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Taxonomic revision of Ediacaran tubular fossils: *Cloudina*, *Sinotubulites* and *Conotubus*

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Abstract.—The Ediacaran tubular fossils *Cloudina*, *Sinotubulites*, and *Conotubus* are taxonomically revised with type materials. It is proposed that *Aulophycus lucianoi* Beurlen and Sommer, 1957, is not a senior synonym of *Cloudina hartmannae* Germs, 1972. Instead, most of its syntypes may be assigned to *Sinotubulites* or other taxa. Lectotypes of *Sinotubulites baimatuoensis* Chen et al., 1981, and *Conotubus hemiannulatus* Zhang and Lin in Lin et al., 1986, are designated from rediscovered syntypes. *Sinotubulites baimatuoensis* Chen et al., 1981, is reported from the Mooifontein Member of Nama Group at Aar Farm, Namibia. *Cloudina waldei* Hahn and Pflug, 1985, is assigned to *Sinotubulites baimatuoensis*, and thus its occurrence range is extended to Brazil. The lectotype of *Conotubus hemiannulatus* shows corrugations and annulations on the surface distinguishing it from *Cloudina* and other collared Ediacaran tubular fossils. Based on the taxonomic revision, we propose a *Cloudina hartmannae* Interval Zone for the terminal Ediacaran with the upper boundary defined by the first appearance datum of *Protohertzina anabarica* (i.e., the index fossil of the early Cambrian *Anabarites trisulcatus*-*Protohertzina anabarica* Assemblage Zone).

Introduction

Ediacaran tubular fossils are the earliest skeletal metazoans, thus being important for understanding early metazoan evolution. Studies in the last few decades have made significant progresses in their phylogenetic affinity (Grant, 1990; Hua et al., 2005; Vinn and Zatoń, 2012; Schiffbauer et al., 2020; Selly et al., 2020; Yang et al., 2020b), paleoecology (Bengtson and Yue, 1992; Cai et al., 2013; Penny et al., 2014; Cortijo et al., 2015a; Becker-Kerber et al., 2017; Wood et al., 2017a; Mehra and Maloof, 2018; Shore and Wood, 2021), biomineralization (Grant, 1990; Chen et al., 2008; Wood et al., 2017c; Pruss et al., 2018; Wood, 2018; Yang et al., 2020b), taphonomy (Grant, 1990; Cai et al., 2010; Pacheco et al., 2011; Becker-Kerber et al., 2019; Walde et al., 2019; Yang et al., 2020b), paleobiogeography (Warren et al., 2014, 2017), and biostratigraphy (Gaucher and Germs, 2009; Yang et al., 2016; Zhu et al., 2017; Cai et al., 2019).

Although these organisms are considered useful markers for identifying the latest Ediacaran (Xiao et al., 2016) with proposed biozonations (Gaucher and Germs, 2009; Adorno et al., 2017; Zhu et al., 2017), there is no consensus on their utility for global correlation. One of the main obstacles is their taxonomic confusion. Thus, the goal of this study is to provide a systematic revision of key Ediacaran tubular taxa, as well as a comprehensive review. To do this, we return to the type materials for the Ediacaran tubular taxa, *Cloudina*, *Sinotubulites*, and *Conotubus*, discussing their systematic treatments following the regulation of International Code of Zoological Nomenclature (ICZN, 1999).

Materials and methods

More than 200 tubular specimens of *Cloudina* and *Sinotubulites* from Namibia, US, and Paraguay were ground and polished to produce uncovered thin-sections. Both longitudinal and transversal sections were obtained, observed with binocular microscopes, and documented with digital cameras. Published and collected specimens of *Cloudina* were measured with the software of ImageJ 1.48V. Statistical data were subsequently obtained with Origin Pro. 8.6.

Repositories and institutional abbreviations.—Types, figures, and other specimens examined in this study are deposited in the following institutions: Institute of Geology, Chinese Academy of Geological Sciences (IGCAGS), Beijing, China; Geological Museum of China (GMC), Beijing, China; Iziko South African Museum (IZIKO), Cape Town, South Africa; Earth Sciences Museum—Brazilian Geological Survey, Rio de Janeiro, Brazil; Northwest University (NU), Xi'an, China.

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Systematic paleontology

Family Cloudinidae Hahn and Pflug, 1985
Genus *Cloudina* Germs, 1972

Type species.—Cloudina hartmannae Germs, 1972, from the Schwarzkalk Limestone Member of Kuibis Formation (=Omkyk Member of the Zaris Formation, Kuibis Subgroup), Driedoornvlakte Farm near Schlip, Namibia, by original designation.

Other species.—Cloudina carinata Cortijo et al., 2010, and *Cloudina xuanjiangpingensis* Cai et al., 2017.

Original diagnosis (Germs, 1972).—The calcareous tubes are sinuous, composed of stacked cones so arranged as usually to give the appearance to the composite structure of having two walls. The outer wall bears annular ridges and depressions. The inner wall is smoother and in some specimens shows very fine annular ridges. The inner tubes are ordinarily not centrally located in transverse section. The apex has nearly always been found open, while the distal end has always been found open. Two species are recognized, *C. hartmannae* and *C. riemkeae*, as described below.

Emended diagnosis.—Sinuous or straight tubular microfossils with regularly arranged collar-structures. Collars usually flare away at the upper part of the tubes with annulations, longitudinal crests, or weak ridges occasionally observed on their surfaces. The tubes have a smooth inner wall and a circular cross section. Closed proximal ends and dichotomous branchings are occasionally observed. The tube wall is composed of multi-layered laminae.

Cloudina hartmannae Germs, 1972
Figures 1.1, 1.2, 3–5, 7.1, 8.1

1972 *Cloudina hartmannae* Germs, p. 753, text-fig. 3C, pl. 1, figs. 1–7.
1972 *Cloudina riemkeae* Germs, p. 755, text-fig. 3D, pl. 1, figs. 8–13.
1976 *Cloudina hartmanae*; Glaessner, p. 266, text-fig. 3, pl. 1, fig. 2, pl. 2, fig. 5.
1983 *Coleolella* sp.; Mount et al., p. 225, figs. 3C, D.
?1983 *Coleolella* sp.; Signor et al., p. 416, fig. 3b.
?1983 Multiple–walled tubular fossil; Signor et al., p. 416, fig. 3e.
?1985 *Cloudina hartmannae*; Hahn and Pflug, p. 422, pl. 2, fig. 5.
[non] 1985 *Cloudina waldei* Hahn and Pflug, p. 423, text-fig. 7, pl. 1, figs. 1, 2, pl. 2, figs. 3, 4.
?1987 *Cloudina lucianoi* (Beurlen and Sommer, 1957); Zaine and Fairchild, p. 804, figs. 1–7.
1987 *Nevadatubulus dunfeei* Signor, Mount, and Onken, p. 429, figs. 3, 4.1–4.14.
1990 *Cloudina* cf. *hartmannae*; Conway Morris et al., p. 252, fig. 4.
1990 Cloudinid-like tube; Conway Morris et al., p. 254, fig. 5.
1990 *Cloudina hartmannae*; Grant, p. 261, figs. 4, 6A, 8D.
1990 *Cloudina riemkeae*; Grant, p. 261, figs. 5, 7A, B, 8C.
1990 *Cloudina* sp.; Grant, p. 261, figs. 7C, D, 10B.
?[non] 1990 *Cloudina* sp.; Grant, p. 275, fig. 8B.
1992 *Cloudina hartmannae*; Bengtson and Yue, p. 368, figs. 2, 3.
1992 *Cloudina* sp.; Li et al., p. 94, text-figs. 3–6, 7:7, 8, pl. 8, figs. 4, 16, 17.
1992 *Cloudina sinensis* Zhang, Li, and Dong in Li et al., p. 93, text-figs. 3–6, 7:1–6, 10, pl. 8, figs. 1–3, 5, 7–12, 14, 15, 18.
1992 *Cloudina lijiagouensis* Zhang, Li, and Dong in Li et al., p. 94, text-fig. 3–6, 7:9, pl. 8, fig. 6.
1992 *Conotubus varius* Zhang, Li, and Dong in Li et al., p. 92, text-fig. 3–7, 8:9, pl. 9, figs. 3, 4, 6, 9.
2000 *Cloudina sinensis*; Zhang and Hua, p. 326, text-fig. 1–6, pl. 1, figs. 2, 17.
2000 *Cloudina lijiagouensis*; Zhang and Hua, p. 332, pl. 1, fig. 3.
2000 *Cloudina* sp.; Zhang and Hua, p. 326, text-figs. 2, 7, 8:9, pl. 1, figs. 1, 6, 9, 14, 18.
2000b *Cloudina* sp.; Hua et al., p. 513, pl. 2, fig. 3.
2000b *Cloudina lijiagouensis*; Hua et al., p. 513, pl. 2, fig. 4.
2001 *Cloudina*; Brain, p. 478, figs. 1, 2.
2001 *Cloudina sinensis*; Chen and Sun, p. 195, pl. 1, figs. 1–13, pl. 2, figs. 1–8, pl. 3, figs. 1–5.
?2001 *Cloudina*; Hofmann and Mountjoy, p. 1093, figs. 2G, H, J.
?[non] 2001 *Cloudina*; Hofmann and Mountjoy, p. 1093, fig. 2I.
2003a *Cloudina hartmannae*; Hua et al., p. 456, figs. 2D–H.
2003a *Cloudina hartmannae*; Hua et al., p. 457, fig. 3.
2003b Morphotype II; Hua et al., p. 197, pl. 2, fig. 1.
2003 *Cloudina lucianoi*; Gaucher et al., p. 261, figs. 10A, B, D–K.
2005 *Cloudina hartmannae*; Hua et al., p. 278, figs. 1A–P.
2007 *Cloudina hartmannae*; Hua et al., p. 269, figs. 5:4, 5:6, 6:3–5.
2008 *Cloudina*; Chen et al., p. 39, fig. 2D.
2010 *Cloudina hartmannae*; Cai et al., p. 492, fig. 4M.
2011 *Cloudina lucianoi*; Warren et al., p. 384, figs. 2D, 3A–E, 4A–G.
2012 *Cloudina* sp.; Warren et al., p. 692, fig. 2A.
?2012 *Cloudina* ex gr. *C. riemkeae*; Zhuravlev et al., p. 209, figs. 3A, C–E
?2012 *Cloudina* ex gr. *C. hartmannae*; Zhuravlev et al., p. 209, figs. 3B, F–H.
2012 *Cloudina hartmannae*; Zhuravlev et al., p. 215 figs. 6C, D.
2014 *Cloudina*; Warren et al., p. 393, figs. 2A–G.
2015a *Cloudina*; Cortijo et al., p. 421, figs. 2, 3.
2015b *Cloudina hartmanae*; Cortijo et al., p. 189, figs. 3A–D, F, I–L, 4, 5.
?2015 *Cloudina lucianoi*; Walde et al., p. 219, figs. 4F, 5A–D, 6 (part).
[non] 2015 *Cloudina waldei*; Walde et al., p. 219, fig. 4E.

