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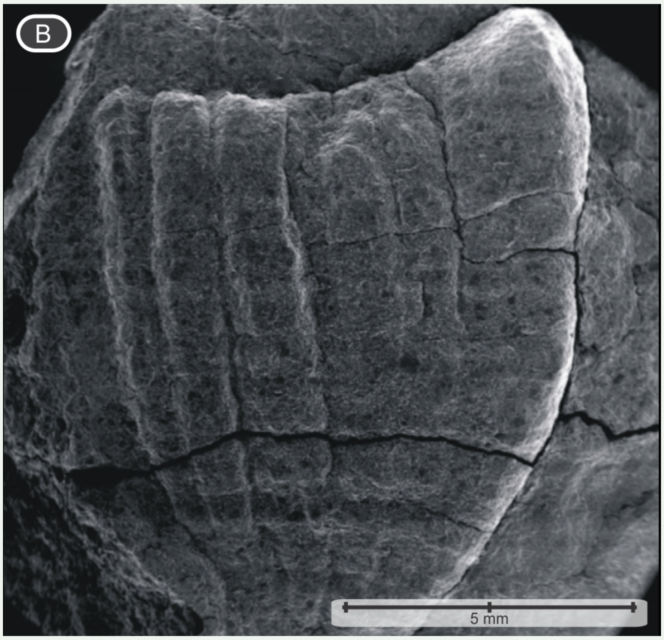

Mouro & Saldanha, 2021. *Paleontologia em Destaque*, v. 36, n. 75, 2021, p. 51, Figura 2B.

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ABSTRACT

The Brazilian fossil record holds crucial information regarding the evolutionary history of many invertebrate groups (e.g., cnidarian, bryozoan and brachiopods). Most of them are well-distributed through the formations of intracratonic basins (Amazonas, Paraná, Sergipe-Alagoas and others), which have been studied since the first expeditions in the second half of the 19th century. Among the invertebrate groups, the phylum Porifera, recognized as one of the earliest-branching of metazoan kingdom, is rarely recovered and studied. Beyond the taphonomic biases, one of the reasons for the scant occurrence may be related to lack of interest and inability to recognize the organisms. Thus, aiming to ratify the poriferan presence in time and space on the Brazilian rocks, here we present a review. Despite previously reported, complete sponges are restricted to Carboniferous–Permian interval.

Keywords: Porifera, South America, Brazilian basins, Phanerozoic.

RESUMO

Esponjas fósseis do Brasil: revisão e perspectivas. O registro fossilífero brasileiro contém informações cruciais sobre a história evolutiva de muitos grupos de invertebrados (e.g., cnidários, briozoários e braquiópodes). A maioria está bem distribuída pelas formações das bacias intracratônicas (Amazonas, Paraná, Sergipe-Alagoas e outras), que vêm sendo estudadas desde as primeiras expedições da segunda metade do século XIX. Dentre os grupos invertebrados, o filo Porifera, reconhecido como uma das ramificações mais basais do reino Metazoa, é raramente descoberto e estudado. Além dos vieses tafonômicos, uma das razões pela escassa ocorrência pode estar relacionada à falta de interesse e incapacidade de reconhecer os organismos. Assim, visando ratificar a presença de poríferos no tempo e no espaço nas rochas brasileiras, aqui apresentamos uma revisão. Apesar dos relatos anteriores, esponjas completas estão restritas ao intervalo Carbonífero–Permiano.

Palavras-chave: Porifera, América do Sul, bacias brasileiras, Fanerozoico.

INTRODUCTION

Sponges (phylum Porifera) are organisms with a long and successful evolutionary history. They are considered as one of the most primitive animals, being crucial for understanding the metazoan phylogeny. Even with their intermittent fossil record from the Cambrian onwards and being normally restricted to sites of exceptional preservation, poriferans are found in most aquatic environments, and may comprise a significant portion of many benthic communities, both fossil and recent (Bond, 1992; McClintock *et al*., 2005; Carballo & Bell, 2017). Thereby, they are generally regarded as ecosystem engineers, actively influencing local physical-chemical processes and enhancing biodiversity; thus, being a powerful group for performing paleoecology studies (see Jiménez & Ribes, 2007; De Goeij *et al*., 2008; Mohamed *et al*., 2010).

In recent years, fossil sponges have been reported in Brazilian rocks, specially to the Carboniferous–Permian interval. These findings have provided interesting data about the taphonomic pathway and allowed paleoenvironmental reconstructions (Mouro *et al*., 2014; 2020; Ng *et al*., 2019). Apart from these complete bodies, most of the reports of fossil

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sponges on Brazilian formations (from Silurian to Quaternary) are about loose spicules, usually mixed and transported, which are normally ignored by an unaware paleontologist. However, several reliable information can be obtained from the loose spicules, such as insights of sponge diversification and evolution (see Mostler, 1990; Mehl, 1998; and many others).

Therefore, here we present a review of all the sponge fossil occurrences from the Brazilian rocks, seeking to explore the phylum potential. Contrary to other invertebrate groups, which are well-distributed through the formations of almost all intracratonic basins (Amazonas, Paraná, Sergipe-Alagoas and others), the poriferans are possibly neglected.

SPONGE OCCURRENCES IN THE BRAZILIAN BASINS

Precambrian to Devonian

Since the establishment as a metazoan, the phylum Porifera has been subject to uncertainty over its life evolution through time. Conflicts between the unequivocal first appearance of fossil sponges at Cambrian period, the much earlier diversification (Tonian–Ediacaran) implied by molecular clock predictions (Sperling *et al.*, 2010; Dohrmann *et al.*, 2013) and questionable porifera-like fossils (Antcliffe *et al.*, 2014; Muscente *et al.*, 2015) have been dominating the paleospongiology research over the last few years.

Brazilian Ediacaran basins are well-known by the presence of macroscopic and complex benthic communities associated to Avalon and Nama biota (see Van Iten *et al.*, 2014; Pacheco *et al.*, 2015; Becker-Kerber *et al.*, 2020, and others). For the Itajaí Basin, Santa Catarina State (642±12 Ma – 581±48 Ma, Silva *et al.*, 2002; Basei *et al.*, 1987), Netto & Da Rosa (1997) and Da Rosa (2005) described millimetric low relief discoid forms with sub millimetric radial lines that form larger and smaller crowns, suggesting similarity to the Choiidae group, which dates from Middle Cambrian to the Early Ordovician (Figures 1A–C, 7; see also Botting, 2007; Botting *et al.*, 2013). Despite the morphologic similarities, Becker-Kerber *et al.* (2020), based on geochemical and petrographic analysis, have argued against the Choiidae occurrence. These authors recognized yellow flat discs composed by Fe, similar to pyrite/marcasite discs, associated with the Itajaí specimens (Figure 1D–F; Seilacher, 2001). Thereby, these choia-like structures are discoidal inorganic minerals, a nice trick pseudofossil.

Another dubious occurrence has been suggested to the rocks of Tamengo Formation (543 ±3 Ma, Ediacaran–Cambrian boundary, Babinski *et al.*, 2008), Corumbá Group. Adôrno (2019) reported the presence of sparse microscopic acicular structures (with a carbonate composition) in siltstones, limestones and calcarenites from three distinct sites (Table 1; Figures 1G, 7). The author described elongated 3-D globular centimetric structures, formed by cross-linked needles, assigning as probable arrangement of the sponge body (Figure 1H). On the same sample, he also suggested the chamber microfossil as poriferan gemmules.

No taxonomic affiliation has been suggested for the specimens and the gemmules are probably sponge resting bodies. Despite the original composition is still not defined, if the Tamengo Formation specimens were a truly poriferan with a calcium carbonate composition, then sponge early evolution may have begun before the Cambrian Explosion. Furthermore, the Corumbá Group could one more time be seen as a crucial site to understand life evolution.

