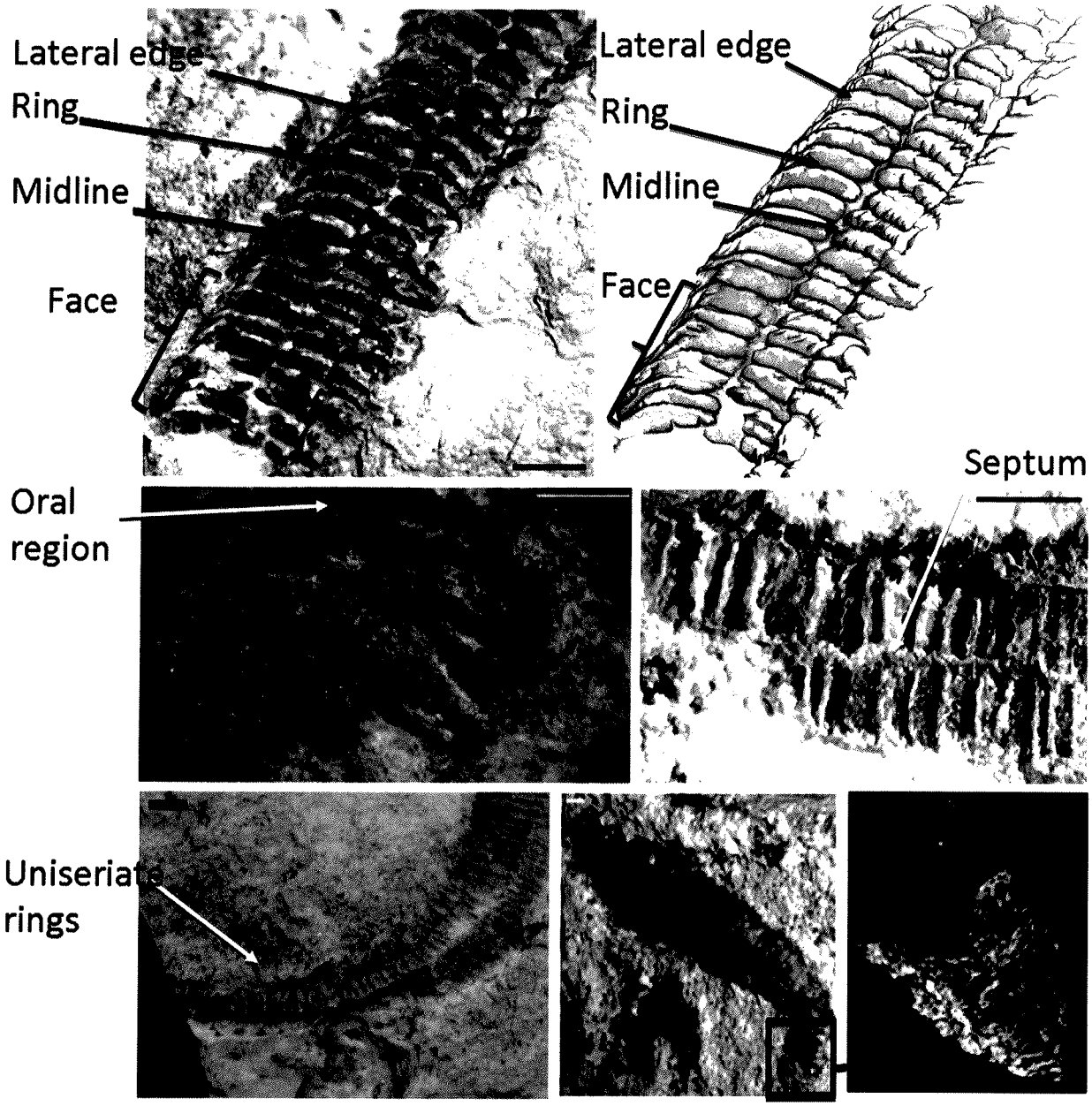
Figure captions

Figure 1. General morphology for *CorumbellaI* (A) Polyhedral part with midline, septa, lateral edges, rings and faces evidenced; (B) draw with morphological details; (C) Oral region; (D) Polyhedral part with detail for septum; (E) Aboral part wilt uniseriate rings; (F) attachment portion observed by the means of (G) microCT. Scale bar: 1mm.

Figure 2. *Corumbella.* Reconstitution of morphological structures: (A) Geometric modeling based on Pacheco *el al.* (2011) and Figure 1. Detail for pyramidal outlook; (B) Oral region; (C) Polyhedral part with midline, septa and lateral edge; (D) Aboral region with detail (E) to attachment structure. Scale bar: 1mm.

Figure 3. *Corumbella*: ultrastructure of exoskeleton. (A) MicroCT of *Corumbella* exoskeleton. (B) Interior view and detail for lamellae microfabric and plates. (C) Detail of lamellar plates by SEM and (D) pores in plates. Explanations: white arrow, midline; black arrow, lamellae; dotted arrow, pores; scale bar for (A) and (B): 1mm.

Figure 4. Cladistic tree (length=125 steps, consistency index=0.77, retention index=0.74). We assume *Corumbella* as sister group of conulariids. Together with conulariids, *Corumbella* formed Paleoscyphozoa: a sister group with coronates