2016	*Cloudina hartmannae*; Yang et al., p. 210, figs. 4A–D, G, H, 5D.
2016	*Cloudina hartmannae*; Chen et al., p. 98, fig. 3C, D.
2016	*Cloudina riemkeae*; Xiao et al., p. 544, fig. 4G, H.
2017	*Cloudina hartmannae*; Cai et al., p. 150, fig. 4.
2017	*Cloudina ningqiangensis* Cai et al., p. 153, fig 6.
2017	*Cloudina hartmannae*; Becker-Kerber et al., p. 4, figs. 2, 3A, C, D, F–I.
2017	*Cloudina hartmanae*; Adorno et al., p. 30, fig. 10A, C.
[non] 2017	*Cloudina hartmanae*; Adorno et al., p. 30, fig. 10B.
2017	*Cloudina hartmannae*; Adorno et al., p. 30, fig. 11A.
2017	*Cloudina riemkeae*; Adorno et al., p. 30, fig. 11C.
?2017	*Cloudina lucianoi*; Adorno et al., p. 30, fig. 11B.
?2017	*Cloudina lucianoi*; Adorno et al., p. 29, figs. 9, 10D, E, 12K.
?[non] 2017	*Cloudina lucianoi*; Adorno et al., p. 32, fig. 12A–J, L–S.
2019a	*Cloudina*; Min et al., p. 19, figs. 1A–D, 2.
2019a	*Multiconotubus*; Min et al., p. 19, fig. 1E–K.
2019	*Cloudina*; Becker-Kerber et al., p. 3, 8, figs. 3, 8.
?[non] 2020	*Cloudina ningqiangensis*; Liang et al., p. 4, fig. 3.
2020	*Cloudina hartmannae*; Liang et al., p. 5, fig. 4.
?2020	*Cloudina* cf. *carinata*; Liang et al., p. 6, fig. 5c.
2020	*Cloudina hartmannae*; Shore et al., p. 878, figs. 1C, 3I, J.
2020a	*Cloudina hartmannae*; Yang et al., p. 450, figs. 2A–C.
2020b	*Cloudina hartmannae*; Yang et al., p. 4, figs. 2D, E, 3A, B, 5A.

Holotype.—S.A.M.K. 1071 (Fig. 1.1), Iziko South African Museum, Cape Town, South Africa.

Diagnosis.—Organisms forming tubular exoskeletons with collar structures. Elongate collars are close to the tubular body near the base to lower part and flare away at the upper part of the tubes. The tube wall is composed of multi-layered laminae, smooth inner wall, and a circular cross section. Closed proximal end and dichotomous branching are occasionally observed.

Occurrence.—Omkyk (Germs, 1972; Grant, 1990; Brain, 2001), Nasep (Germs, 1995), Mara? (Germs, 1983), Mooifontein (Germs, 1983; Grant, 1990; Yang et al., 2020b; Figs. 3, 4), Kliphoek? (Grant, 1990), Huns (Grant, 1990; Germs, 1995), and Spitskop (Germs, 1995) members of the Nama Group, South Namibia; Tamengo Formation, Corumbá Group, Mato Grosso do Sul State, Brazil (Beurlen and Sommer, 1957; Adorno et al., 2017; Becker-Kerber et al., 2017); Sete Lagoas Formation, Bambuí Group, Januária area, central Brazil (Warren et al., 2014); Tagatiya Guazu Formation, Itapucumi Group, northeastern Paraguay (Warren et al., 2011, 2017; this study); Shibantan (Chen and Wang, 1977; Fig. 7) and Baimatuo (Liang et al., 2020) members of Dengying Formation, Yichang City of Hubei Province, China; Dengying Formation, Shennongjia area of Hubei Province, South China, (Steiner et al., 2007; Yang et al., 2020a); Dengying Formation (Conway Morris et al., 1990; Hua et al., 2005; Cai et al., 2017), Ningqiang County of Shaanxi Province, South China; Kuanchuanpu Formation, Ningqiang County of Shaanxi Province, South China (Yang et al., 2020b); Deep Spring Formation (Mount et al., 1983; reported as *Coleolella* sp.; Signor et al., 1987; reported as *Nevadatubulus*; this study), western USA; Villarta Limestone of Ibor Group, Villarta de los Montes Village, Bada-joz Province, Spain (Cortijo et al., 2015b); Byng Formation of Miette Group, Salient Mountain area, British Columbia, Canada (Hofmann and Mountjoy, 2001); Ara Formation of Huqf Group, Birba Area, Oman (Conway Morris et al., 1990); Ust'-Yudoma Formation, Uchur-Maya region, Southeast Siberia (Zhuravlev et al., 2012; Zhu et al., 2017); Tarzhul' Formation in Kuznetsk Alatau (Terleev et al., 2011) and Raiga Formation in Tomsk Region (Kontorovich et al., 2008), West Siberia, Russia.

Description.—Straight or sinuous tubular constructions exist with both closely or widely expanding collared structures. Fossil length varies from hundreds of micrometers to several centimeters, with a diameter range of hundreds of micrometers to ∼5 mm. Cross sections are usually circular, but sometimes oval due to compression. Wall thickness is between 10–30 μm. Multi-layered laminae of the tube wall range from 1–5 μm in thickness and preserve organic residues.

Measurements.—The width and spacing of collar structures of previously described species of *Cloudina* were measured to provide a statistic assessment on the size variation of the genus and its different species (Fig. 2). The data are based on the type material, additional published material, as well as our collected specimens (Supplemental data). Only specimens that were preserved in a state of preservation that secured an exact size measurement were measured, which resulted in 190 data sets that were obtained based on literature and our own material. It is emphasized that the size measurements can partly be affected by the fossil preservation (e.g., recrystallization and additional cement growth on tubes) and may have been biased by selective sampling and preparation methods (e.g., specimens extracted by acid or presented by thin-section). Despite this, general size trends indicated by the data are considered to be useful as a support of the systematic work. The measurements show that collar width and spacing have a wide range of variation (60 to ∼4600 μm and 36 to ∼3750 μm, respectively; Fig. 2.1) while they are relatively well correlated in an approximately linear trend. *Cloudina carinata* is generally larger than most individuals of *Cloudina hartmannae* and other species. However, some of the specimens of *Cloudina hartmannae*, including its holotype, are larger than most of the other collected specimens. The majority of specimens of *Cloudina hartmannae* are of smaller size, indistinguishable from the type specimens of *C. riemkeae*, which originally was distinguished by an alleged size difference (Germs, 1972). The size statistics of the collar width shows that the diameter of *Cloudina hartmannae* has a size peak ∼500 μm (Fig. 2.2). The size peak at 3000 μm is contributed by *Cloudina carinata* (Fig. 2.2; Supplemental data).