From Cambrian to Silurian, isolated spicules were reported only for Pitinga Formation, Trombetas Group, Amazonas Basin (Early Silurian; Derby, 1878; Cardoso, 2005). Until 2020, the sparse and scant porifera presence were also observed on the rich Devonian Brazilian seas. Silva (1987) recovered isolated spicules in the sandstones of Uerê Formation, Solimões Basin. Based on siliceous mono-, tri- and tetraxonic spicules, he suggested the presence of shallow marine Demospongiae related to Frasnian transgression (Table 1; Figures 2A–B, 7; Supplementary Material 1). To the same unit, Lima & De Ross (2002) ratified the presence of random diactins with low fragmentation. This signature implies a weak transportation and probably a concentration formed by storm events, forming spiculites and hybrid sandstones (Figure 2A–B). The intense eodiagenesis with the replacement by chalcedony, microquartz and carbonate cement, identified by the authors, allowed them to suggest that the sponges were abundant and the main source of silica at the Late Devonian Solimões units.

Mouro et al. (2018) reported the occurrence of 3-D siliceous oxeas and hexactins associated to the Hexactinellida class, in sandstones from the Ponta Grossa Formation in Mato Grosso do Sul (Figure 2C–D). Recently, Chahud & Farchild (2020) described a possible sponge body to the Lower Devonian of Paraná Basin. Along with the rich Malvinocafric fauna, three compressed conical shaped specimens were recovered from the siltstones of the Jaguariaíva Member, Ponta Grossa Formation (Emsian; Table 1; Figures 2E–F, 7; Supplementary Material 1). Specimens, from rounded base to

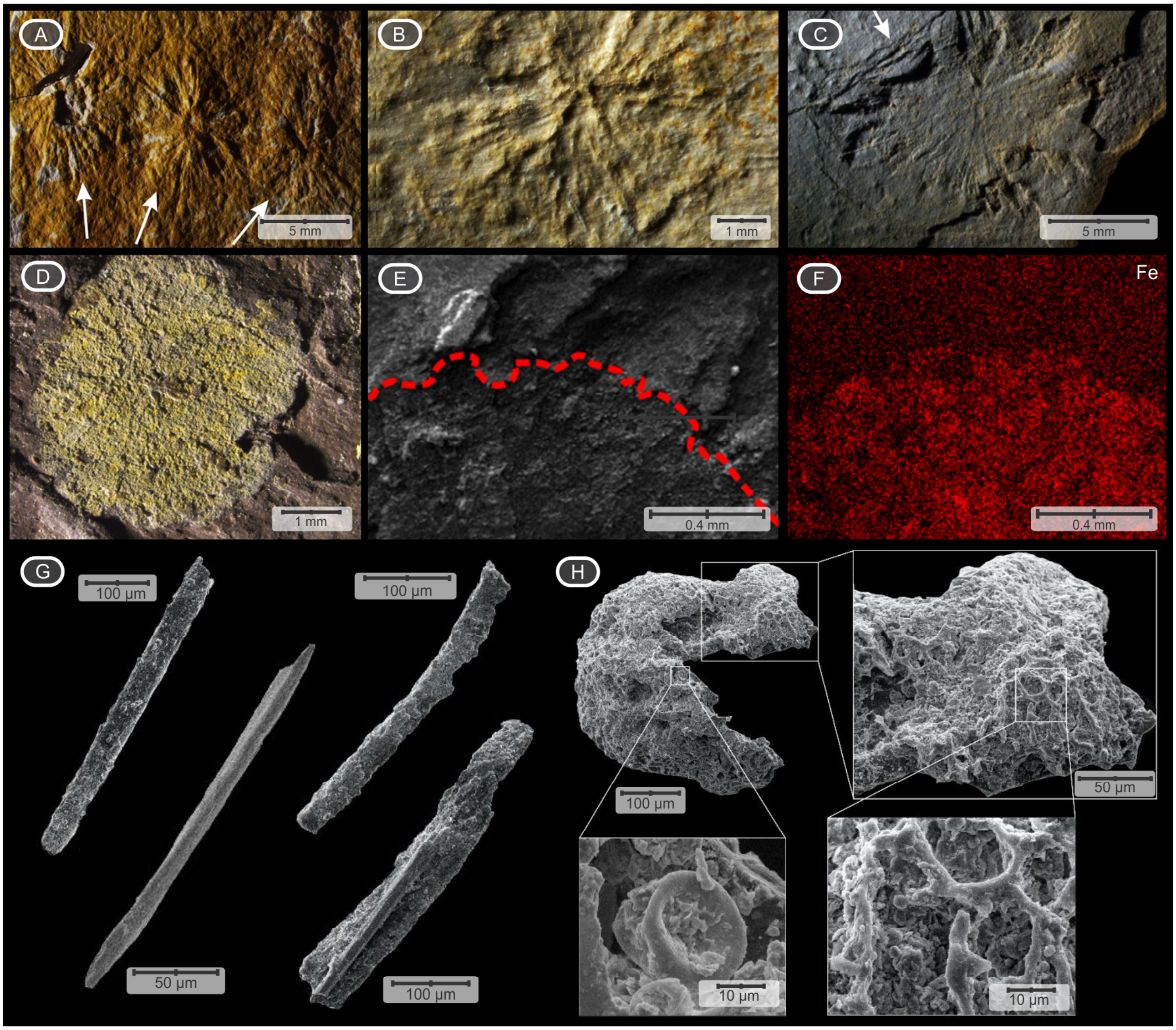

Figure 1. Questionable Precambrian Brazilian sponges. **A–F**) Itajaí Basin dubiofossils: **A–C**) 3-D discs of putative choiidae; **D–F**) flat yellow discs possible pyrite/marcasite; **E**) Dubiofossil marking; **F**) EDS analysis of Fe composition in yellow disc (Becker-Kreber et al., 2020); **G–H**) Tamengo Formation sponges: **G**) isolate spicules; **H**) possible sponge wall fragment with detailed reticulated structures, chambers and spicular arrangement (Adôrno, 2019).

Figura 1. Possíveis poríferos do Pré-Cambriano brasileiro. **A–F**) dubiofosséis da Bacia do Itajaí: **A–C**) discos 3-D associados a Choiidae; **D–F**) forma discoide achatada possivelmente construções de pirita/marcasita; **E**) Dubiofossil assinalado; **F**) análise composicional EDS, assinalando a presença de Fe na morfologia discoide amarelada (Becker-Kerber et al., 2020); **G–H**) esponjas da Formação Tamengo: **G**) espículas isoladas; **H**) fragmento corpóreo com estruturas reticulares, câmaras e arranjos espiculares associados a poríferos (Adôrno, 2019).

upper edge, were about 1 cm of height, and internally dubios quadrules grooves with 1 mm are observed (Figure 2 F; Chahud & Farchild, 2020). Despite no spicules have been identified, the overall morphology associated with specimens texture, which is similar to other Devonian sponges, suggested the affinity to the phylum.

Upper Paleozoic

Until now, the most well-preserved and abundant sponge specimens have been observed in the latest Carboniferous Lontras Shale Macrofossiliferous Interval (LSMI), Campo Mourão Formation, Itararé Group, Paraná Basin, South of Brazil (Table 1; Supplementary Material 1). After the Late Paleozoic Ice Age, the Lontras paleo-fjord bay was a nursery place to sponge flourishment as well as a high-efficient setting to preservation (Mouro *et al.*, 2017). Ruedemann (1929)

Table 1. Summary of Brazilian fossil sponges occurrence, based on: composition, sedimentary matrix, paleoenvironment, geological unit, age, and regional location.
Tabela 1. Distribuição dos poríferos no registro fossilífero brasileiro, em relação a sua composição, matriz sedimentar, paleoambiente, unidade geológica, idade e localização regional.