Lateral edge
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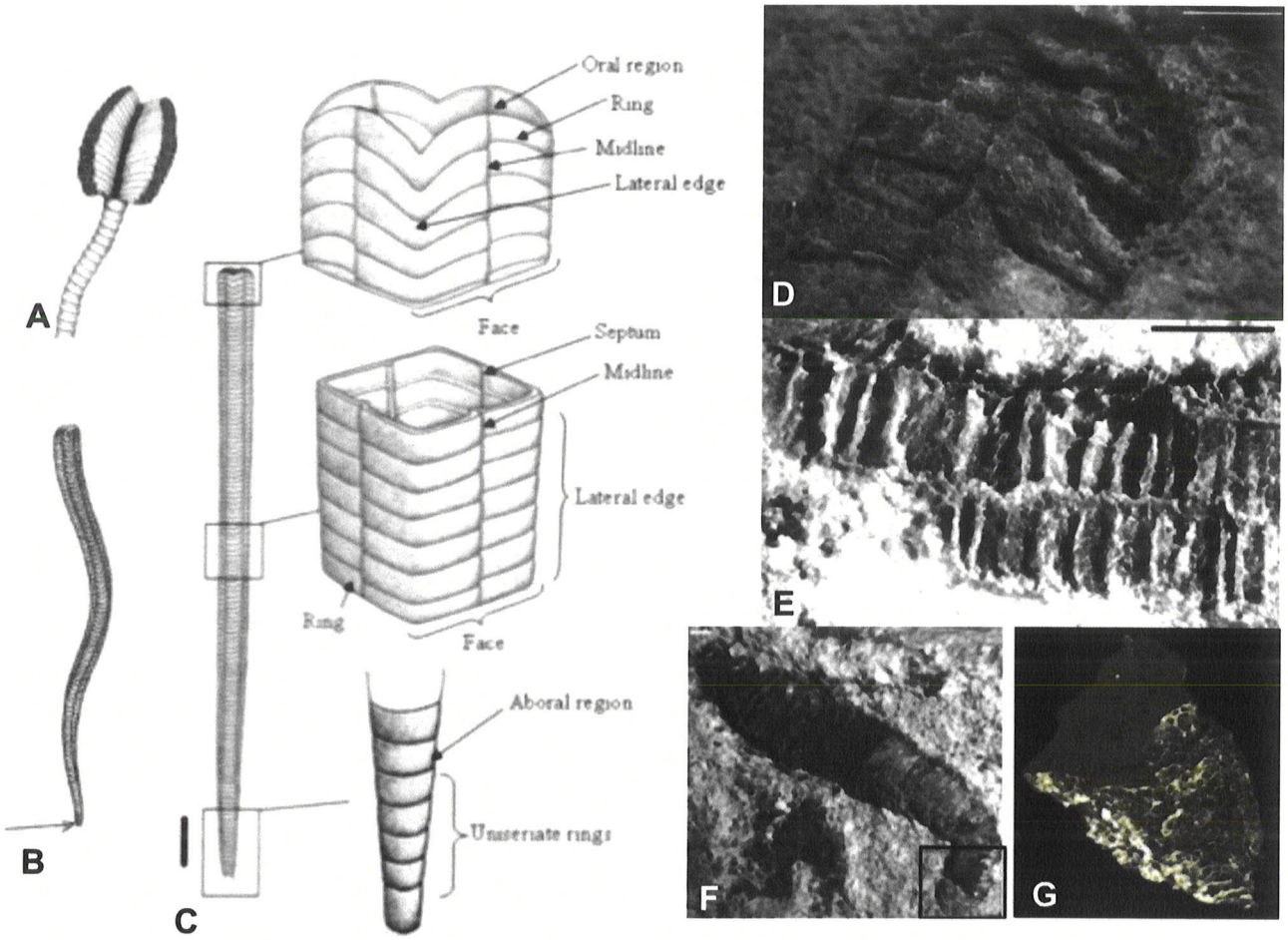
Midline
Face
Lateral edge
Ring
Midline
Face
Septum
Oral region
Uniseriate rings


Oral region
Ring
Midline
Lateral edge
Face
Septum
Midline
Lateral edge
Ring
Face
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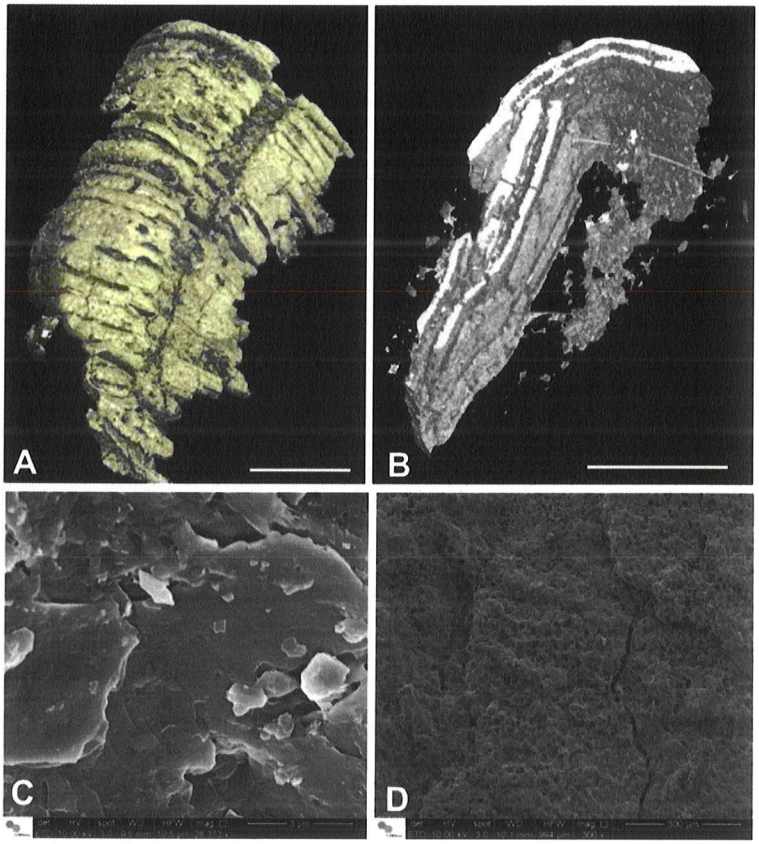
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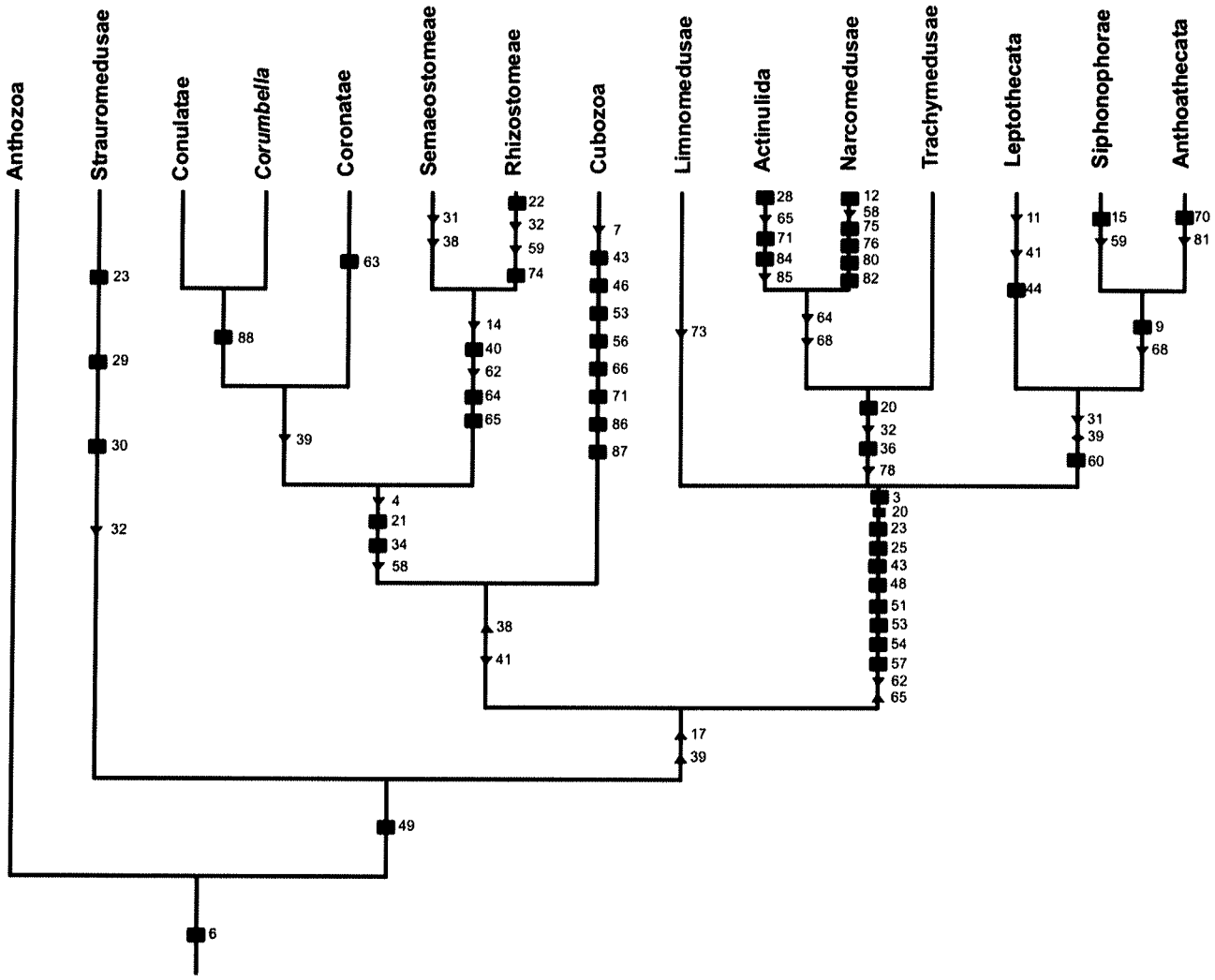
Anthozoa
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Conulatae
Corumbella
Coronatae
Semaeostomeae
Rhizostomeae
Cubozoa
Limnomedusae
Actinulida
Narcomedusae
Trachymedusae
Leptothecata
Siphonophorae
Anthoathecata
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CAPÍTULO 4