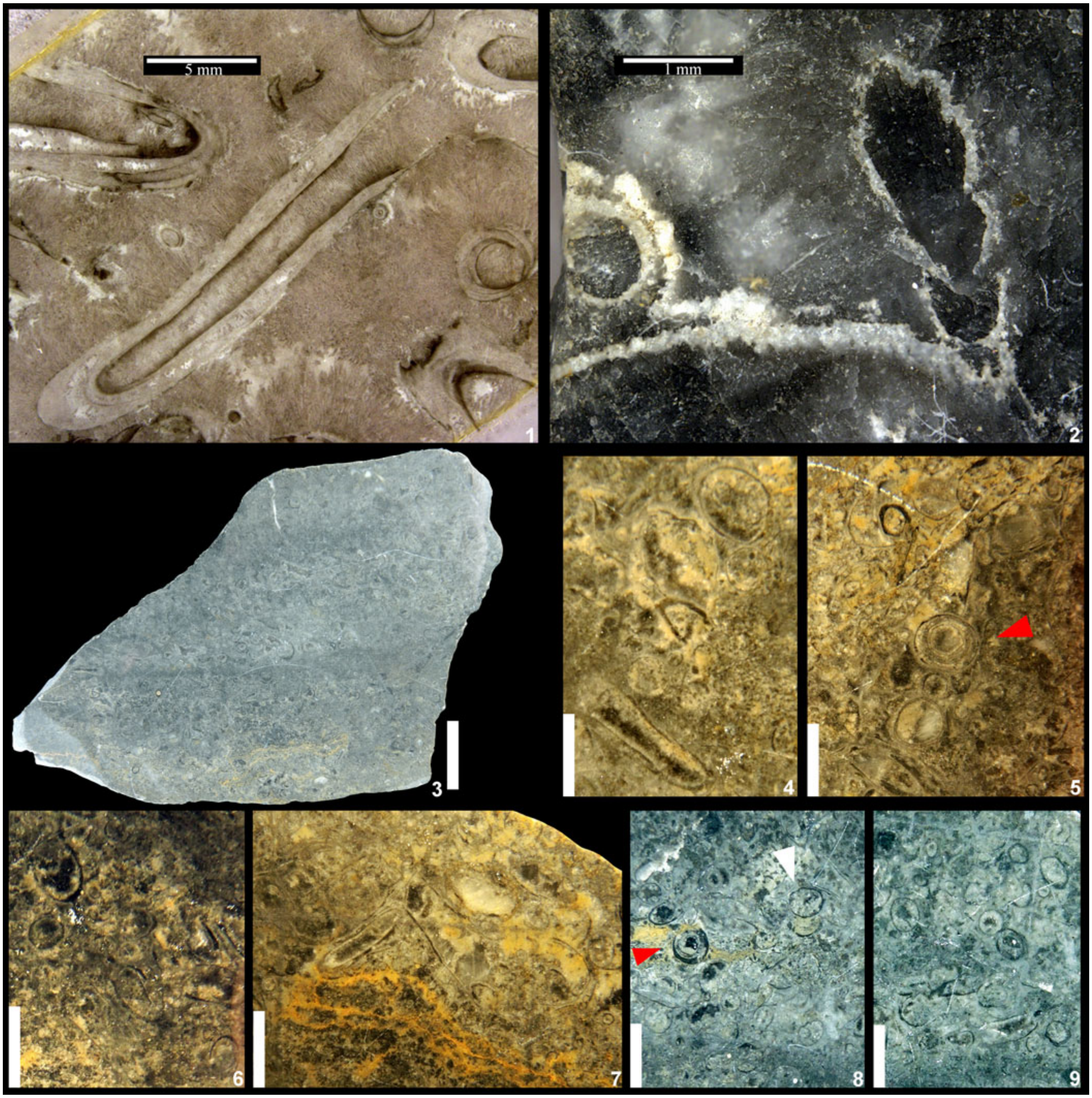

Figure 1. Originally published materials of *Cloudina* (**1, 2**) from the Omkyk Member (formerly named Schwarzkalk Limestone Member) of the Zaris Formation at Driedoornvlakte Farm near Schlip, Namibia (Germs, 1972; photo courtesy of the Iziko Museum of South Africa from specimens housed at this institution) and *Aulophycus* (**3–9**) reported from the Tamengo Formation, Corumbá Group, Ladário Town, Mato Grosso do Sul State, Brazil (Beurlen and Sommer, 1957; photo courtesy of the Earth Sciences Museum—Brazilian Geological Survey, from specimens housed at this institution). (**1**) Holotype of *Cloudina hartmannae*, S.A.M.K. 1071. (**2**) Holotype of *Cloudina riemkeae* (=*Cloudina hartmannae*), S.A.M.K. 1072. (**3**) Holotype of *Aulophycus lucianoi*, D.G.M. 1149. (**4**) Close-up photograph of (**3**) showing cross-sections with single wall and one longitudinal section with a single wall. (**5**) Close-up photograph of (**3**) showing multi-walls and angular folds resembling *Sinotubulites* (red arrow); the photograph also shows cross sections with various diameters. (**6**) Close-up photograph of (**3**) showing cross-section specimens with a single wall. (**7**) Close-up photograph of (**3**) showing longitudinal sections with a single wall and specimens with various diameters. (**8**) Specimens from paratype D.G.M. 1156 shows specimens with various diameter and single wall, some of which resemble *Namacalathus* (e.g., white arrow); one specimen with multi-walls and angular folds resembles *Sinotubulites* (red arrow). (**9**) Specimens from paratype D.G.M. 1156 show cross sections with a single wall and various diameters. Scale bars: (**1**) 5 mm; (**2**) 1 mm; (**3**) 2 cm; (**4–7**) 300 µm; (**8, 9**) 500 µm.

Remarks.—Germs (1972) named two species, *Cloudina hartmannae* and *Cloudina riemkeae,* from Namibia, attributing a Precambrian age to these organisms. The holotype of *C. hartmannae* (Fig. 1.1) shows weakly preserved collars and a pervasive recrystallization of calcite crystallites. The type specimen of *Cloudina riemkeae* (Fig. 1.2) is also preserved in a sample with strongly recrystallized spar calcite. The size statistics show that *Cloudina* has a broad variation

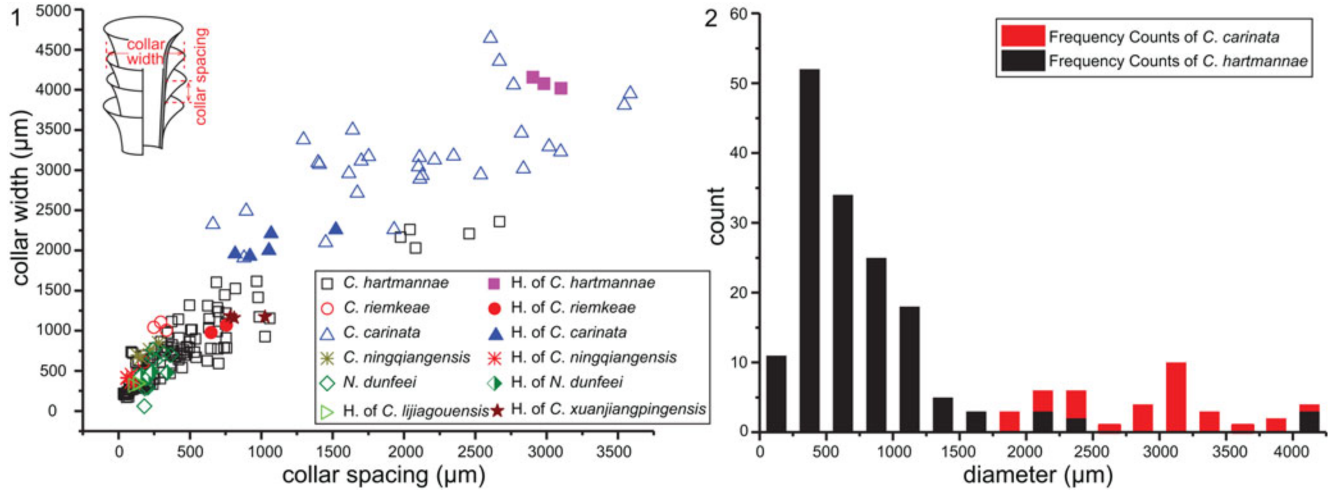

Figure 2. (**1**) Scatter plot of collar width and spacing in *Cloudina*. It is noted that the collar widths and spacing are relatively proportional for *Cloudina*; species designations are according to the original publications instead of the taxonomic revision herein. Some specimens originally described with genus designation were identified to species level herein. (**2**) Frequency distribution histograms of the diameters of *Cloudina hartmannae* and *Cloudina carinata*; note the peak at 3000 μm reflects specimens of *Cloudina carinata* (in red). The data of *Cloudina hartmannae* (see original data and relevant references in the supplementary file) are based on the new taxonomic assignment in this study. Abbreviations: *C.* = *Cloudina*; *N.* = *Nevadatubulus*; H. = Holotype.

(60 to ∼4600 μm) of collar width (i.e., the outer diameter). Although sampling and preservational bias may have led to relatively fewer large specimens presented in thin-sections and publications, the size of holotype of *C. riemkeae* is well within the size cluster of measured *C. hartmannae* (Fig. 2.1). Although morphologic details are obscured as a result of recrystallization, the preserved characters demonstrate that *C. riemkeae* shares the same tubular collared-structures with *C. hartmannae* (Fig. 1.1) and contradicts the original observation of strong size differentiation (Germs, 1972). We therefore do not see an objective basis for a distinction of *C. riemkeae*, and hence support Yang et al. (2016) in synonymizing it with *C. hartmannae*.

Aulophycus lucianoi Beurlen and Sommer, 1957, was initially reported as a middle–late Cambrian alga from the Tamengo Formation of Corumbá Group, Brazil, although the specimen donor, Dr. Luciano Jacques de Morais, considered it to be of animal origin (Beurlen and Sommer, 1957). The original description (translated from the original description in Portuguese) of the type materials is: "…*These are tubiform stems, straight or somewhat curved, not segmented, from less than 1 mm to more than 5 mm in diameter, with wall of variable thickness, thin or not; in the specimens preserved in relief, the wall appears wrinkled, in the polished slabs these wrinkles are represented by thin, sinuous lines. In the same polished surfaces, we find transverse and oblique cuts, frequently, showing several surrounding layers, sometimes concentric or not, with cross-sections presenting circular, round, polygonal and oval contours. Absence of preferential orientation within the strata bearing the clusters of specimens analysed, where alternate beds of higher incidence with other with sparse stems (st. I; V a, b). Stand out the terminations of the stems for their rounded ends (est. II a; III b; V b). The carefully studied sample surfaces do not authorize to speak of ramifications of stalks, nor isolated nodules. The analysed figures don't show that it cannot be interpreted as section made through a circular or oval tube, with closed ends or not, rounded or slightly tapered, the whole stem rarely reaching its 10 mm in length*…" (Beurlen and Sommer, 1957, p. 32).

Zaine and Fairchild (1987) subsequently re-combined *A. lucianoi* to *Cloudina lucianoi*. Recent studies further suggested the synonymy of *Cloudina lucianoi* with *Cloudina hartmannae* (Adorno et al., 2017, but see Becker-Kerber and Pacheco, 2018), and modified the systematic treatment, considering *Cloudina hartmannae* to be a junior synonym of *Cloudina lucianoi* or vice versa (Yang et al., 2016). An examination of type specimens of *Aulophycus lucianoi* (Fig. 1) is carried out herein. Considering *Aulophycus lucianoi* was later reassigned from algae to metazoans (e.g., Hahn and Pflug, 1985; Zaine and Fairchild, 1987), the holotype sample (D.G.M. 1149) containing multiple tubular remains is therefore treated as an assemblage of syntypes (ICZN, 1999, Article 72.1) and examined here (Fig. 1.3–1.9; image credit to Dr. Rafael Costa da Silva from Earth Sciences Museum—Brazilian Geological Survey). The specimens show circular cross sections with single or angularly folded multiple walls, but none of them can be undoubtedly assigned to *Cloudina* because they lack collar structures. In consideration with the other type specimens and their original descriptions (see above, Beurlen and Sommer, 1957), most of them (Fig. 1.5, 1.8) may be assigned to *Sinotubulites* or other unknown taxa based of their corrugated multi-layered walls in cross-section. Nonetheless, it is possible that a few of the specimens (on other type samples, but not the holotype sample) might be compared to *Cloudina* (e.g., specimens on paratype sample 1157). Hahn and Pflug (1985) tentatively suggested that *A. lucianoi* was synonymous with *Cloudina waldei* Hahn and Pflug, 1985, while the latter is herein reassigned to *Sinotubulites baimatuoensis* (see discussion below). We thus suggest that *Cloudina hartmannae* should be retained as a species and not synonymized with *Aulophycus lucianoi*.