Class	Occurrence Body/spicule	Composition	Sedimentary matrix	Paleoenvironment	Stratigraphic unit	Age	Brazilian State	Reference
Demospongiae	Megascleres, microscleres, gemmulescleres and body parts	silica	mud to sand deposits	Lacustrine, fluvial and lagoonal	Pleisto-Holocene Sedimentary deposits	Pleistocene-Holocene	Goiás, Rio Grande do Norte, Mato Grosso do Sul and São Paulo	Parolin *et al.* (2007); (2008); Kuerten *et al.* (2011); Santos, 2011; Machado, (2014); Docio, (2020); Docio *et al.* (2021)
Demospongiae	Monaxonic spicules	silica	siltstones	Fluvial	Boa Vista Formation, Tacutu Basin	Neogene	Roraima	Cruz *et al.* (2017)
Demospongiae	Monaxonic spicules	silica	siltstones	Fluvial	Itaquaquecetuba and São Paulo Formations, São Paulo Basin	Oligocene-Miocene	São Paulo	Jacinto and Campanha (1989); Fittipaldi and Simões (1989)
Demospongiae	Monaxonic spicules	silica	shale	Lacustrine	Tremembé Formation – Taubaté Basin, São Paulo	Oligocene	São Paulo	Wickert (1947)
?	Monaxonic spicules	silica?	carbonate	Marine – reef	Cotinguiba Formation, Sergipe-Alagoas Basin	Upper Cretaceous	Sergipe	Silva *et al.* (2019)
Demospongiae	Oxeas Solid skeleton	silica?	sandstones and siltstones	Marine to continental	Guatá and Passa Dois groups, Paraná Basin	Permian	Goiás, Mato Grosso, Paraná, São Paulo and Rio Grande do Sul	Washburn, (1930); Almeida and Barbosa, (1953); Fulfaro, (1967); Amaral, (1971); Maranhão and Petri, (1996); Ng *et al.*, (2019)
Demospongiae	oxeas	?	calcarenite	Marine	Aracaré Formation, Sergipe-Alagoas Basin	Lower Permian	Sergipe	Silva *et al.* (2020)
Demospongiae	Ichnofossil *Entobia* isp. and *Clionolithes* isp.		shell molds heterolites	Marine	Rio Bonito Formation, Guatá Group, Paraná Basin	Lower Permian	Santa Catarina and Rio Grande do Sul	Schmidt-Neto *et al.* (2018)
Heteractinida or Calcarea?	oxeas, triactins, tuning-fork, tetractins, triaene, pentactins and polyactins	carbonate	siltstone	Marine?	Rio do Sul Member, Taciba Formation, Paraná Basin	Upper Carboniferous	Santa Catarina	Mouro *et al.* (2011); Saldanha & Mouro (2018)
Demospongiae Hexactinellida	Diactins and stauractins Pentactins and hexactins	silica	shale	Marine	Budó facies, Upper Itararé Group, Paraná Basin	Upper Carboniferous	Rio Grande do Sul	Pinto (1947) Mouro *et al.* (2012)
Demospongiae non-lithistid	Body sponge?	silica	shale	Marine – fjordbay	Lontras Shale, Campo Mourão Formation, Paraná Basin	Upper Carboniferous	Santa Catarina	Mouro & Fernandes (2012); Mouro (2017)
Hexactinellida	Body sponge Unnamed sponge	silica	shale	Marine – fjordbay	Lontras Shale, Campo Mourão Formation, Paraná Basin	Upper Carboniferous	Santa Catarina	Saldanha *et al.* (2018)
Hexactinellida	Body sponge *Microhemidiscia greineti*	silica	shale	Marine – fjordbay	Lontras Shale, Campo Mourão Formation, Paraná Basin	Upper Carboniferous	Santa Catarina	Ruedemann (1929); Mouro *et al.* (2014); Mouro *et al.* (2020)
Demospongiae	Mono-, tri- and tetraxonic spicules	silica	sandstones	Marine	Uerê Formation, Solimões Basin	Middle Devonian	Amazonas	Silva (1987); Lima and De Ross (2002)
Hexactinellida	Oxea, hexactins, possible dermal layer	silica	sandstones	Marine - deltaic	Ponta Grossa Formation, Paraná Basin	Lower Devonian	Mato Grosso do Sul	Mouro *et al.* (2018)
?	Body sponge *Pontagrossia reticulata*		shales	Marine	Jaguariaíva mb., Ponta Grossa Formation, Paraná Basin	Lower Devonian	Paraná	Chahud and Farchild (2020)
?	Spicules	silica	shales and diamictites	Marine	Pitinga Formation, Trombetas Group, Amazonas Basin	Lower Silurian	Pará	Breitback (1957)
?	Monaxonic spicules Sponge wall Gemmule?	carbonate	siltstone, calcarenite, carbonate	Shoreface offshore	Tamengo Formation – Corumbá Group	Late Ediacaran	Mato Grosso do Sul	Adôrno (2019)

was the first to report the presence of several isolated hexactins, "hairlike sponges spicules" (Figure 3C), which in 2014 were identified as new species within the Order Hemidiscosa, Hexactinellida class, Microhemidiscia greinerti (Mouro *et al.*, 2014; Figure 3A–E). These sponges have conical-cylindrical shape with skeletal-net composed of hexactins of ranked sizes with sub-parallel rays of each rank and well-delimited hemidiscs, pentactins and root tufts (Figure 3A–E).

Still in LSMI, Mouro & Fernandes (2012) identified a small basal portion of a conical shape sponge, formed by monaxonic siliceous spicules associated with few isolated tetraxonic. The authors assigned it as a non-lithistid Demospongiae (Figure 3 H). Saldanha *et al.* (2018, 2019) recovered some intriguing sponge morphotypes erroneously assigned as protomonaxonids (Figure 3F–G). Reviewing these specimens and considering divergent splays of highly elongate monaxonic spicules and few small stauractins and monactins, the morphotypes may be related to an Hexactinellid genus associated with the Pyritonemidae family (the material is understudy; Figure 3F–G). The co-existence of hexactinellid species suggests the presence of two epibentonic tiers, one with the abundant M. greinerti (heights between 40–151 mm) inhabiting the lowest level, up to 10 cm; and the second with the unnamed sponge (more than 130 mm high) above 10 cm.

Furthermore, using micro-CT we have observed that both delimited bodies and sponge spicules (isolated hexactins, monactins and stauractins) comprise most of the matrix on LSMI, suggesting that sponge association may flourish over skeletal architecture of dead poriferans, as seen on recent sponge gardens (fjords of southern British Columbia, Canada; Marliave *et al.*, 2009). Ongoing research is recovering possible silica nodules which may suggest horizon of silica chert into LSMI levels.

Above the Carboniferous Campo Mourão Formation lies the Taciba Formation (Lower Permian), a transitional paleodepositional setting which is under a paleoclimatic amelioration and comprises isolated spicules along its intervals (Table 1; Supplementary Material 1). Pinto (1947) recovered a bulk of isolated monoaxon and hexactin from several outcrops related to the Budó facies, a shallow marine setting (Muratori & Lopes, 1963; Barcellos, 1973; Pinto & Pupper, 1974; Cazzulo-Klepgzig *et al.*, 1980).

Decades later, Mouro *et al.* (2012b) revised few samples from Budó facies (Figure 4A), which were stored at National Museum, and recognized two set of spicules: one formed by smaller diactins associated with smaller stauractins related to Demospongiae; and other comprising pentactins and dubious hexactins associated with Hexactinellida.

On the north section of the Taciba Formation, close to the Santa Catarina and Paraná state border, Mouro *et al.* (2012a) recovered a large number of monaxons and a possible sponge-body without spicule articulations (Figures 4B–H, 7; Supplementary Material 1). These specimens were associated with non-Lithistid Demospongiae. Saldanha & Mouro (2018), studying new samples for the same outcrops, observed a package of confusing delimited sponges formed by calcarean spicules. At first, they suggested the presence of oxeas, triactins, tuning-forks, tetractins, triaens, pentactins and polyactins (Figure 4C–H), which could be related to Heteractinida or Calcarea. These samples are under investigation and already establish the calcium composition as a secondary process.