Distribuição paleoambiental de cnidários ediacaranos: potenciais indicadores de limites estratigráficos.

Texto inédito.

O Grupo Corumbá é caracterizado por apresentar a maior assembléia de formas de vida neoproterozoicas, registradas na América do Sul (Almeida, 1945, 1958a, b, 1964, 1965, 1968, 1984; Hahn *et al.*, 1982; Zaine & Fairchild, 1987; Zaine, 1991; Boggiani *et al.*, 1993, 2010; Boggiani, 1998; Gaucher *et al.*, 2003; Babcock *et al.*, 2005; Fairchild *et al.*, 2012; Pacheco *et al.*, 2011, 2015; Van Iten *et al.*, 2014; 2016; Walde *et al.*, 2015; Morais *et al.*, 2017; Becker-Kerber *et al.*, 2017; Adorno *et al.*, 2017; Parry *et al.*, 2017) (Figuras 4.1 e 4.2). Nas últimas décadas, pesquisas paleontológicas, realizadas nesta unidade litoestratigráfica, revelaram a existência de organismos que atestaram à importância da transição Proterozoico/Cambriano, no Brasil (vide revisão em Fairchild *et al.*, 2012). Tal conteúdo fóssil, presente no Grupo Corumbá é representado por e estromatólitos, microfósseis (p.ex. "*Vase-shaped microfossils*" (VSMs), *Sphaerocongrerus variabilis*), metáfitas (*Tyrasotaenia* sp.) e metazoários (*Paraconularia* sp., *Corumbella werneri* e *Cloudina lucianoi*). Estes últimos constituem as mais antigas evidências dos Metazoa na América do Sul (Almeida, 1945, 1958a, b, 1964, 1965, 1968, 1984; Hahn *et al.*, 1982; Zaine & Fairchild, 1987; Zaine, 1991; Boggiani *et al.*, 1993, 2010; Boggiani, 1998; Gaucher *et al.*, 2003; Babcock *et al.*, 2005; Pacheco *et al.*, 2011, 2015; Warren *et al.*, 2011, 2012; Van Iten *et al.*, 2014; 2016; Becker-Kerber *et al.*, 2017). Portanto, a análise paleontológica do Grupo Corumbá apresenta papel fundamental na elucidação da história da explosão adaptativa de metazoários macroscópicos que marcou a transição do Proterozoico para o Fanerozoico. De fato, a ocorrência de *Corumbella werneri*, *Paraconularia* sp., juntamente com as conchas cônicas de *Cloudina lucianoi,* tem sido usada para correlacionar os fósseis da Formação Tamengo com a biota de Ediacara (Almeida, 1945, 1958a, b, 1964, 1965, 1968, 1984; Hahn *et al.*, 1982; Boggiani, 1998; Zaine, 1991; Gaucher *et al.*, 2003; Babcock *et al.*, 2005; Warren *et al.*, 2012; Pacheco *et al.*, 2015; Walde *et al.*, 2015; Van Iten *et al.*, 2014; 2016; Becker-Kerber *et al.*, 2017; Adorno *et al.*, 2017).