It is noted that the correction of *C. hartmannae* to *C. hartmanae* (e.g., Glaessner, 1976; Adorno et al., 2017) is considered

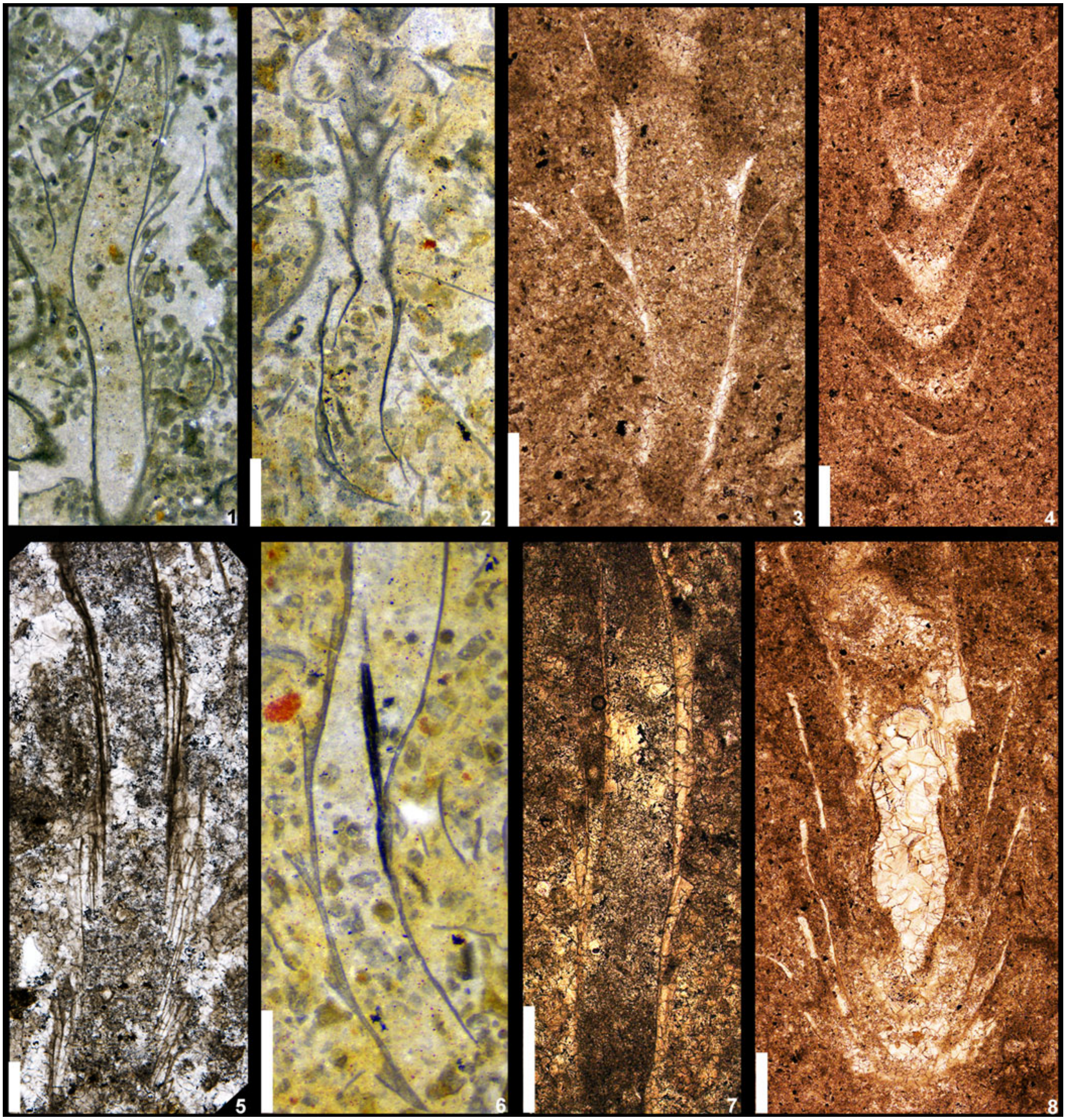

Figure 3. *Cloudina hartmannae* from the Mooifontein Member of Nama Group in Aar Farm, Namibia (**1, 2, 5–7**) and Tagatiya Guazu Formation, Itapucumi Group, northeastern Paraguay (**3, 4, 8**); note the evident morphological variations between distinct specimens, some of which (**5**) resemble *Multiconotubus chinensis* Cai et al., 2017. (**1**) A0803. (**2**) A1201. (**3**) PGC010202. (**4**) PGC010501. (**5, 7**) NFA210103–2. (**6**) A01–02. (**8**) PGC010602. Scale bars: (**5**) 200 µm; others, 500 µm. Specimens are deposited at the Institute of Geology, Chinese Academy of Geological Sciences (CAGS).

invalid. Germs (1972) initially present a corrected spelling of the source name (Professor Olga Hartman) with a consistent presentation of the taxonomic name *C. hartmannae* through the text. Thus we consider this species name is after an inappropriate latinization and should be considered valid according to the ICZN (1999, Article 32.5.1).

Cloudina lijiagouensis Zhang et al. in Li et al., 1992, is defined by a single specimen with a spherical shell adhered to the collared tubular body (Li et al., 1992, pl. 8, fig. 6). It is considered here that the spherical shell represents a branch fragment of the main tubular body, as reported commonly in other studies (Hua et al., 2003a; Min et al., 2019a). *Cloudina sinensis* Zhang

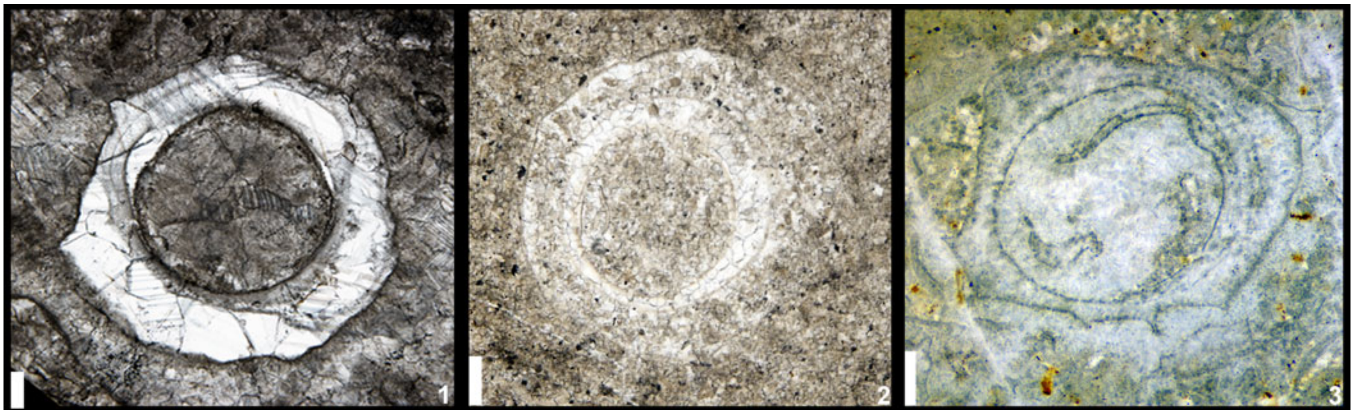

Figure 4. Transversal views of *Cloudina hartmannae* Germs, 1972 from Mooifontein Member of Nama Group, Aar Farm, Namibia (**1**), northeastern Paraguay (**2**) and Deep Spring Formation of Mount Dunfee in Nevada, USA (**3**). (**1**) NFA210202–2. (**2**) PGC010603. (**3**) ELG370501. Scale bars: (**1, 2**) are 200 μm; (**3**), 500 μm. Specimens are deposited at the Institute of Geology, CAGS.

et al. in Li et al., 1992, originally was differentiated from *Cloudina hartmannae* based on its smaller diameter, a lack of dichotomous branching, and ornamentations on the surface. Size statistics revealed the broad range of *Cloudina hartmannae* (Fig. 2). Dichotomous branching is more common in the three-dimensional specimens from South China compared to those from Namibia (Germs, 1972; Shore et al., 2020) and South America (Warren et al., 2014), which are usually studied in thin-sections. We agree with the opinion by Cai et al. (2017), synonymizing *C. sinensis* and *C. lijiagouensis* with *Cloudina hartmannae*. *Nevadatubulus dunfeei* was considered to be distinct from *Cloudina hartmannae* in size and its coarse layering (Signor et al., 1987). While its size variation is within the size range of *C. hartmannae* (Fig. 2.1), the coarse layering is considered to have resulted from taphonomic effect and acid maceration. Due to similarity in the described collar structures, the species is suggested to be synonymized with *C. hartmannae* (Yang et al., 2016; Cai et al., 2017). On the other hand, *Cloudina carinata*, from the Villarta Limestone of the Ibor Group of Spain (Cortijo et al., 2010) and Tamengo Formation of Brazil (Adorno et al., 2019), is distinguished from *C. hartmannae* by its longitudinal crests. The putatively recrystallized *Cloudina carinata* in Siberia (Terleev et al., 2011) cannot be unequivocally confirmed by observations through thin-sections. *Cloudina* cf. *carinata* (Liang et al., 2020) needs further examination because it displays irregular longitudinal ridges, which may have resulted from diagenetic alteration during silicification.

Coleolella sp. and other problematic tubular fossils (see synonym list above) from the Deep Spring Formation and the upper Reed Dolomite (White-Inyo Mountains of California and Esmeralda County, Nevada) is reassigned to *Cloudina hartmannae* (Fig. 5). The *Wyattia* Taylor, 1966, reported from the Reed Dolomite in the White-Inyo Ranges, USA, also could be synonymous with *Cloudina* (Grant, 1990; Zhuravlev et al., 2012). However, the pervasive recrystallization and obscuration of features, such as the collared structure, leave this synonymization tenuous. Reports of *Cloudina*? sp. from Antarctica (Yochelson and Stump, 1977) and *Cloudina*? *borrelloi* Yochelson and Herrera, 1974, lack key characteristics of *Cloudina*, such as collars and multiple layers, rendering this identification dubious.

Conotubus varius Zhang et al., 1992 (Li et al., 1992) is suggested to be *Cloudina hartmannae* by its typical collared structures instead of transversal ridges (Fig. 8.4; see the diagnosis of *Sinotubulites* below).