When we draw attention to later Permian groups and formations from interior basins of Brazil (Table 1; Supplementary Material 1, 2), such as the Paraná Basin (Guatá Group: Rio Bonito and Palermo formations; Passa Dois Group: Irati, Serra Alta, Teresina, Rio do Rasto formations) and Sergipe-Alagoas Basin (Aracaré Formation), almost all the formations have isolated oxeas associated to the Class Demospongiae (Washburn, 1930; Almeida & Barbosa, 1953; Fulfaro, 1967; Amaral, 1971; Maranhão & Petri, 1996; Silva *et al.*, 2018; Ng *et al.*, 2019; Figure 5 G–H).

Although no spicules were found at the Rio Bonito Formation, Guatá Group in the Paraná Basin, Schmidt-Neto *et al.* (2018) described sponge borings (Entobia isp.) of several Clionid ontogenetic stages (Figures 5A–D, 7). These fossils suggested a wave-agitated setting and ratified the paleoclimatic change after the Late Paleozoic Ice Age (observed in the Itararé Group).

In the Passa Dois Group, since the early 20th Century, abundant monaxons were recovered and reinforce the hypothesis of a large eperic sea during the Artinskian-Capitanian times. Ng *et al.* (2019) established 13 microfacies to the Passa Dois Group (mainly in the Central Domain) and among them they recognized isolated monoaxonic spicules with preserved axial canal and possible soft filament (Figures 5E–F, 7). The Central Domain comprises a set of mixed carbonate-siliciclastics lithofacies associated with the Irati and Teresina formations. Moreover, the authors recovered a solid skeleton of sponge in the chert layers. These samples are under-study and may have soft tissues preserved.

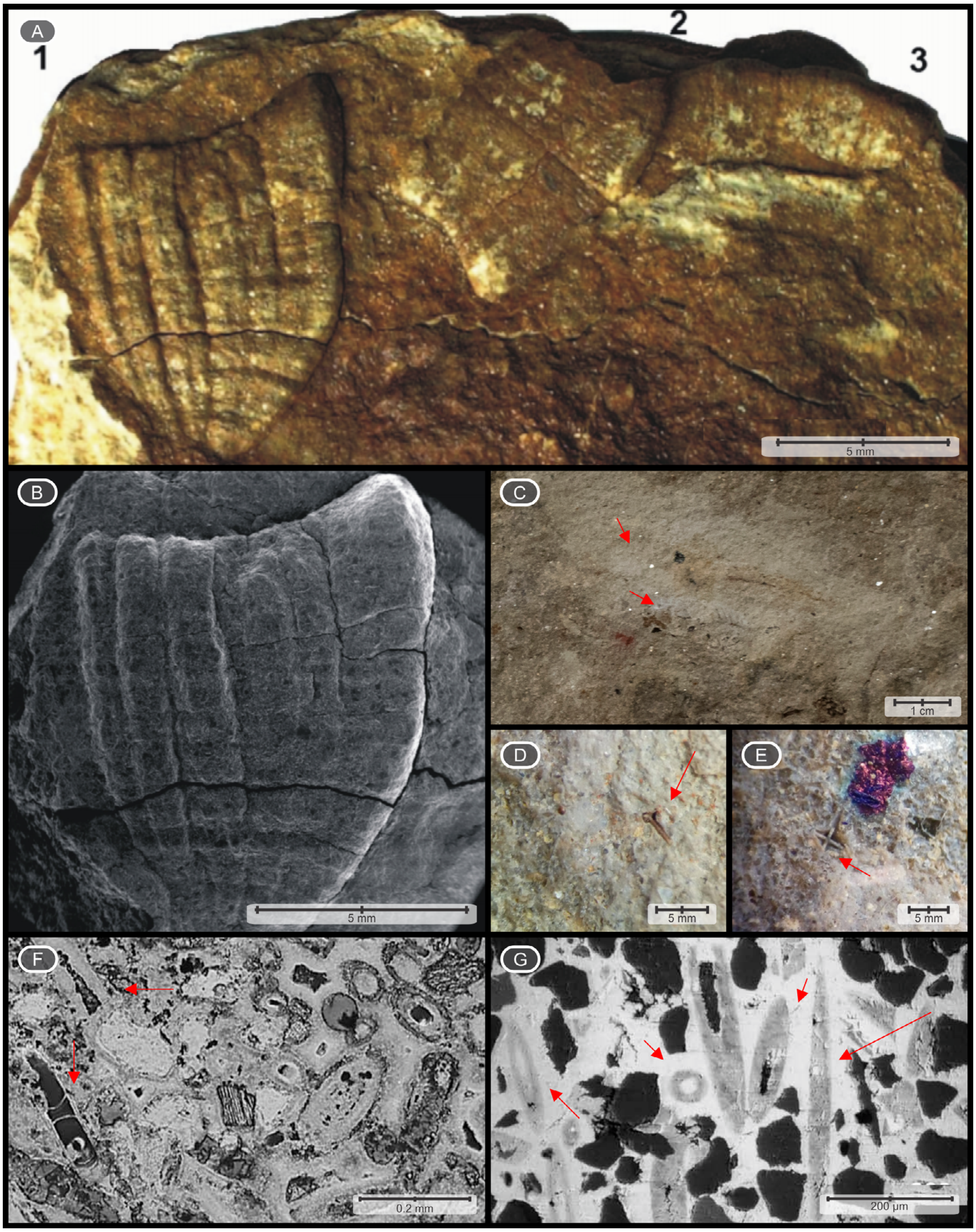

Figure 2. Figure 2. Devonian Brazilian sponges. **A–B**) Chalice-like reticulate fossil of Ponta Grossa Formation, *Pontagrossia reticulata*: **A**) lateral occurence of three fossils; **B**) SEM analysis of sample number 1 (Chahud & Farchild, 2020); **C–E**) Ponta Grossa Formation spicules and possible dermal layer: **C**) whitish material possible sponge dermal layer that embedded spicules; **D–E**) 3-D hexactins (Mouro *et al.*, 2018); **F–G**) Uerê Formation spicules in sandstones: **F**) phomicrograph of spiculite with chalcedony; **G**) BSE image of "ghost" spicules replaced by dolomite (Lima & De Ross, 2002).

Figura 2. Poríferos devonianos brasileiros. **A–B**) *Pontagrossia reticulata*, espécime associado ao Filo Porifera devido ao formato de cálice-reticulado: **A**) visão lateral dos três espécimes; **B**) análise de MEV-EDS do exemplar 1 (Chahud & Farchild, 2020); **C–E**) espículas e fragmento da pinacoderme encontrados na Formação Ponta Grossa: **C**) material esbranquiçado, possivelmente resquício da camada dermal da esponja, com espículas embebidas (assinaladas pelas setas vermelhas); **D–E**) hexactinas 3-D (Mouro *et al.*, 2018); **F–G**) Uerê Formation spicules in sandstones: **F**) espículas dos arenitos da Formação Uerê; **G**) imagem de elétrons retrodispersos (BSE) do resquício espicular substituído por dolomita (Lima & De Ross, 2002).