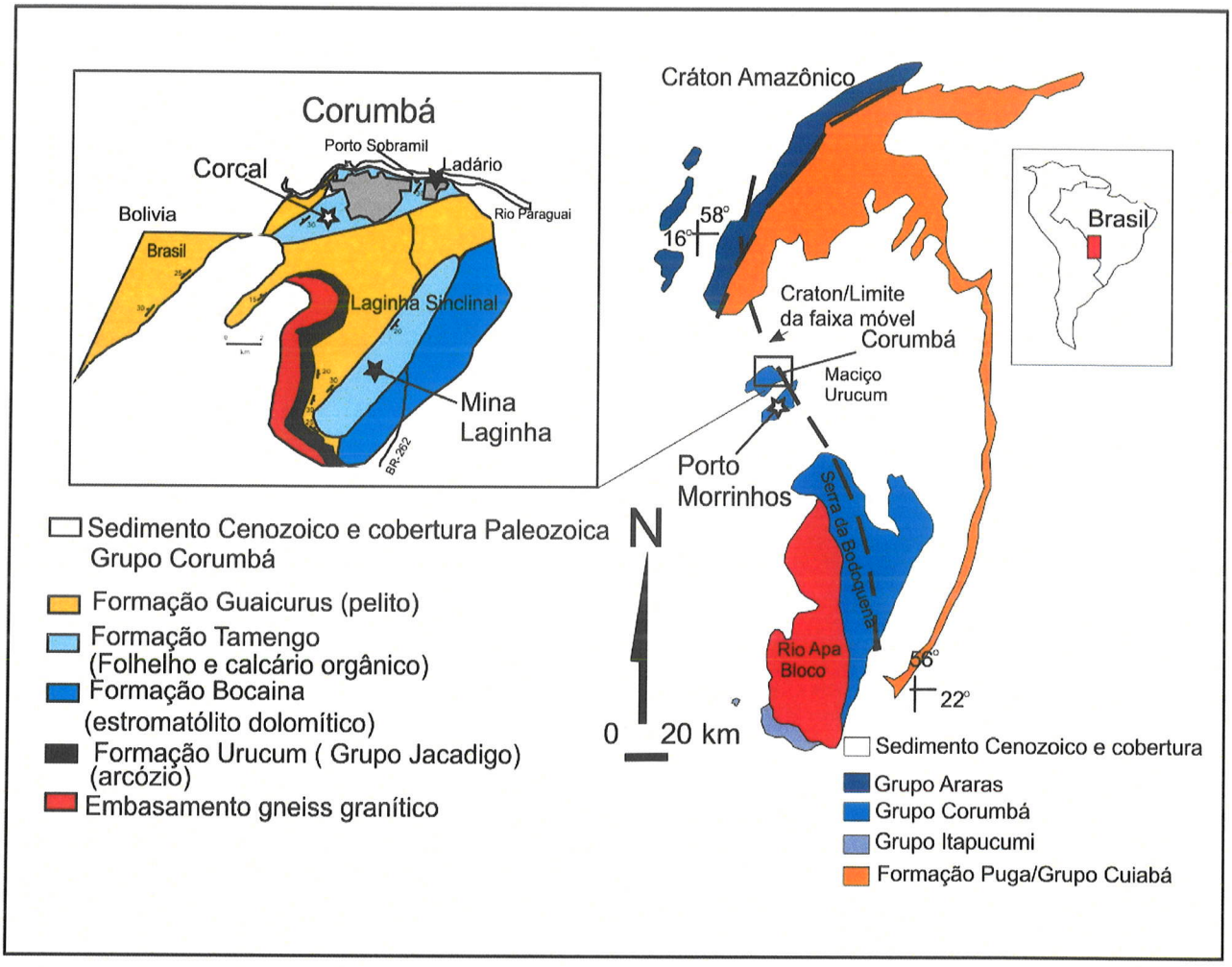

Figura 4.1. Mapa geológico da região de Mato Grosso do Sul com enfoque ao Grupo Corumbá, retirado de Van Iten *et al.* (2016) e Diniz (2017).

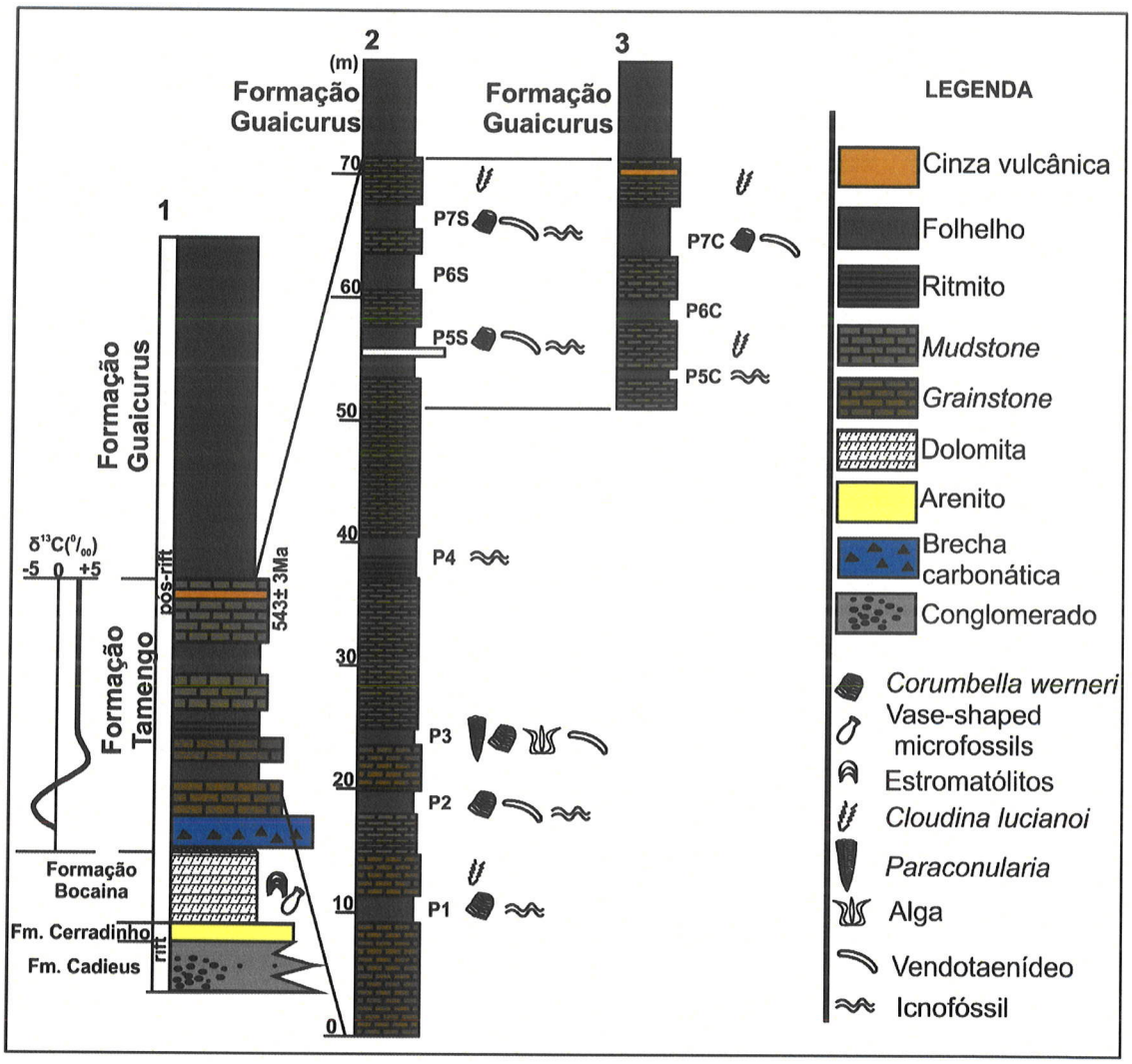

Figura 4.2. Coluna estratigráfica do Grupo Corumbá 1: formações do Grupo Corumbá, 2: detalhe da Fm. Tamengo, 3: correlação do topo da Fm. Tamengo na Mina Corcal. Modificada de Van Iten *et al.* (2016) e Diniz (2017).

Boggiani (1998) dividiu a Formação Tamengo em nove fácies carbonáticas compostas por: fácies de quatzo-arenito sugerindo um retrabalhamento eólico dos grãos. Fácies de brechas intraformacionais originárias da Formação Bocaina retrabalhadas e depositadas na Formação Tamengo, indicando o limitide da borda do talude. Fácies *rudstones* com clastos arredondados delimitando o ambiente em talude continental com alta energia. Fácies de mudstones calcíticos pretos, interpretado como um ambiente de deposição com baixa energia rico em matéria orgânica. Fácies de margas carbonosas rica em matéria orgânica indicando uma deposição em zona fótica de baixa energia.

Também foram delimitadas as fácies de ritmitos *mudstones*/folhelho carbonoso com presença de material fóssil, interpretada como um ambiente de maior profundidade podendo ter condições hemipelágicas. Fácies *ooids grainstones* com fragmentos de *C. lucianoi* podendo ser formadas em águas rasas sobre a plataforma durante a transgressão marinha ou podem indicar deposição em águas mais profundas através de processos de

ressedimentação. Fácies de *rudstones* interpretado como um ambiente com alto nível do mar em águas mais profundas (Boggiani, 1998).

Oliveira (2010) também estudou as fácies carbonáticas da Formação Tamengo, subdividindo-as em duas associações: A associação *shoreface* e a associação *shoreface/offshore*.