It is emphasized that *Cloudina hartmannae* has a wide morphological variation in collar size (Figs. 2–4), density, and angles. *Multiconotubus* Cai et al. (2017) was defined as tubular fossils with multi-layered and nested cone-shaped layers. Compared with most of the known specimens of *Cloudina hartmannae*, this indicates that it consists of tubes with collars of high density and small divergent angles. This species requires further study to determine if there are genus-level differences or merely inter-/intraspecific variations, as observed among various specimens (e.g., Fig. 3). The *Cloudina*-like fossil *Feiyanella manica* Han et al., 2017, is a tubular fossil with multi-layered shells and wrinkled/folded outer walls, as well as two orders of dichotomous branchings, forming three generations of tubes (Han et al., 2017). The fossils superficially resemble branching algae, such as *Epiphyton* from the Dengying Formation of the same area (Min et al., 2019b). The published *Cloudina* specimens from Mexico (Sour-Tovar et al., 2007; Hodgin et al., 2020) show typical corrugated surfaces and irregularly distributed longitudinal and transversal ridges, but the typical collar-structure was missing (McMenamin, 1985; Sour-Tovar et al., 2007, text-figs. 2D, E). As a result, most of these individuals can be assigned to *Sinotubulites*. *Cloudina waldei* Hahn and Pflug, 1985, from the Tamengo Formation, Corumbá Group in southwest Brazil likely developed a “strongly wrinkled outer wall” (Hahn and Pflug, 1985, p. 423) instead of collars because the outer wall is described as (translated from the original description in German): “Transverse ridges are interrupted by narrow, irregularly running transverse furrows; transverse ridges can also occur (pl. 1, fig. 1c). In some specimens there are also external longitudinal ridges which, in conjunction with the transverse ridges, can produce a cassette-like field of the outer surface…” (Hahn and Pflug, 1985, p. 425). These descriptions, as well as the illustrated specimens (Hahn and Pflug, 1985, pls. 1, 2.3, 2.4), support our assignment of the species to *Sinotubulites baimatuoensis*.

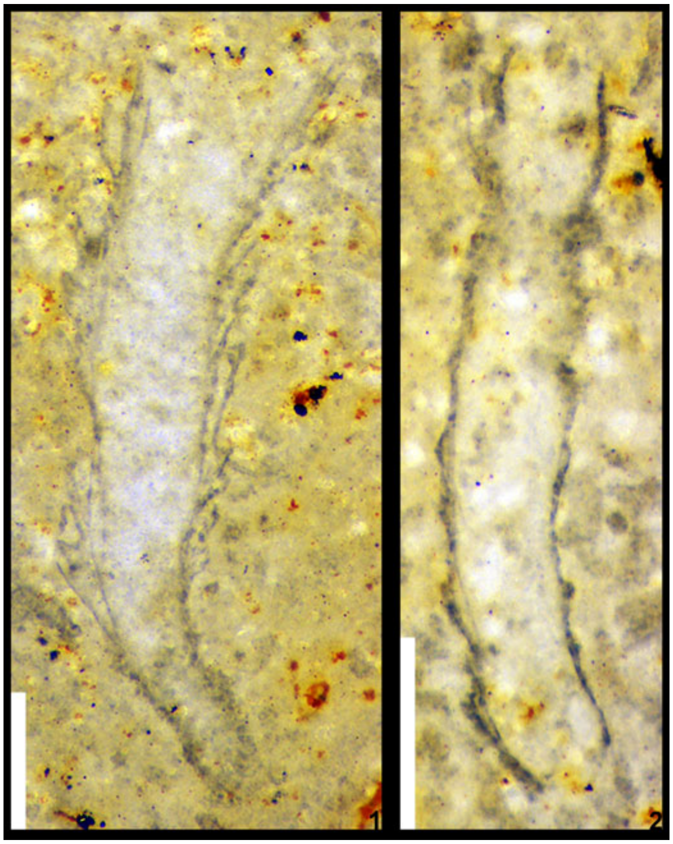

Figure 5. *Cloudina hartmannae* Germs, 1972, from the Deep Spring Formation of Mount Dunfee in Nevada, USA. (**1**) ELG370401. (**2**) ELG370402. Scale bars are 500 µm. Specimens are deposited at the Institute of Geology, CAGS.

Branching individuals of *Cloudina* have been reported rarely from South China (Hua et al., 2005; Min et al., 2019a), Spain (Cortijo et al., 2010; Cortijo et al., 2015a), Brazil (Warren et al., 2014), and Namibia (Germs, 1972; Shore et al., 2020). Considering the strong recrystallization and that post-mortem stacking of specimens could result in apparent branching, the branching features observed in *Cloudina* specimens from Namibia (Germs, 1972; Shore et al., 2020) and Brazil (Warren et al., 2014) are awaiting further confirmation. Disproportionate reports for the rarity of branching specimens might indicate the possibility that these specimens indicate particular ecological conditions that forced local development of budding and branching during reproduction in distinct habits, or even that they might be assigned to a different species. Another possible explanation is based on the taphonomic bias (i.e., phosphatic specimens can be extracted in great numbers by acid digestion compared to calcitic specimens), which are mainly observed with thin sections. Furthermore, multiple taphomodes lead to morphological variations of *Cloudina*. Specifically, three-dimensionally preserved phosphatic specimens exhibit characteristics of closed ends and fine decorations on the shell surfaces, whereas such features cannot be easily observed in thin-sections of calcitic specimens (Figs. 3, 4). Nonetheless, two-dimensional (thin-section) data of the ultrastructure, compositional comparison, as well as statistics of the collar width and spacing (Fig. 2) are equally beneficial for taxonomic understanding. There also exists the possibility that the closed end is simply a diagenetic feature created by a cover of phosphate cement.

Phylum, Class, Order, Family uncertain
Genus *Sinotubulites* Chen, Chen, and Qian., 1981

Type species.—*Sinotubulites baimatuoensis* Chen, Chen, and Qian, 1981, from the Middle (=Shibantan) Member of the Dengying Formation, Shibantan of Yichang City, China, by original designation.

Other species.—*Sinotubulites triangularis* Cai et al., 2015; *Sinotubulites pentacarinalis* Cai et al., 2015; and *Sinotubulites hexagonus* Cai et al., 2015.

Emended diagnosis.—Straight or curved tubular fossils with variable diameter, decorated with corrugations, transverse annulations, and discrete longitudinal ridges. The annulae of the external decoration partially show Y-shaped arrangements. The shell wall is relatively thick and multi-layered. The cross-section is circular or irregularly polygonal due to the presence of longitudinal ridges. Inner wall is smooth, and the margin of the inner wall is always circular in cross-section.

Sinotubulites baimatuoensis Chen, Chen, and Qian, 1981
Figures 6, 7.3, 8.2–8.4, 9

1977 *Cloudina*? sp.; Chen and Wang, p. 220, figs. 1a, b (part).
1981 *Sinotubulites baimatuoensis* Chen et al., p. 119, pl. 1, figs. 1, 2, pl. 2, figs. 1–6 (part).
1981 *Skolithos miaoheensis* Chen, Chen, and Qian, p. 117, pl. 1, figs. 4, 5 (part).
1983 *Salanytheca* sp.; Mount et al., p. 225, fig. 3A.
?1983 *Salanytheca* sp.; Mount et al., p. 225, fig. 3B.
1983 *Salanytheca* sp.; Signor et al., p. 416, fig. 3c.
1983 Smooth, single-walled shell; Signor et al., p. 416, fig. 3f.
1983 Irregularly annulated tube; Signor et al., p. 416, fig. 3g.
1983 Regularly annulated tube; Signor et al., p. 416, fig. 3h.
1985 *Cloudina waldei* Hahn and Pflug, p. 423, fig. 7, pl. 1, figs. 1, 2, pl. 2, figs. 3, 4.
1985 *Sinotubulites cienegensis* McMenamin, p. 1417, figs. 3.2–3.6, 4.1, 4.2, 4.4–4.7, 5.2, 5.5, 5.6.
?1985 Invaginated tubular or narrow conical shells with thin wall; McMenamin, p. 1422, fig. 5.3.
1985 *Sinotubulites baimatuoensis*; McMenamin, p. 1416, fig. 6.
1987 *Sinotubulites cienegensis*; Signor et al., p. 431, fig. 5.1.
?1987 *Salanytheca* sp.; Signor et al., fig. 5.2.
1992 *Qinella shaanxiensis* Zhang, Li, and Dong in Li et al., p. 94, pl. 7, figs. 1–5, 8–10, pl. 9, figs. 5, 7, 10.
1992 *Qinella levis* Zhang, Li, and Dong in Li et al., p. 96, pl. 7, fig. 6.
1992 *Qinella lijiagouensis* Zhang, Li, and Dong in Li et al., p. 96, text-fig. 6-3, pl. 7, fig. 7.
1992 *Qinella* cf. *lijiagouensis*; Li et al., p. 97, pl. 14, figs. 6a–c.
?1992 *Qinella* sp.; Li et al., p. 98, pl. 14, fig. 4.
?1992 *Sinotubulites baimatuoensis*; Li et al., p. 98, pl. 16, fig. 1.
1993 *Sinotubulites miaoheensis* Ding et al., p. 120, pl. 2, figs.1–6.