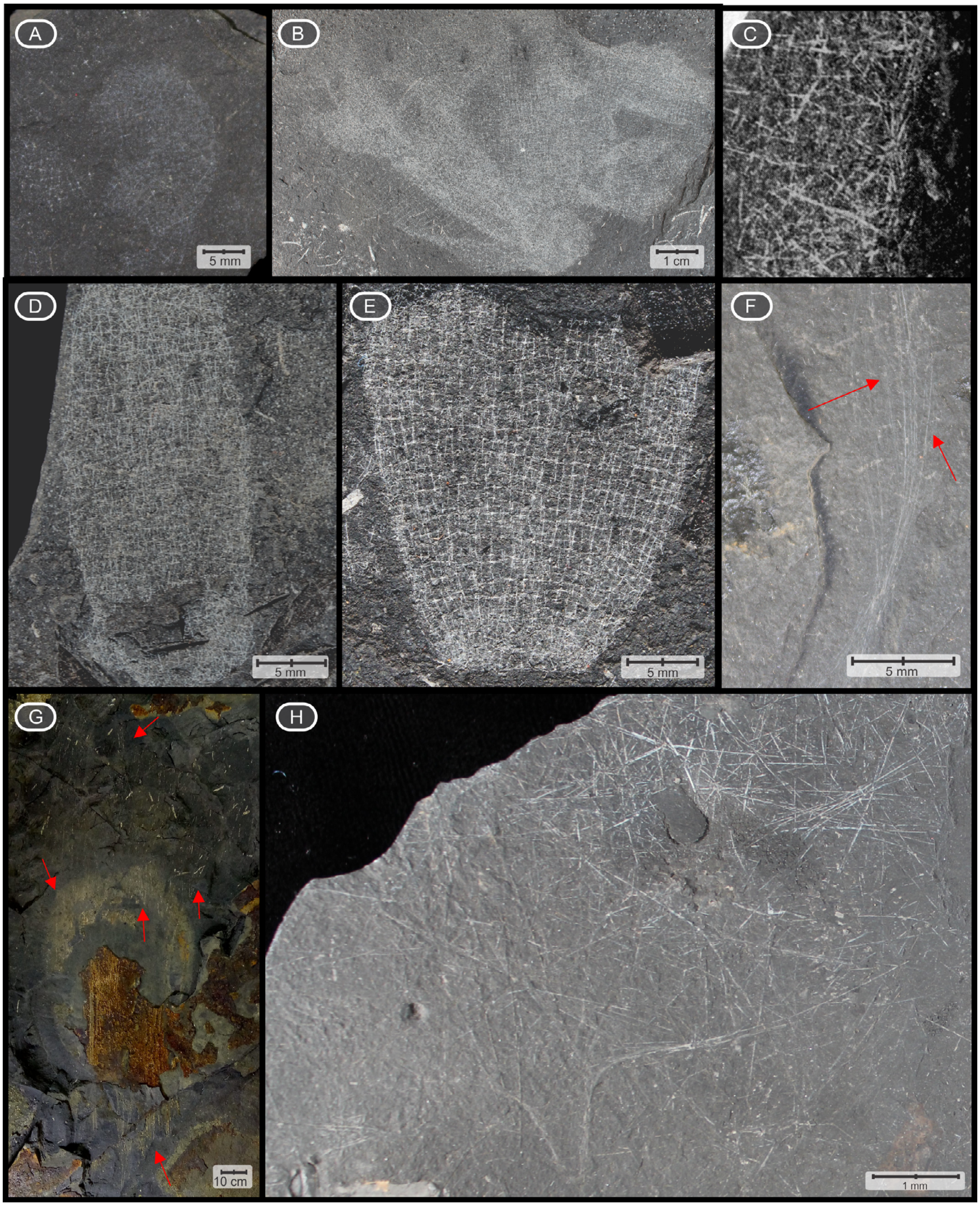

Figure 3. LSMI sponges. **A–E**) *Microhemidiscia greinerti*: **A**) well-delimited upper portion; **B**) sample denoting possible gregarious habit; **C**) "hairlike sponge spicules", the first image of a Brazilian fossil sponge made by Ruedemann 1929; **D–E**) well-arranged Hexactinellida specimens (Mouro *et al*., 2014): **D**) completed specimen of *Microhemidiscia greinerti*; **E**) well-delimited lower portion with root tufts; **F–G**) possible Pyritonemidae sponge body: **F**) long monaxons shaping the sponge elongate oval body, spicules marked with red arrows; **G**) divergent splay of highly elongate monaxonic spicules, marked with red arrows (Saldanha *et al*. 2018); **H**) well-delimited lower portion of a probable Demospongiae non-lithisthid, full of monaxonic siliceous spicules (Mouro, 2017).

Figura 3. Esponjas do Intervalo fossilífero do Folhelho Lontras (IFSL). **A–E**) *Microhemidiscia greinerti*: **A**) morfologia ovalada com delimitação da porção superior; **B**) amostra denotando possível hábito gregário; **C**) primeira imagem de espículas de espongiários do IFSL (Ruedemann, 1929); **D–E**) exemplares corpóreos bem delimitados de Hexactinellida (Mouro *et al*., 2014): **D**) espécime completo de *Microhemidiscia greinerti*; **E**) porção inferior de Hexactinellida bem delimitada com tufo de fixação; **F–G**) possível espécime de Pyritonemidae: **F**) longas espículas monoaxônicas que cruzam toda extensão do espécime (espículas assinaladas pelas setas em vermelho) (Saldanha *et al*., 2018); **H**) porção inferior formada por espículas silicosas monoaxônicas, espécime possivelmente associado ao grupo de esponjas Não-Litistida da Classe Demospongiae.