A associação *shoreface* apresenta barras oolíticas e três fácies, sendo a primeira de *grainstone* intraclástico maciço formado a partir do retrabalahmento por fluxo oscilatório. A segunda formada por *grainstone* oolítico maciço lateralmente contínuo, criados a partir da precipitação carbonática em um ambiente com atividade constante de correntes ou ondas, ou seja, um ambiente de alta energia. A terceira caracterizada por ritmito com ocorrência eventual de *Cloudina lucianoi* em posição de vida formado a partir da alternância da de processos de baixa (precipitação dos folhelhos) e alta energia (influxo de grãos terrígenos. Oliveira (2010) propõe um ambiente de alta energia para essa associação, devido à presença de ooides e intraclastos, mas seria uma região plana com migração de formas de leito em barras a partir da ação de correntes litorâneas. Atribui a presença de ritmitos carbonosos e carapaças de *C. lucianoi* devido ao desenvolvimento de barras ooliticas que serviriam como proteção contra a ação de ondas de tempestade e que auxiliariam na construçãi de ambientes protegidos caracterizados por baixa energia.

A associação *shoreface/offshore* teria sido influenciada por tempestades e composta por quatro fácies: calcário cristalino com estratificação cruzada *hummocky* com presença de fragmentos de *C. lucianoi* formada a partir da deposição por fluxo combinado dominantemente oscilatório por ondas de tempestades. Calcário cristalino maciço criado a partir da precipitação química de carbonato em ambiente com energia moderada a alta. Pelito carbonático maciço formado a partir da suspensão química. Folhelho rico em matéria orgânica depositado a partir da suspensão em um ambiente de baixa energia.

Segundo (Fazio *et al.*, 2016) a Formação Tamengo teria um possível aporte sedimentar baixo devido a áreas baixas ao seu redor seguido de uma subida no nível do mar (Boggiani, 1998) e por consequência um aumento na taxa de acomodação (Catuneanu, 2006; Catuneanu *et al.*, 2011) criando um ambiente de talude com uma comunicação abrupta de ambientes de água rasa situados a oeste para águas mais profundas e oceânicas a Leste (Boggiani, 1998). As águas mais profundas, abaixo do nível de base de ondas de tempestade, e, de baixa energia, seriam responsáveis pela deposição de materiais finos como pacotes de ritmitos com folhelhos, siltito e argilitos onde viveriam *C. werneri*.

A partir da análise estratigráfica e litológica realizada, foi encontrada a alternância de 5 litotipos diferentes como argilito, siltito, folhelho, arenito e calcário que também se apresentam na forma de camadas homogêneas ao longo da seção com presença de registro fossilífero, todos possuem granulometria fina, também são encontrados de forma

homogênea calcários *grainstones* e *mudstones* podendo ter estratificação cruzada *hummocky* e em algumas localidades, especificamente no topo da formação podem estar associadas com espécimes de *Cloudina lucianoi*.

Analisando detalhadamente os pacotes pelíticos, a litologia apresentada indica um ambiente deposicional calmo e de baixa energia capaz de sedimentar materiais finos o que pode ser corroborado por estarem abaixo de *grainstones* com estratificação cruzada estilo *hummocky* inferindo menor influência de ação de ondas de tempestade e a presença de registro fossilífero da espécie de *Corumbella werneri*, que por possuir uma carapaça mais orgânica e frágil, poderia ser preservada em ambientes mais calmos. Já a presença de *C. lucianoi* em calcários pode inferir que viveriam em ambientes de plataforma rasas que foram retrabalhados para partes mais profundas através de (Boggiani, 1998; Oliveira, 2010).

Portanto, a ocorrência de *Corumbella werneri* preferencialmente nos pelitos, enquanto, *Cloudina lucianoi* nas camadas de calcário, indica que provavelmente habitaram ambientes diferentes, ou pelo menos o modo e a capacidade de preservação das carapaças deveriam ser distintos (Guimarães *et al.*, 2014). De fato, a diferença da composição mineralógica entre as carapaças de *C. lucianoi* composta de $CaCo_3$, e *C. werneri* mais orgânica, composta por uma película escura de carbono, pode ser um fator limitante na preservação desses fósseis.

Entretanto, a ocorrência de *C. werneri* juntamente com macroalgas (Figura 4.3) pode indicar condições de águas mais rasas, ainda em zona fótica. Esse novo dado mostra que, talvez, mesmo ocorrendo em pelitos, indicando deposição em águas calmas, seria possível que *C. werneri* tivesse condições paleoecológicas de habitat desde águas mais rasas, acima do nível de base de ondas de tempestades até mesmo, mais profundas. No entanto, conforme os resultados observados, os níveis de ocorrência e de maior abundância de *C. werneri* devem estar associados a momentos de aumento na taxa de sedimentação e deposição de partículas finas, em substrato com baixa influência de ondas de tempestades.

Outra evidência de que seria provavelmente condições de águas mais rasas é a presença de *Paraconularia* sp, completamente achatada, incompleta, preservando apenas a região mediana (Van Iten *et al.*, 2016). Segundo (Rodrigues *et al.*, 2003), nas rochas sedimentares da Formação Ponta Grossa (Devoniano), Bacia do Paraná, em geral, nos intervalos mais rasos do Trato de Sistemas Transgressivo, raras são as ocorrências de fósseis de conulários. Quando presentes, as tecas estão achatadas lateralmente e rasgadas, apenas com a região mediana preservada. Essas tecas foram submetidas a algum tipo de transporte, possivelmente curto, antes de sua deposição final (Figura 4.3).