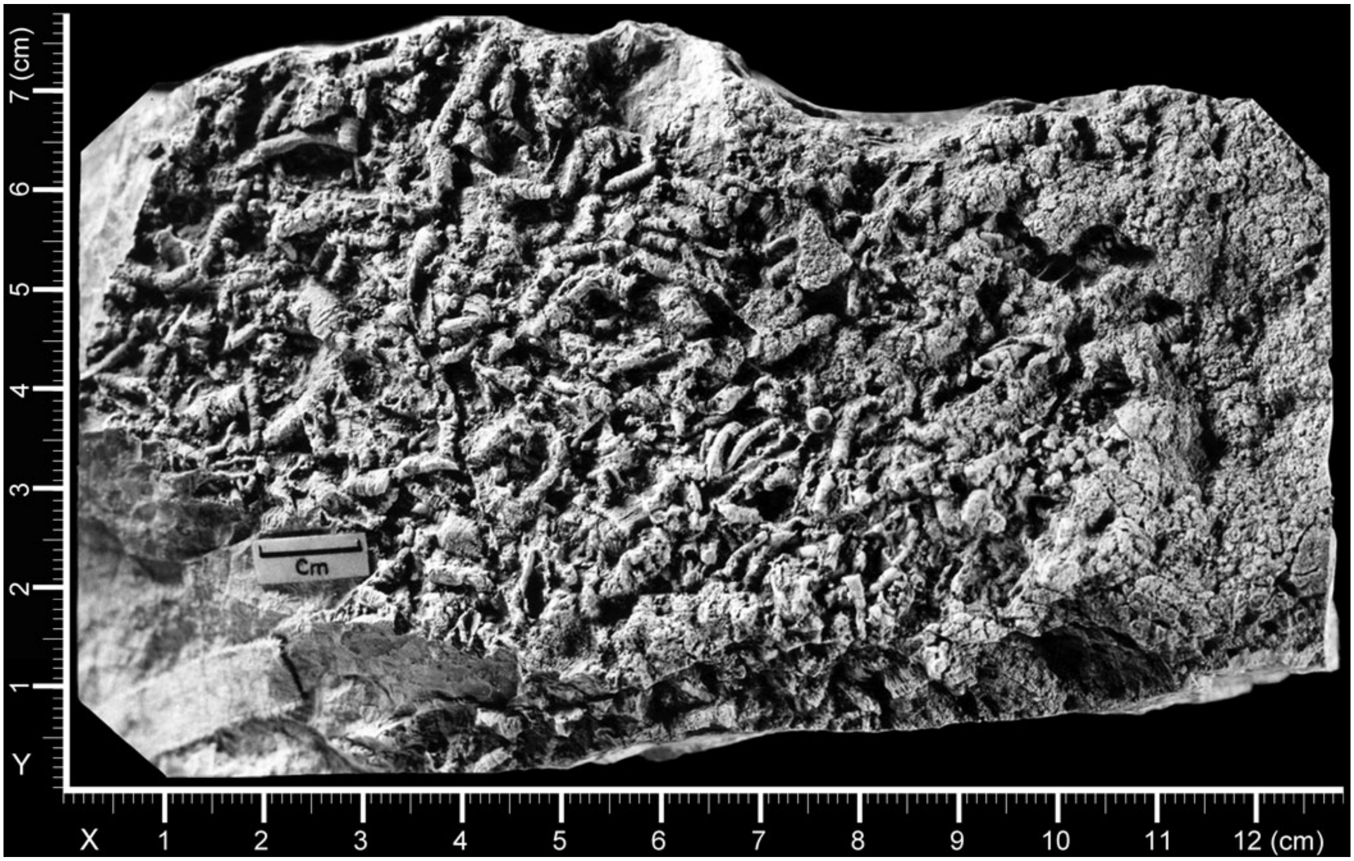

Figure 6. Rescanned original photograph of previous syntypes of *Sinotubulites baimatuoensis* Chen et al., 1981, displaying the originally reported specimen from the Middle Member (Shibantan Member), Dengying Formation in the Three Gorges region of Hubei Province, China, YG-96-1. Detailed fossil information is presented in Figures 7 and 8. The numbers along X and Y axes provide precise locations as well as a centimeter scale for individual specimens.

2000a *Qinella levis*; Hua et al., p. 386, pl. 1, figs. 1, 3, 4, 9–12.
2000a *Sinotubulites cienegensis*; Hua et al., p. 386, pl. 1, figs. 5–8, pl. 2, figs. 1–5, 6a, b, 14.
2000b *Sinotubulites cienegensis*; Hua et al., p. 513, pl. 1, fig. 1b, pl. 2, fig. 6.
2001 *Sinotubulites shaanxiensis*; Chen and Sun, p. 196, pl. 3, fig. 7, pl. 4, figs. 1, 2.
2003a *Sinotubulites cienegensis*; Hua et al., p. 456, figs. 2A–C.
2003b Morphotype I; Hua et al., p. 197, pl. 1, fig. 2.
2007 *Sinotubulites*; Hua et al., p. 269, figs. 5.7, 5.8.
2007 silica-replaced cloudiniids; Sour-Tovar et al., p. 171, text-figs. 2D, E.
2008 *Sinotubulites*; Chen et al., p. 39, figs. 2A–C, E, 3A–G, 4A–G.
2010 *Sinotubulites baimatuoensis*; Cai et al., p. 492, fig. 4N.
?2012 *Sinotubulites* sp.; Zhuravlev et al., p. 212, fig. 5.
2012 *Sinotubulites*; Sun et al., p. 110, figs. 3, 4.
2015 *Sinotubulites baimatuoensis*; Cai et al., p. 14, figs. 3, 4.
2015b *Sinotubulites baimatuoensis*; Cortijo et al., p. 191, fig. 6.
2016 *Sinotubulites*; Xiao et al., p. 544, fig. 4I.
2019 *Sinotubulites baimatuoensis*; Walde et al., p. 345, figs. 9A–E.
2020 *Cloudina*; Hodgin et al., p. 117, figs. 2D, E.
2020 *Sinotubulites*; Liang et al., p. 6, fig. 6.
2020a *Sinotubulites baimatuoensis*; Yang et al., p. 450, figs. 2D, E.

Lectotype hereby designated.—YG-96-5 (Fig. 8.4), deposited at Geological Museum of China, Beijing, China.

Paralectotype hereby designated.—The specimens in Figure 8.2 and 8.3, from a hand slab deposited at Geological Museum of China, Beijing, China (original number of whole sample is YG-96-1).

Emended diagnosis.—Small straight or slightly curved tubular fossils, millimetric to centimetric size, with surface ornamentation of transversal rings. Irregular rugae, discontinued transversal and longitudinal ridges can be preserved and arranged in Y-shaped patterns. The wall is relatively thick and multi-layered. The inner wall is originally smooth, and the cross-section is circular to oval or polygonal at the outer wall due to discrete longitudinal ridges.

Occurrence.—Shibantan Member of Dengying Formation, Yichang City, China (Chen et al., 1981; Figs. 6–8); Dengying Formation of Shennongjia area of Hubei (Yang et al., 2020a) and South Shaanxi provinces (Chen and Sun, 2001; Chen et al., 2008; Cai et al., 2015, 2019), South China; Deep Spring Formation, Mount Dunfee, Nevada, USA (Mount et al., 1983, reported as *Salanytheca* sp.; Signor et al., 1983, reported as *Salanytheca* sp.); La Ciénega Formation, Sonora, Mexico (McMenamin, 1985; Signor et al., 1987; Sour-Tovar

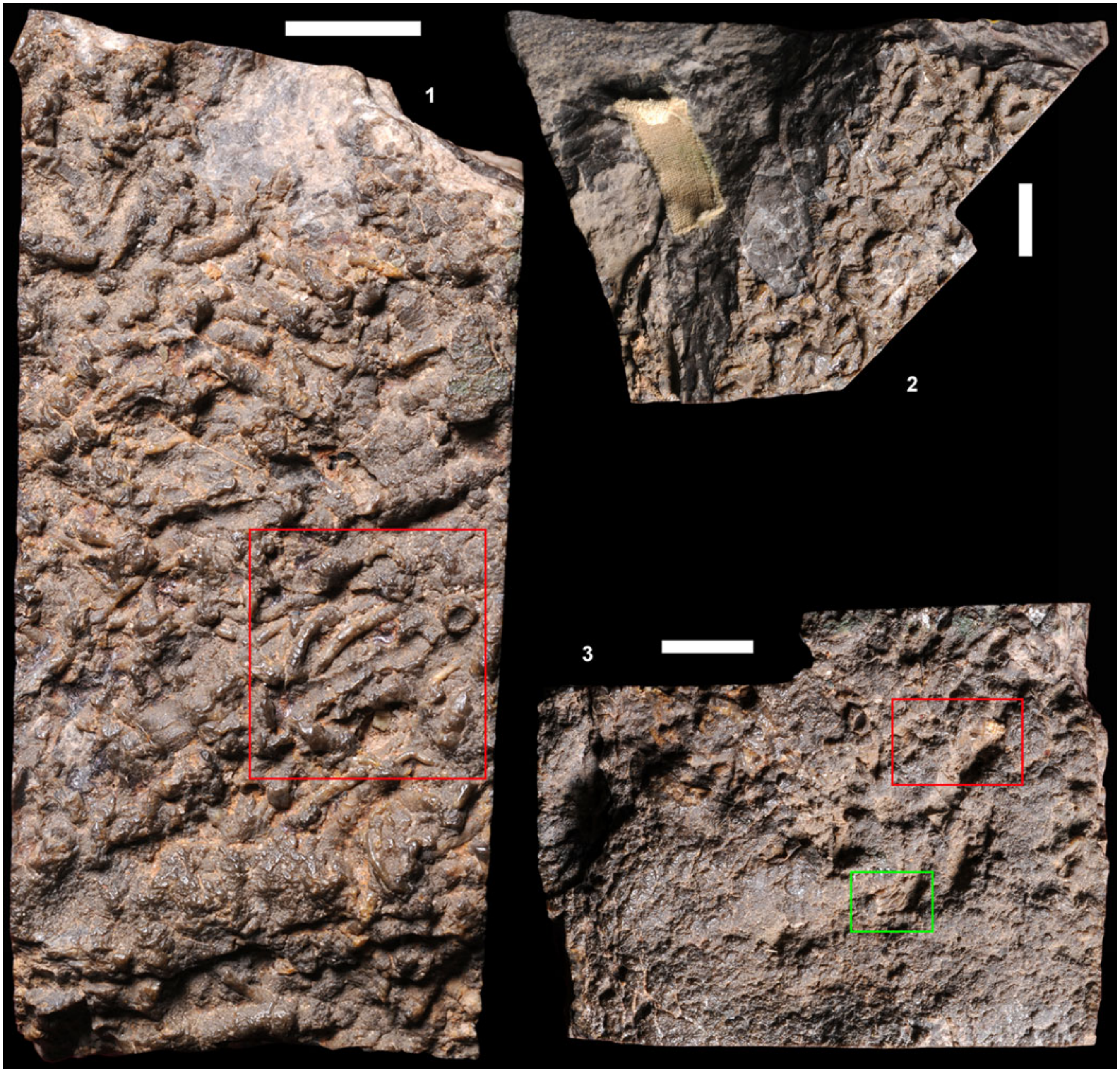

Figure 7. Specimens acquired from the previous type material (YG-96-1, Fig. 6) of *Sinotubulites baimatuoensis* Chen et al., 1981. The specimens contain *Cloudina hartmannae*: (**1**) smooth tubular fossils (**1, 2**) as well as *Sinotubulites baimatuoensis* Chen et al., 1981, (**3**). Scale bars are 1 cm. Specimens are deposited at the Geological Museum of China, Beijing, China.

et al., 2007, reported as silica-replaced cloudiniids); Villarta Limestone of Ibor Group, Villarta de los Montes village, Bada-joz Province, Spain (Cortijo et al., 2015b); Tamengo Formation, Corumbá Group, Mato Grosso do Sul State, Brazil (Hahn and Pflug, 1985, originally reported as *Cloudina waldei*); Mooifontein Member, Nama Group, Aar Farm, South Namibia (Fig. 9).