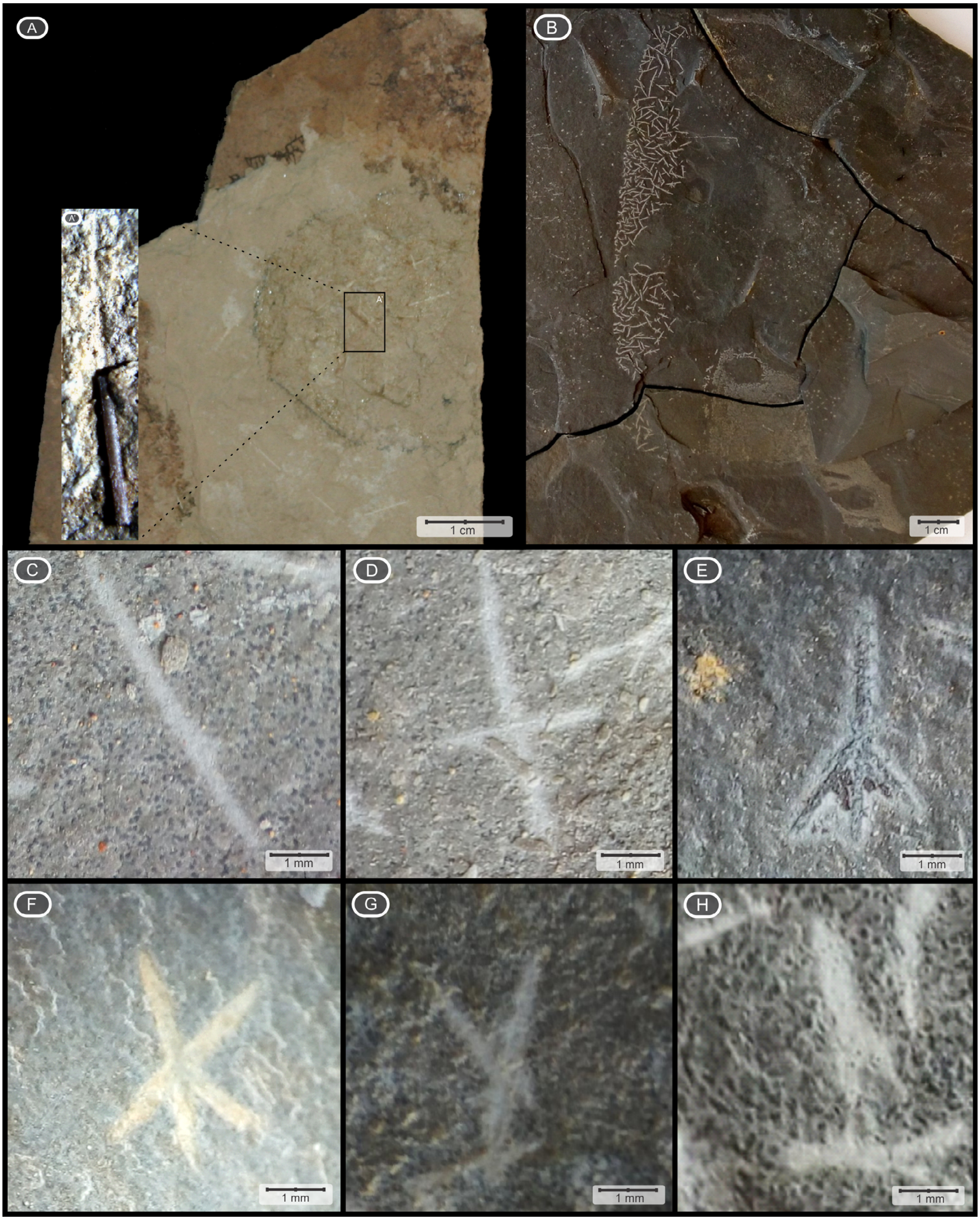

Figure 4. Taciba Formation sponges. **A**) Budó facies spicules, detailed 3-D monaxon (Mouro *et al.* 2012b); **B–H**) Upper Taciba spicules: **B**) elongate and oval organization of loosely packed spicules regarding two sponge bodies, center and lower agglomerates; **C–H**) possible spicules: **C**) oxea; **D**) stauractin; **E**) triaene; **F**) pentactin; **G**) triactin; **H**) tuning-fork (Saldanha & Mouro, 2018).

Figura 4. Esponjas da Formação Taciba. **A**) espículas monoaxônicas tridimensionais encontradas na fácies Budó (Mouro *et al.*, 2012); **B-H**) espículas da porção superior da Formação Taciba. B, dois corpos de poríferos bem delimitados em formato alongado e oval, preenchido com espículas soltas. **C-H**) estruturas orgânicas possivelmente espículas: **C**) oxea; **D**) estauractina; **E**) triaena; **F**, pentactina; **G**) triactina; **H**) espícula em formato de gancho (Saldanha & Mouro, 2018).

Mesozoic to Cenozoic

It is well-known that Mesozoic sponge faunas diverge sharply from the Paleozoic sponges (see Pisera, 2006), and that crucial physic-chemical changes happened during the transition between Paleozoic to Mesozoic seas. Thereby, considering the Brazilian paleogeographic conditions during Mesozoic times, especially in Cretaceous, it was expected that sponge fauna could be well represented. However, poriferans are almost unknown, being the only register of spicules in the Cotinguiba Formation, Sergipe-Alagoas Basin (Cretaceous Table 1; Supplementary Material 2). Silva *et al.* (2019) recognized these poorly isolated monaxons in a bioclastic wackestone. Previously, Mouro & Fernandes (2011) erroneously had set two specimens from Spongiliidae and Paleospongillidae described by Ott & Volkheimer (1972) and Volkmer-Ribeiro & Reitner (1991) to Brazilian rocks. These two fossils were gemmule-bearing freshwater sponges from the Aptian of Argentina.

As seen in the Mesozoic, Brazilian sponges are also rare in the Cenozoic Era (Table 1; Supplementary Material 2). Isolated spicules of Demospongiae occur in the shales of São Paulo Basin (fluvial deposits of Itaquaquecetuba and São Paulo formations, Oligo–Miocene) and Taubaté Basin (lacustrine facies of Tremembé Formation, Oligocene) in the State of São Paulo (Wickert, 1974; Fittipaldi & Simões, 1989; Mezzalira, 2000). This last unit comprises several fossils of plants, insects, crustaceans, mollusks, fish, reptiles, amphibians, mammals in a playa-lake type lacustrine environment (Bergqvist & Almeida, 2004; Melo, 2007; De Oliveira & Romano, 2007; Ribeiro, 2010). Although the occurrence of spicules can provide more information about the benthic fauna related to the lake, there is no new data from the group besides the cores described by Wickert (1974). Since both basins have similar tectonic origin and evolution, it is plausible to assume that spicules can be found in the lacustrine and fluvial facies, at São Paulo and Taubaté basins.

Furthermore, Ferreira & Fernandes (1997) reported three species of complete sponges for the Pirabas Formation (Oligocene–Miocene Northern Brazil). The specimens assigned as Aphrocallistes lobata Pomel, 1872, Aphrocallistes estevoui Termier & Termier, 1981 and Manzonia aprudina Giattini, 1909, were described as globular organisms, colonial forms with several honeycomb-like holes, without spicules and with carbonate composition. By comparison with fossil species from Spain, these samples were assigned to hexactinellids, replaced by carbonate in diagenesis (Ferreira & Fernandes, 1997).

Muricy *et al.* (2016) using SEM, stereomicroscope and light microscopy of transverse sections, restudied the three species and, considering the lack of spicules, morphological structures and the ecological incongruity, refuted the possibility of sponges (Figures 6A–C, 7). The paleometry analysis allowed the authors to set the specimens as a Celleporaria bryozoan based on zooecia, avicularia and ooecia features. Thereby, the three corporeal fossils of the Oligocene–Miocene are not sponges.

Cruz *et al.* (2017) identified isolated sponges in Boa Vista Formation, Tacutu Basin, Roraima (Table 1; Supplementary Material 2). They applied petrography and SEM-EDS and recognized siliceous spicules and a dubious encrusting body with pores associated with siltstones. The analyzed material was related to freshwater sclerosponges deposited in fluvial-alluvial facies related to hemi graben installation and accommodation (Cruz *et al.*, 2017; Menezes *et al.*, 2020).

Sponges and spicules have a good applicability in paleoenvironmental reconstruction along the Quaternary. A great number of studies have been using the Brazilian sponges (freshwater and marine) to address the climate changes in the near past and ancient environments as paleorivers, paleolakes and paleolagoons (Table 1; Figures 6D–G, 7; Parolin *et al.*, 2007, 2008; Kuerten *et al.*, 2011; Santos *et al.*, 2011; Machado, 2014; Volkmer-Ribeiro & Machado, 2017; Santos, 2020; Santos *et al.*, 2021).

Furthermore, generally core samples from sandy and muddy sediments are assigned as spiculite or contain isolated spicules. These occurrences ratify the installation and evolution of water bodies recording wetter and drier periods related to the Pleistocene–Holocene glacial cycle. Nevertheless, marine spicules have little resolution and continental sponges need to be associated with other proxies to delimit paleoclimatic conditions (Santos *et al.*, 2011; Machado, 2014; Santos *et al.* 2021).