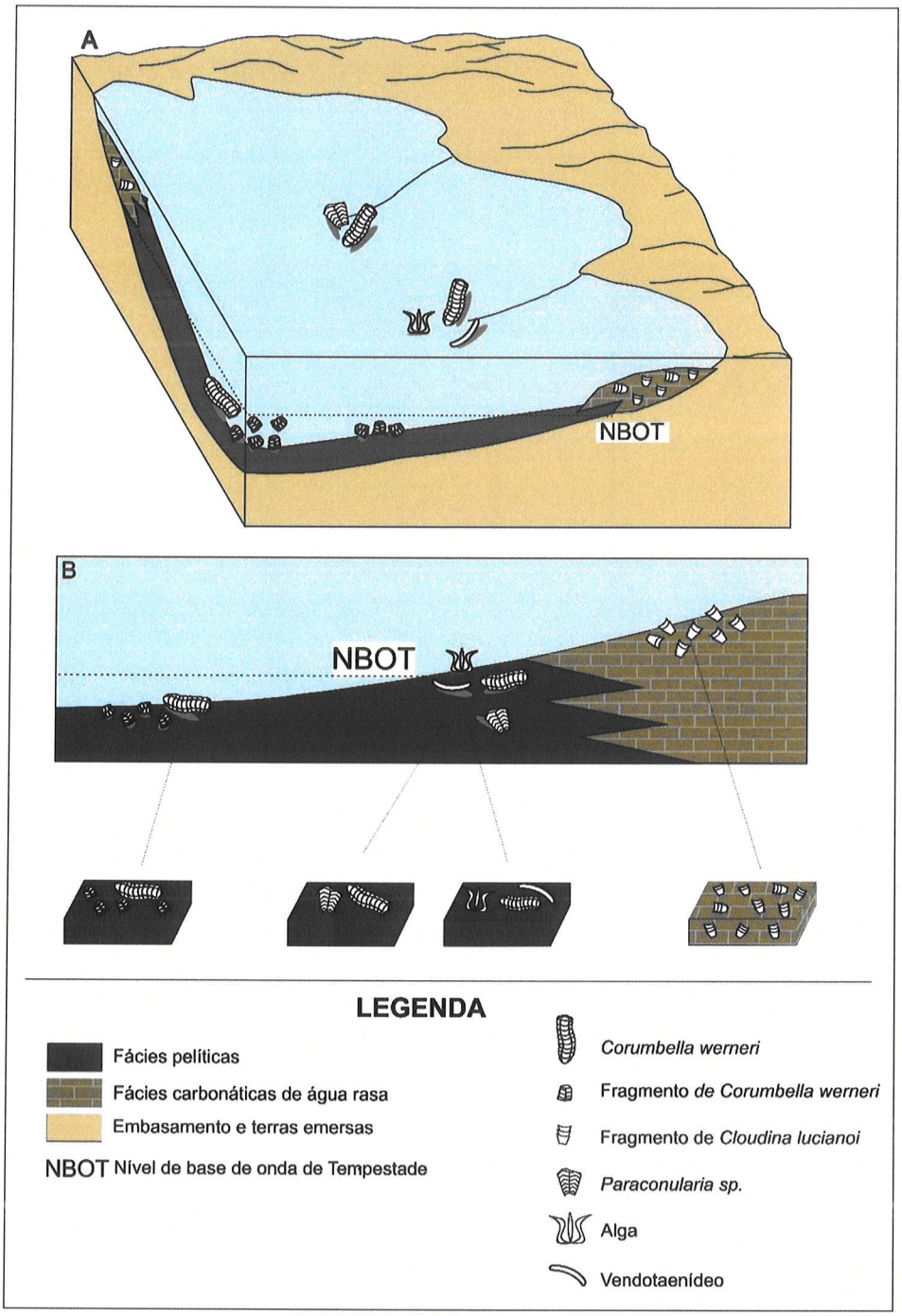

Figura 4.3: Representação paleoeambiental de *C. werneri*, *Paraconularia* sp., *C. lucianoi* e outros fósseis da Formação Tamengo. Modificado de Rodrigues *et al.*, (2003) e Matos *et al.* (2017), Diniz (2017).

Evidências estratigráficas, tafonômicas e anatômicas sugerem, fortemente, que conulários e *C. werneri* distribuíam-se nos fundos acima do nível de base de ondas de tempestade, no entanto, são preservadas em maior número abaixo do nível de base de ondas de tempestade, graças ao maior potencial de fossilização, sob condições menos energéticas. Tendo em mente os dados acima e examinando a distribuição vertical de *C.*

werneri, Paraconularia sp. e *C. lucianoi* da seção da Formação Tamnego, é notável sua ocorrência em intervalos estratigráficos específicos. Em outras palavras, esses macrofósseis não ocorrem aleatoriamente na seção.

Em termos estratigráficos, a Formação Tamengo apresenta ciclos de raseamento marcando de duas a três parassequências. Recentemente, foi descrito um horizonte de fragmentos de *C. werneri,* juntamente com fragmentos de *C. lucianoi.* Esse horizonte corresponde a depósitos de um limite de parassequência, registrando uma superfície de inundação marinha. Correntes de fundo afetaram o substrato remobilizando e fragmentando as carapaças de invertebrados da epifauna. Sob tais condições, o retrabalhamento dos bioclastos no fundo será ampliado e, graças à remobilização dos biclastos, os organismos bentônicos ficarão preservados como fragmentos (Miller *et al.* 1988, Brett 1995, Brett *et al.* 1997; Ribeiro, 2001, Rodrigues *et al.*, 2003). Dessa forma, a identificação de um horizonte de fragmentos de *C. werneri,* juntamente com fragmentos de *C. lucianoi* pode contribuir para a indicação do limite entre parassequências (Figura 4.4).

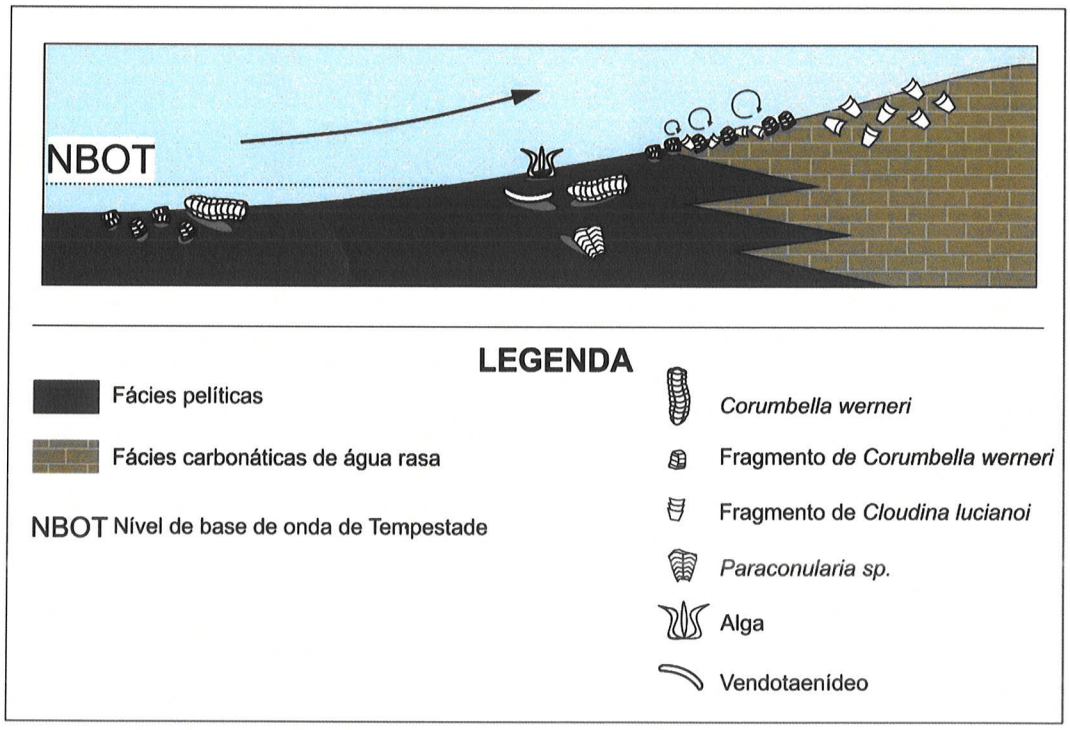

Figura 4.4: Horizonte de fragmentos de *C. werneri,* juntamente com fragmentos de *C. lucianoi,* registrando um limite entre parassequências.

Os resultados obtidos indicam consistentemente que os dados tafonômicos são um importante complemento às análises estratigráficas, especialmente como evidência independente para as interpretações paleoambientais. Por outro lado, os dados tafonômicos contribuem também para o melhor entendimento da paleobiologia desses grupos de cnidários extintos, mostrando ser essa ciência ferramenta indispensável à análise do registro sedimentar.