Description.—Straight or sinuous, nearly cylindrical tubular fossils with a length of 2–18 mm. Outer cross sections are round or irregularly polygonal. Inner wall is smooth, circular to oval in cross section. Tube surfaces are ornamented with regular or irregular rugae, or annulations, which are sometimes arranged in a Y-shape. Some of the specimens have longitudinal ridges, which are often developed along the entire length of tubes, but occasionally are interrupted. The tubes have a thick, irregularly corrugated multi-layered wall.

Remarks.—Abundant tubular fossils were reported from one silicified dolostone bed within the Shibantan Member of Dengying Formation of the Three Gorges Region and identified as *Cloudina*? sp. (Chen and Wang, 1977). The subsequent study (Chen et al., 1981) recognized morphological differences between these fossils and *Cloudina*,

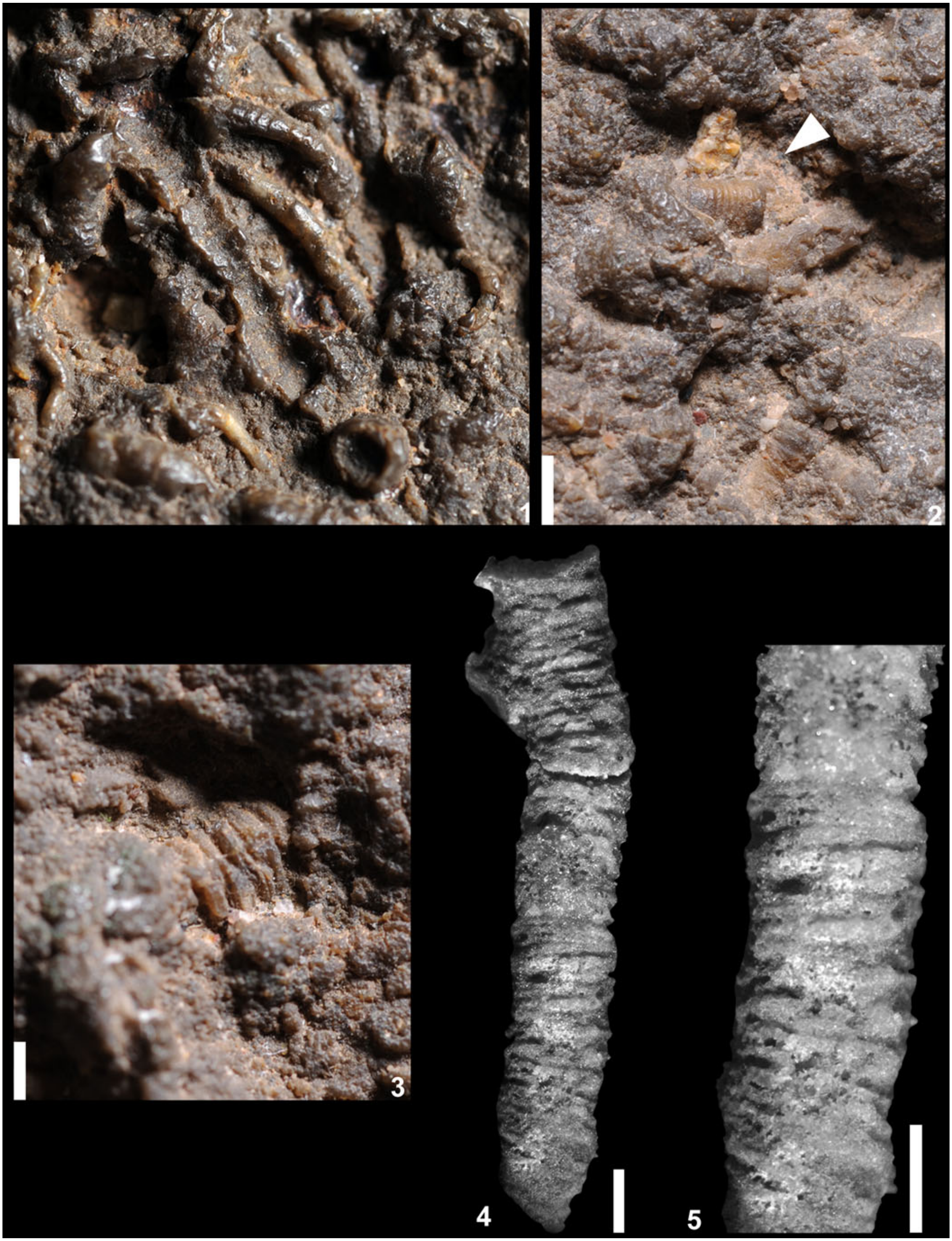
1
2
3
4
5

Figure 8. Detailed views of tubular fossils from the specimens shown in Figure 7. (**1**) Proximal view of *Cloudina hartmannae* and smooth tubular fossils (Fig. 7.1, red box, 90° clockwise rotation) with a coordinate of (6.6, 3.5; Fig. 6). (**2**) Proximal view of one paralectotype of *Sinotubulites baimatuoensis* Chen et al., 1981 (white arrow, red box in Fig. 7.3, rotated 90° counterclockwise) showing undeformed annulations. (**3**) Proximal view of one paralectotype of *Sinotubulites baimatuoensis* Chen et al., 1981 (green box in Fig. 7.3, 90° rotation counterclockwise) showing a longitudinal ridge; coordinate of (11.2, 4.6; Fig. 6). (**4**) Lectotype of *Sinotubulites baimatuoensis* Chen et al., 1981, YG-96-5. (**5**) Proximal view of (**4**) showing corrugated annulations on the surface. Scale bars: (**1–3**) 2 mm; (**4, 5**) 100 µm. Specimens are deposited at the Geological Museum of China, Beijing, China.

leading to the establishment of *Sinotubulites baimatuoensis*. Chen et al. (1981) described the hand-specimen "YG-96-1" (Fig. 6) containing multiple individuals as the genotype of *Sinotubulites*. This designation is invalid according to the regulation on genotype (ICZN, 1999). Therefore, all the described specimens of *S. baimatuoensis* presented in the study of Chen et al. (1981) are regarded as syntypes. The repository of the type materials was unknown for a long time, but recently, syntype materials of *Sinotubulites baimatuoensis* were recovered at the Geological Museum of China, allowing us to carry out a detailed re-examination (Figs. 7, 8). The rediscovered samples include the specimen "YG-96-5" (with part of it lost) and one small specimen preserved without numbering, as well as a rock slab "YG-96-1," which is heavily silicified, showing limited details of the fossils. Given the varied preservation of all these specimens, we designate the specimen "YG-96-5" as the lectotype and the previous neotype (Cai et al., 2015) is considered invalid (see ICZN, 1999, Article 75.8). Other existing type specimens are converted into paralectotypes. After its original documentation (Fig. 6, refigured from original photographs in Chen et al., 1981), the specimen "YG-96-1" rock slab was later sectioned into four pieces by the original authors, with one piece, unfortunately, now missing. Each of the remaining three parts contains several tubular fossils (Fig. 7). After a careful examination of the syntype sample, we were able to recognize three distinct morphotypes of tubes (sensu Chen et al., 1981) in the sample. One morphotype with typical collar structures can now be assigned to *Cloudina hartmannae* (Fig. 8.1). Another morphotype, with corrugations, ridges, and rings, is designated as *Sinotubulites baimatuoensis* (Fig. 8.2, 8.3). The last type, with a smooth tube surface, is considered as a steinkern or weathered specimen of unknown tubular fossils.

Cai et al. (2015) proposed new species of *Sinotubulites* based on different aperture shapes, including: *S. triangularis* Cai et al., 2015; *S. pentacarinalis* Cai et al., 2015; and *S. hexagonus* Cai et al., 2015. *Sinotubulites* tubes with only a single ridge developed and specimens with transitional characteristics have been mentioned (Cortijo et al., 2015b), raising doubts about how to distinguish between different *Sinotubulites* species. The formation of ridges and the morphology of the irregular aperture may have resulted from taphonomic effects. The lamellate walls of the tubes are irregularly corrugated, suggesting that they were once flexible and easily deformed, and might be considered as originally organic in composition. In addition, it has been suggested that *Corumbella* from South America resembles *Sinotubulites* and can be classified as a sinotubulitid due to morphological and ultrastructural similarities (Wood et al., 2017b; Walde et al., 2019). Detailed examination of the two taxa are necessary to test this hypothesis.

Previous studies provided inconclusive proposals for the biological affinities of *Sinotubulites*, with both Chen et al. (1981) and Chen and Sun (2001) tentatively suggesting a potential annelid affinity. On the other hand, there are differences between *Sinotubulites* and dwelling tubes of modern annelids (Chen et al., 2008). *Sinotubulites* is often found in association with *Cloudina*, and both are suspected to be originally of organic composition with multiple lamellae (Yang et al., 2020b). More studies on the lamellar structure and composition are required to understand phylogenetic affinity of *Sinotubulites*.

Phylum, Class, Order, Family uncertain
Genus *Conotubus* Zhang and Lin in Lin et al., 1986

Type species.—*Conotubus hemiannulatus* Zhang and Lin in Lin et al., 1986 from the Lower Member (fifth bed = Gaojiashan Member) of Gaojiashan Formation, Hujiaba Town, Ningqiang County, Shaanxi, China, by original designation.

Other species.—The type species only.

Diagnosis.—As for the type species by monotypy.

Conotubus hemiannulatus Zhang and Lin in Lin et al., 1986
Figure 10

1986	*Conotubus hemiannulatus* Zhang and Lin in Lin et al., p. 12, pl. 1, figs. 6, 10.
1986	*Conotubus hemiannulatus*; Zhang, p. 75, pl. 1, figs. 10, 13.
1986	*Conotubus gaojiashanensis* Zhang and Lin in Lin et al., p. 12, pl. 1, figs 3–5, 7.
1986	*Conotubus gaojiashanensis*; Zhang, p. 76, pl. 1, figs. 1, 3, 9.
1986	*Conotubus impolitus* Zhang and Lin in Lin et al., p. 12, pl. 1, figs. 1, 11.
1986	*Conotubus impolitus*; Zhang, p. 76, pl. 1, fig. 11.
1986	*Conotubus mimicus* Zhang and Lin in Lin et al., p. 12, pl. 1, figs. 2, 9a, pl. 2, fig. 9.
1986	*Conotubus mimicus*; Zhang, p. 76, pl. 1, fig. 6.
1986	*Conotubus hamatus* Zhang, p. 76, pl. 1, figs. 2, 4.
1986	*Conotubus cephalotus* Zhang, p. 77, pl. 1, fig. 7.
1986	*Conotubus adpressus* Zhang, p. 77, pl. 1, figs. 8, 14, pl. 2, fig. 7.
1986	*Conotubus* sp.; Zhang, p. 77, pl. 1, fig. 12.
1992	*Conotubus hemiannulatus*; Li et al., p. 91, pl. 11, figs. 9, 16, 18.
1992	*Conotubus gaojiashanensis*; Li et al., p. 91, pl. 11, fig. 13, pl. 12, figs. 1, 4.
1992	*Conotubus impolitus*; Li et al., p. 92, pl. 11, fig. 14.