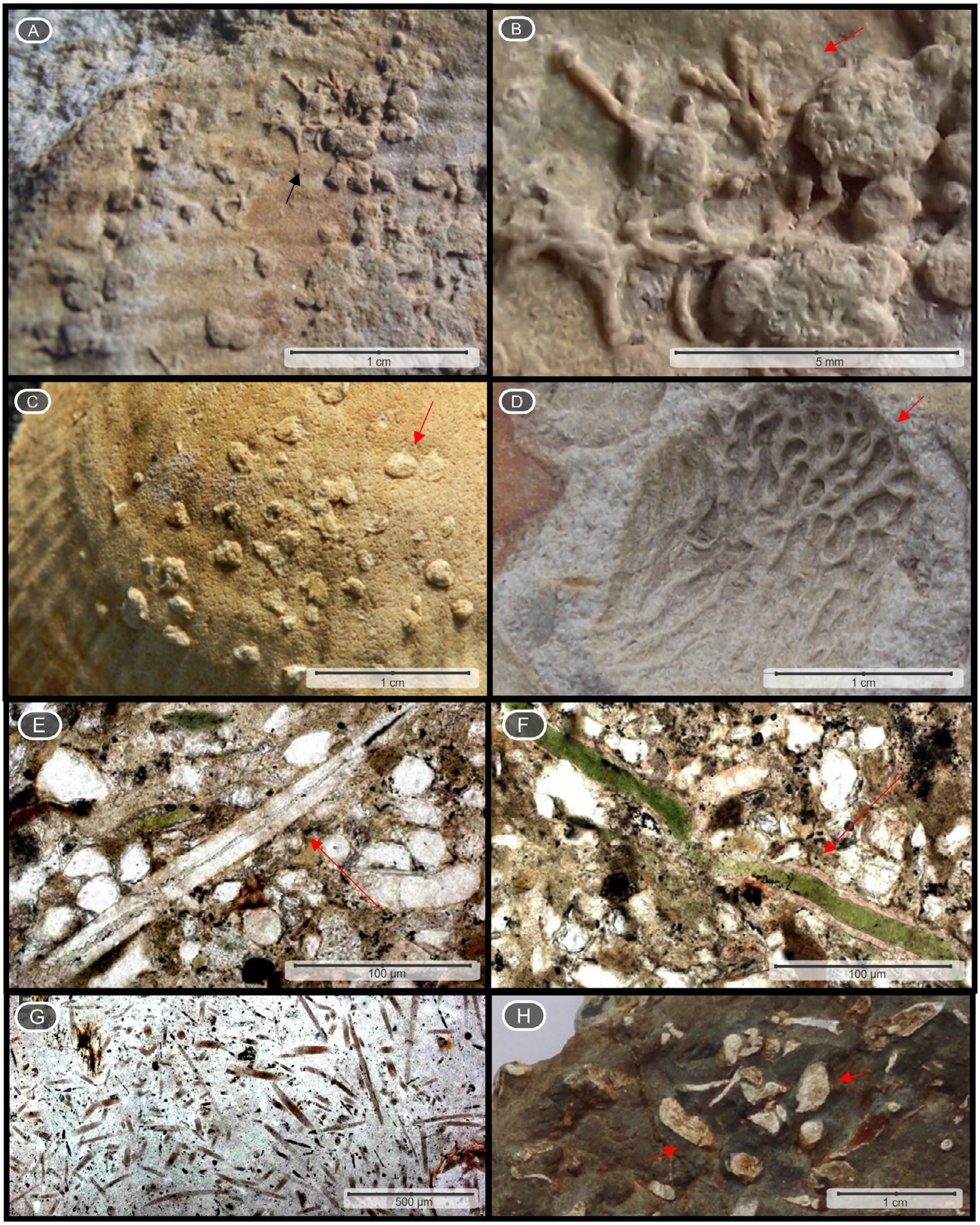

Figure 5. Permian sponges. **A–D**) *Entobia* isp., biogenic structure associated to Clionidae (pointed with red arrows) preserved in molds of *Heteropecten* shells of Rio Bonito Formation (Schmidt-Neto *et al.*, 2018); **E–H**) well-preserved sponges of Guatá and Passa Dois groups of Paraná Basin: **E–G**) photomicrographs of spicules with axial canal and possible organic filament, pointed marked with red arrows; **H**) well-preserved sponge in chert, pointed with red arrows (Ng *et al.*, 2019).

Figura 5. Poríferos do Permiano. **A–D**) Traços do tipo *Entobia* isp. (assinalados em vermelho) associados a esponjas Clionidae, em moldes de conchas de bivalves *Heteropecten* da Formação Rio Bonito (Schmidt-neto *et al.*, 2018); **E–H**) esponjas bem preservadas recuperadas de rochas dos grupos Guatá e Passa Dois, Bacia do Paraná: **E–G**) fotomicrografia das espículas, assinalando o canal axial e um possível resíduo orgânico (marcado pelas setas em vermelho); **H**) registro corpóreo bem preservado de poríferos em chert (Ng *et al.*, 2019).

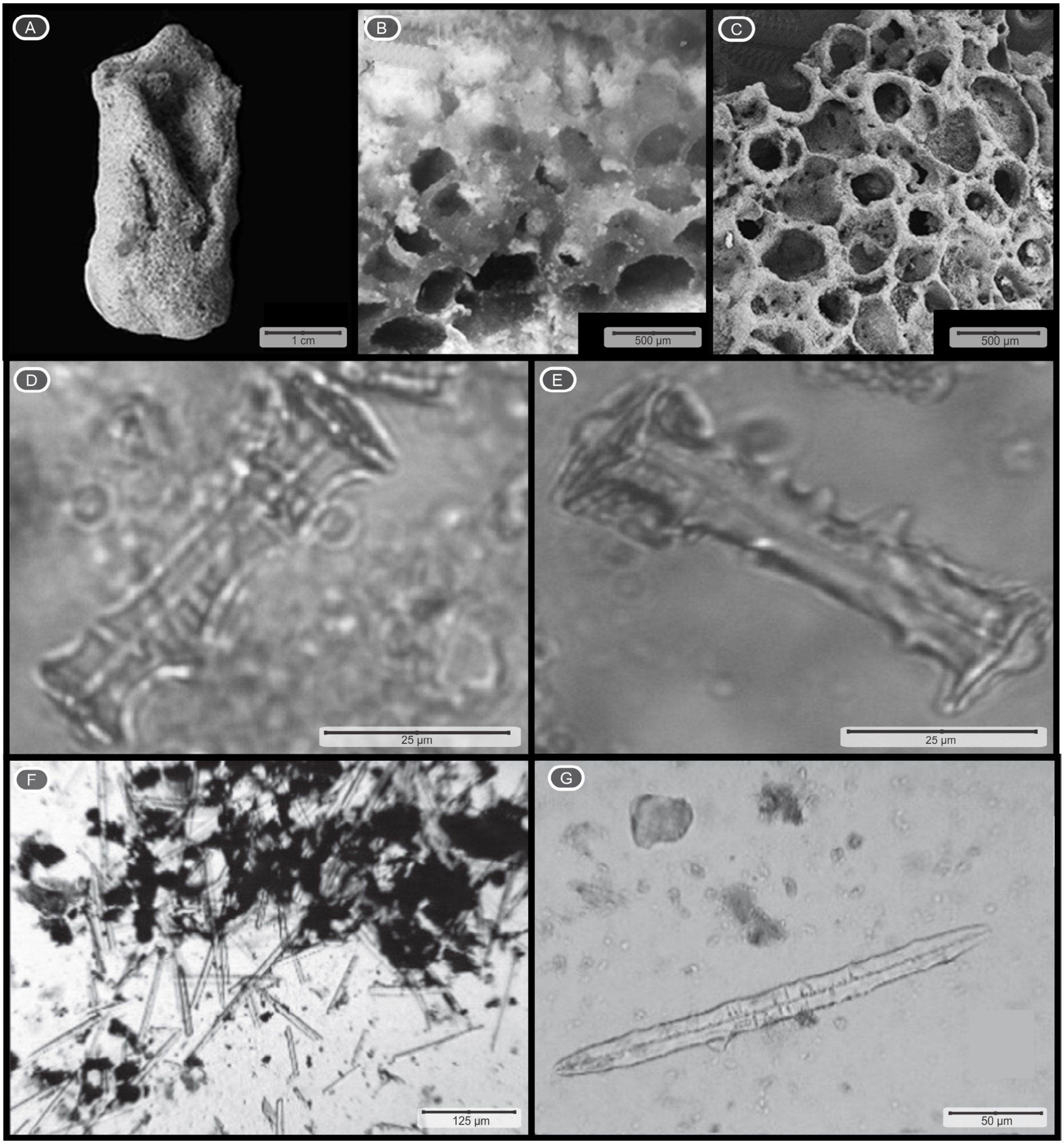

Figure 6. Cenozoic sponges. **A–C**) Bryozoa *Celleporaria pirabasensis* erroneous associate to hexactinellid sponges from Pirabas Formation: **A**) Bryozoa colony; **B–C**) detailed zooecia, orifices and pores (Muricy *et al.*, 2016); **D–G**) micrographs of demospongian freshwater spicules: **D**) *Heterorotula fistula*; **E**) *Ephydatia* sp. (Santos *et al.*, 2021); **F**) isolated spicules; **G**) *Metania spinata* (Parolin *et al.*, 2008).