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CONCLUSÕES

As pesquisas realizadas e resumidas nesse trabalho permitem concluir que:

Os mais antigos cnidários fósseis conhecidos ocorrem em estratos de idade ediacariana e consistem em formas polipóides que eram não-biomineralizados ou fracamente assim. Um possível conulário pode primeiro ter aparecido (635-577 Ma), na Formação Lantian, Sul da China. No entanto, uma nova ocorrência de *Paraconularia* sp., em associação com *Corumbella werneri,* no Ediacarano (c. 543 Ma), Formação Tamengo, Brasil, confirma a origem dos primeiros cifozoários no Neoproterozoico.

As recentes interpretações filogenéticas indicam que, juntamente com os conulários, *Corumbella* fazia parte de um novo subgrupo dentro do Scyphozoa, os Paleoscyphozoa, um grupo irmão de Coronatae atuais. Nesse sentido, os paleocifozoários representariam os primeiros Scyphozoa conhecidos a partir do registro fóssil.

Em relação à Família Conulariidae, a análise filogenética indicou que as subfamílias Conulariina, Paraconulariinae e Ctenoconulariinae previamente reconhecidas não foram sustentadas como monofiléticas. Conulários são cnidários, extintos, com teca fosfática.

Conulários são característicos das faunas do Domínio Malvinocáfrico, sendo abundantes nas concentrações fossilíferas do Devoniano. Outras ocorrências são verificadas na Argentina, Peru, Paraguai, Uruguai e África do Sul. No Brasil, ocorrências de conulários são verificadas nas bacias do Amazonas, do Parnaíba e do Paraná e, mais recentemente, no Ediacarano, Formação Tamengo.

Corumbellídeos tinham uma teca espessa, mas flexível e provavelmente viviam com a sua parte basal ancorada no sedimento, bem como *Conotubus.* Quando considerados juntos, esses resultados sugerem que *Corumbella* foi um dos primeiros cnidários a construir um exoesqueleto, empregando uma microfábrica lamelar semelhante aos conulários.

A associação entre *Corumbella* e macroalgas, incluindo os vendotaenídeos, pode indicar condições de águas mais rasas, ainda em zona fótica, ou seja, numa profundidade que receberia luz solar suficiente para que ocorresse a fotossíntese, indicando que teria condições paleoecológicas de habitat desde águas mais rasas, acima do nível de base de ondas de tempestades até mesmo, mais profundas. Adicionalmente, a presença de um exemplar de *Paraconularia* sp., completamente achatada, incompleta, preservando apenas

a região mediana, também reforça a hipótese de que *Corumbella*, deve ter habitado água mais rasas.

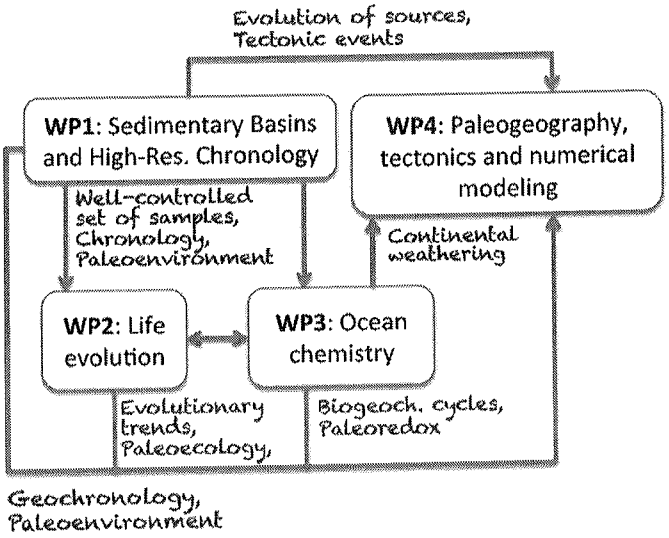
A ocorrência de *Corumbella werneri* preferencialmente nos pelitos, enquanto, *Cloudina* nas camadas de calcário, indica que provavelmente habitaram ambientes diferentes, ou pelo menos o modo e a capacidade de preservação das carapaças deveriam ser distintos.

A identificação de um horizonte de fragmentos de *C. werneri,* juntamente com fragmentos de *Cloudina lucianoi* pode contribuir para a indicação de limite entre parassequências.

PERSPECTIVAS FUTURAS

Mudanças significativas na composição e na dinâmica da Terra são observadas no final do Neoproterozoico. Neste período ocorreu um dos principais saltos evolutivos na biosfera, com o aparecimento de formas complexas de vida. Ocorreram também variações importantes no clima e na configuração dos continentes. Neste contexto, os processos de inovação biológica são comumente relacionados às mudanças ambientais em uma relação de causa-e-efeito. No entanto, ainda se conhece pouco acerca do Sistema Terra do Neoproterozoico, quando condições climáticas e tectônicas extremas podem ter amplificado os efeitos diretos e indiretos do meio ambiente na biologia e vice-versa.

Em agosto de 2016 foi aprovado o Projeto Temático FAPESP (16/06114-6) "*The Neoproterozoic Earth System and the rise of biological complexity*" o qual pretende compreender acerca do Sistema Terra do Neoproterozoico a partir da integração de dados sobre a composição química dos oceanos, a evolução da vida e a configuração paleogeográfica do planeta entre o Criogeniano e o Cambriano inferior. Para tal, no projeto Temático serão desenvolvidos de forma integrada quatro grupos de trabalho (Work packages): (1) estudo sedimentológico e geocronológico de alta resolução de quatro bacias no Brasil e na África, compreendendo o intervalo de interesse, (2) análise detalhada do registro paleontológico dessas sucessões sedimentares (3) um estudo geoquímico e isotópico das mesmas sucessões sedimentares de modo a gerar um registro multi-proxy das variações dos ciclos biogeoquímicos nos oceanos, (4) reconstruir a paleogeografia do Neoproterozoico. Portanto o objetivo maior onde estão inseridas as pesquisas em andamento é entender as conexões existentes entre a vida, o meio ambiente e a tectônica no Neoproterozoico, em particular os efeitos do aumento da concentração de oxigênio e de nutrientes na origem dos metazoários.



Integração entre os grupos de trabalho propostos no projeto Temático-FAPESP.

Dessa forma, os projetos em andamento e futuros vão atender as questões do segundo grupo de trabalho "Life Evolution" que irá estudar e compreender os aspectos paleoecológicos e paleoevolutivos do Grupo Corumbá (Neoproterozoico). Como primeiros resultados desse projeto foram publicados em 2017, dois artigos internacionais:

PARRY, L.; BOGGIANI, P.C.; CONDON, D.; GARWOOD, R.; LEME, J. M.; McILROY, D.; BRASIER, M. D.; TRINDADE, R.; CAMPANHA, G. A. C.; PACHECO, M.L.A.F.; DINIZ, C. Q. C.; LIU, A. G. 2017. Ichnological evidence for meiofaunal bilaterians from the Ediacaran?Cambrian transition of Brazil. *Nature Ecology and Evolution*, v. 5, p. 1-36.

BECKER-KERBER, B.; PACHECO, M. L. A. F.; RUDNITZKI, I. D.; GALANTE, D.; RODRIGUES, F.; LEME, J. M. 2017. Ecological interactions in *Cloudina* from the Ediacaran of Brazil: implications for the rise of animal biomineralization. *Scientific Reports*, v. 7, p. 5482.

Atualmente, estão sendo desenvolvidos os seguintes projetos, relacionados abaixo. O desenvolvimento desses projetos está alinhado à projetos de Pós-Doutorado, de Doutorado e de Iniciação Científica.

a) *Icnofósseis da Formação Tamengo e Guaicurus (Grupo Corumbá, Ediacarano-Cambriano)*. (Projeto Doutorado-FAPESP).

A Explosão Cambriana representa um dos eventos mais críticos da história da Terra. Esse aumento na diversidade e complexidade de fósseis e de icnofósseis é marcado pela ampliação na exploração do sedimento, o que causou uma mudança drástica no ambiente e permitiu a formação de novos habitats. No Neoproterozoico, os icnofósseis são mais simples espelhando seus produtores, mas são de suma importância, pois descrever as características dessas atividades em um momento em que os organismos vivos simples estariam começando a se diferenciar e se especializar, auxilia no entendimento evolucionário dos mesmos. Utilizado de forma integrada à análise sedimentológica e estratigráfica, o estudo de icnofósseis vem sendo cada vez mais aplicado como ferramenta adicional à análise paleoambiental e estratigráfica de depósitos sedimentares. No Brasil, o registro de icnofósseis do limite Pré-Cambriano-Cambriano é escasso, tanto pela falta de unidades geológicas, como pela dificuldade de preservação de organismos simples, de corpo mole. No Grupo Bambuí, Formação Sete Lagoas, são encontrados icnofósseis atribuídos a *Palaeophycus* e *Archaeonassa*. Foram descritos icnofósseis de idade Cambriana na parte Norte da Faixa Paraguaia no Grupo Alto Paraguai de *Skolithos linearis*. *Diplocraterion parallelum*, *Arenicolites* sp. Na faixa Paraguai Sul, em Mato Grosso do Sul,

está localizado o Grupo Corumbá, na qual a Formação Guaicurus corresponde ao seu topo e possui contato inferior gradacional com a Formação Tamengo. A Formação Tamengo, de idade 542 Ma, representa rochas do limite superior do Ediacarano. Não é encontrado nenhum registro fossilífero ao longo da Formação Guaicurus, exceto macroalgas e icnofósseis com formato de tubos sinuosos, formando túneis sub-horizontais e uma rede irregular com múltiplas camadas, além de icnofósseis de aparência bilobada. Este projeto será fundamentado em torno de questões paleontológicas envolvendo a taxonomia juntamente com questões paleoecológicas, paleoambientais e bioestratigráficas dos icnogêneros em rochas presentes na Formação Tamengo e Guaicurus do Grupo Corumbá, auxiliando no entendimento da transição da evolução de organismos no limite do Pré-cambriano e avaliando o impacto que bioturbadores causam no ambiente. Em caráter paleontológico estão relacionados a descrição morfológica e identificação taxonômica dos icnofósseis a partir de equipamentos como: estereomicroscópio, microscópio eletrônico de varredura, microtomografia, análise química por EDS e espectroscopia Raman. Descrever e compreender as ocorrências dos icnofósseis dessas localidades, pode auxiliar o entendimento do impacto em que organismos bioturbadores causaram no ambiente, como taxa de oxigenação e revolvimento do substrato, durante o processo de transição evolutiva dos metazoários.

b) *Estudo de microfósseis Pré-Cambrianos (Grupo Corumbá).* (Projeto Pós-Doutorado-FAPESP).

As conexões entre inovações biológicas evolutivas e mudanças ambientais compreendem temas relevantes na área de geociências. Durante o Neoproterozoico a biosfera é caracterizada pelo registro das revoluções biológicas (e.g. aquisição de partes duras e surgimento dos metazoários) associadas a grandes mudanças climáticas e químicas nos oceanos (e.g. glaciações, depósitos ferríferos), porém, pouco se sabe a respeito das reais implicações destes eventos. Este projeto de pesquisa se encaixa no escopo do Projeto temático FAPESP (2016/06114-6), intitulado "The Neoproterozoic Earth System and the rise of biological complexity", pois visa preencher essas lacunas, integrando novas informações sobre a morfologia e composição de microfósseis eucariontes da Faixa Paraguai Sul com informações sobre a química dos oceanos, paleogeografia e tectônica da faixa entre o Criogeniano e o Cambriano.

c) *Distribuição estratigráfica de Corumbella e Cloudina da Formação Tamengo (Grupo Corumbá, Ediacarano).* (Projeto Iniciação Científica).

Apesar das interpretações sistemáticas, paleoecológicas e paleobiogeográficas elaboradas sobre *Corumbella weneri* e *Cloudina lucianoi*, muitas questões permanecem em

aberto, como, por exemplo, as relações tróficas, o modo de vida e o habitat destes táxons, bem como os processos e as condições paleoambientais de preservação destes invertebrados.

Dessa forma, é constatado que estudos sobre a distribuição estratigráfica de detalhe, para *Corumbella werneri* e *Cloudina lucianoi*, no Grupo Corumbá, são escassos. Mesmo diante das informações disponíveis, até o momento, muitas questões, de cunho tafonômico, paleoambiental e paleoecológico, ainda não foram totalmente esclarecidas. Associados a outros fósseis, *Corumbella werneri* e *Cloudina lucianoi* corroboram uma conjunção de importantes processos da evolução biológica (como a aquisição de esqueletos mineralizados) e das mudanças que ocorreram no planeta ao longo da sua história geológica. Portanto, as questões relevantes ao estudo destes táxons estão estruturadas na determinação das características estratigráficas, relacionadas às questões tafonômicas para o estabelecimento das condições e paleoambientais e paleoecológicas, refletido pelo habitat, modos de vida e estrutura trófica.

d) *Tafonomia e preservação de fósseis ediacaranos da Formação Tamengo (Grupo Corumbá, Ediacarano).* (Projeto Iniciação Científica).

Não existem ainda estudos sobre a tafonomia de detalhe de fósseis Ediacaranos no Grupo Corumbá. A determinação das características da tafonomia desses fósseis ajudará a elucidar o estabelecimento de condições sobre o habitat e modos de vida.

Portanto, considerando que certos aspectos relacionados ao estudo de fósseis do Grupo Corumbá são essenciais para estabelecer os eventos biológicos ocorridos no Neoproterozoico, este trabalho deve ajudar a uma compreensão mais detalhada dos padrões e processos biológicos e geológicos, subseqüente ao Fanerozoico.

Serão descritas as a orientação dos espécimes, as estruturas sedimentares presentes no nível de ocorrência de fósseis, como abaixo e acima destes, as características biostratinômicas de fósseis, como fragmentação, desarticulação, transporte, alinhamento e convexidade e as características diagenéticas dos fósseis como tipo de fossilização.

Finalmente, os projetos em andamento vão colaborar para a consolidação do estabelecimento da linha de pesquisa em macrofósseis ediacarianos, no âmbito da Paleontologia do Estado de São Paulo.