Figura 6. Esponjas cenozoicas. **A–C**) espécime de Bryozoa, *Celleporaria pirabasensis*, erroneamente identificado como hexactinélideos da Formação Pirabas: **A**) colônia de briozoário; **B–C**) detalhe do zooécio, orifícios e poros (Muricy *et al.*, 2016); **D–G**) microfotografias de espículas de espongiários dulcícolas da classe Demospongiae: **D**) *Heterorotula fistula*; **E**) *Ephydatia* sp. (Santos *et al.*, 2021); **F**) espículas isoladas; **G**) *Metania spinata* (Parolin *et al.*, 2008).

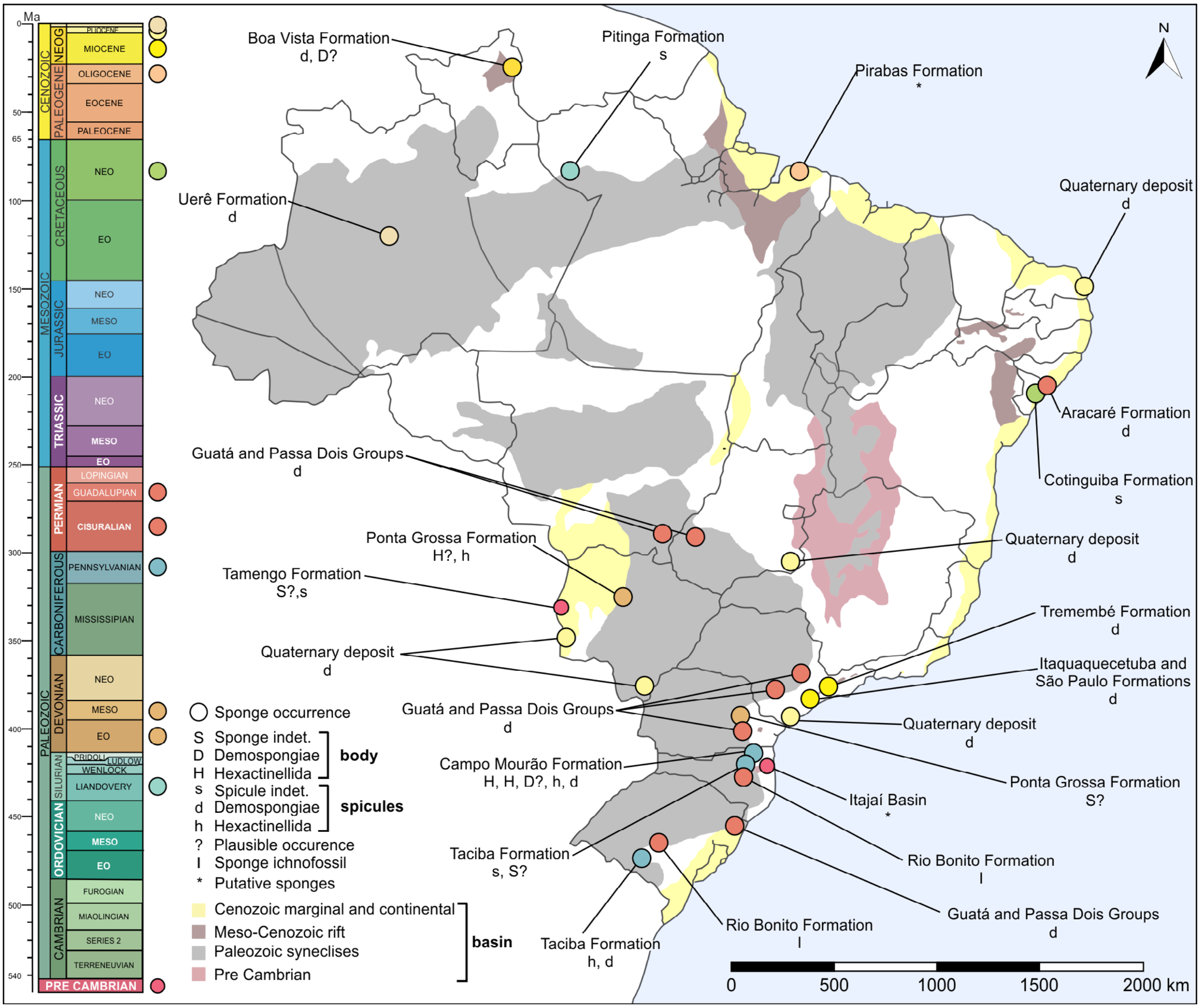

Figure 7. Geographic and stratigraphic distribution of sponge fossils of Brazil. Based on Milani *et al.* (2007).

Figura 7. Distribuição geográfica e estratigráfica dos fósseis de poríferos do Brasil. Baseado em Milani *et al.* (2007).

REMARKS AND FUTURE PERSPECTIVES

As seen above, the record of fossil sponges in Brazil is still rare and poorly studied. This scarcity seems incongruous given the great diversity of paleoenvironments, temporally extensive basins and multiple preservation conditions found in the country. One of the causes of this deficiency may be associated with diagenetic conditions as pointed out by Lima & De Ross (2002) and the difficulty of paleontologists in diagnosing sponges and spicules in the field. After the first reports of fossil spicules by Derby, in 1878, and almost a century, since Ruedemann's pioneer work in 1929, few occurrences have been recorded. The last century was marked by isolated spicules reports and rare determination of sponge-bodies that later turned out to be pseudofossils or other organisms (Netto & Da Rosa, 1997; Ferreira & Fernandes, 1997). On the other hand, in recent decades, there has been a relative advance, probably linked not only to the growth of science in the country, but also to the intensification of the use of high-resolution techniques in paleontology.

This multiproxy approach known as paleometry, (Riquelme *et al.*, 2009; Delgado *et al.*, 2014; Gomes *et al.*, 2019) has helped to detail sponge bodies, as well as to unravel taphonomy and diagenetic processes (Lima & de Ross, 2002;

Cruz *et al.* 2017; Ng *et al.*, 2019; Mouro *et al.*, 2018, 2020; Adôrno, 2019). Additionally, paleometry is helping to identify dubiofossils (Muricy *et al.*, 2016; Becker-Kerber *et al.*, 2020).

This national panorama can be related to the debate that has been focused for two decades in global paleospongiology. The high-resolutions techniques have raised problems in conventional systematics and in the phylogenetic characteristics applied to the phylum, such as the existence of bimineral spicules and Paleozoic Stem Groups (Botting & Butterfield, 2005; Botting *et al.*, 2012; Botting & Muir, 2018; Nadhira *et al.*, 2019). In this sense, fossil sponges of Brazil have the potential to bring new information regarding the fossildiagenesis (Lima & De Ross, 2002; Mouro *et al.*, 2020), as well as the origin and evolution of sponges (which still under extensive debate; see Sperling *et al.*, 2010; Antcliffe *et al.* 2014; Botting & Muir, 2018; Turner, 2021), especially if the spicule-like fossils from Precambrian were ratified (Adôrno, 2019; Becker-Kerber *et al.*, 2020).

Therefore, the need to foster new research and review fossil sponges in Brazil become clear once there is potential to recover sponges and spicules in all Brazilian basins. Thus, combining the current analytical technologies with the fossil potential, Brazilian sponges could help improve the phylum knowledge.

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