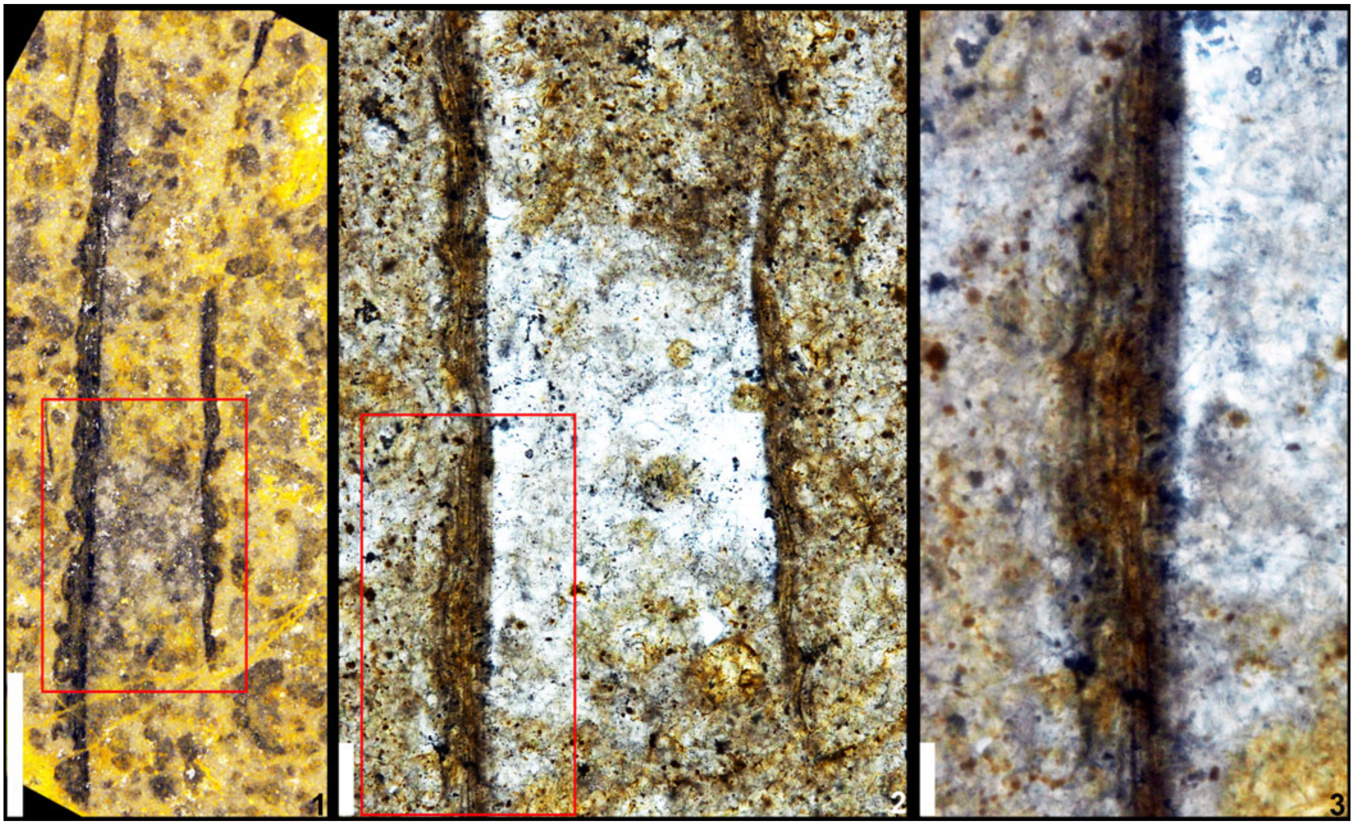

Figure 9. *Sinotubulites baimatuoensis* Chen et al., 1981, from the Mooifontein Member, Nama Group, Aar Farm, Namibia. (**1**) Longitudinal section showing corrugated shell surface, A1404; (**2**) magnified view (**1**, red box) revealing multi–layered shells; (**3**) magnified view (**2**, red box) showing the multilayers on the wall. Scale bars: (**1**) 500 μm; (**2**) 100 μm; (**3**) 50 μm. Specimens are deposited at the Institute of Geology, CAGS.

Figure 10. Lectotype of *Conotubus hemiannulatus* Zhang and Lin in Lin et al., 1986, V1–21. (**1**) General view of the lectotype showing strong and fine annulations; (**2**) lateral view of (**1**) revealing that the specimen has been compressed; (**3**) opposite view of (**1**) showing an uneven facet with no ridges or annulations preserved; (**4**) magnified view of (**1**, white arrow) showing the strong and fine annulations; (**5**) magnified view of the sectioned part of (**2**, white arrow) indicating a pyritized composition and unclear multilayer structure. Specimens are deposited at the Department of Geology, Northwest University, China. Scale bars: (**1–3**) 1 cm; (**4**) 2 mm; (**5**) 1 mm.

Figure 11. Paleogeographic reconstruction of Gondwana at ca. 541 Ma highlighting the distribution of *Cloudina hartmannae* Germs, 1972, *Sinotubulites baimatuoensis* Chen et al., 1987, and *Namacalathus hermanastes* Grotzinger et al., 2000. Base map is modified from Torsvik and Cocks (2013). Occurrences of *C. hartmannae* and *S. baimatuoensis* as given in the systematic description paragraphs; occurrences of *N. hermanastes* according to Penny et al. (2017) and Warren et al. (2017). Dashed line marks potential original outlines of Armorica microcontinent, of which only dispersed blocks remain.

1992 *Conotubus mimicus*; Li et al., p. 92, pl. 11, fig. 2, pl. 12, fig. 2.
1992 *Conotubus hamatus*; Li et al., p. 92, pl. 11, fig. 15.
1992 *Conotubus cephalotus*; Li et al., p. 93, pl. 12, fig. 10.
1992 *Conotubus adpressus*; Li et al., p. 93, pl. 12, figs. 3, 5, 6.
[non] 1992 *Conotubus varius* Zhang et al. in Li et al., p. 92, text-figs. 3–7, 8:9, pl. 9, figs. 3, 4, 6, 9.
2000 *Conotubus hemiannulatus*; Zhang and Hua, p. 329, pl. 1, fig. 8.
2000 *Conotubus* sp.; Zhang and Hua, p. 332, pl. 1, fig. 16.
2000b *Conotubus* sp.; Hua et al., p. 513, pl. 1, fig. 7a.
2007 *Conotubus hemiannulatus*; Cai and Hua, p. 647, fig. 1.
2007 *Conotubus* sp.; Cai and Hua, p. 648, fig. 3c.
2007 *Conotubus*; Hua et al., p. 269, figs. 5:1–5:3, 6:1, 6:2, 7:2, 7:3, 7:5, 8:2a.
2008 *Conotubus* sp.; Cai and Hua, p. 217, figs. 1G, H.
2010 *Conotubus*; Cai et al., p. 492, figs. 4B–F, 8A, B, 9A, 9C–J, 10A, B, 10G–I.
2011 *Conotubus hemiannulatus*; Cai et al., p. 49, figs. 5A, D, E, 6, 7.
[non] 2016 *Conotubus*; Smith et al., p. 913, figs. 3A, B.
2020b *Conotubus hemiannulatus*; Yang et al., p. 49, fig. 5C1.

Lectotype hereby designated.—V1-21 (Fig. 10; numbered as XG15 in Li et al., 1992, pl. 11, fig. 9), deposited at the Department of Geology, Northwest University, Xi'an, China.

Emended diagnosis.—Straight or curved tubular fossils decorated with corrugations and concentric annulations on the surface. The tube wall is composed of multiple layers with smooth inner wall. The cross section is oblate to round.

Occurrence.—Gaojiashan Member of the Dengying Formation, Ningqiang County, South Shaanxi, China (Lin et al., 1986; Li et al., 1992; Hua et al., 2007; Cai et al., 2011).

Description.—Oblate tapered tubes with a length of 40–80 mm and width of 4–10 mm. The fossils are slightly curved, with cross sections oblate or oval. The tubes show ridges and annulations on the surface, which are raised to the tapered end. The tube wall is composed of two or more laminae.

Remarks.—Conotubus hemiannulatus Zhang and Lin in Lin et al., 1986 was originally defined without a designation of holotype or paratype. Following ICZN (1999, Articles, 72.1.1, 73.2), the only two specimens of *Conotubus hemiannulatus* illustrated in the original publication became syntypes. The location of the two syntypes has been unknown for a long time. Here, we report one of these two syntypes from the collections of Northwest University, Xian, China, designating it as a lectotype. Based on characters such as prominent ridges and annulations of the lectotype, the specimens reported by Cai et al. (2011, figs. 3C, D) may not belong to *Conotubus*, but show a similarity to tubular fossils with collar structures (e.g., *Saarina* from Nevada; Selly et al., 2020; or possibly *Cloudina*). The cf. *Cloudina* sp. reported from the Wood Canyon Formation in the Death Valley region (Hagadorn and Waggoner, 2000) is probably comparable to the subsequently reported *Conotubus* from the same deposits (Smith et al., 2017), as well as the Deep Spring Formation of Mt. Dunfee, Nevada (Smith et al., 2016). Both of them resemble *Costatubus* Selly et al., 2020, *Saarina* Sokolov, 1965, and *Zuunia chimidtsereni* Yang et al., 2020b, in overall morphology as well as collar-structures.

The lectotype of *Conotubus* indicates a limonitic composition, likely resulting from diagenetic replacement of an original carbonaceous composition of tube walls. The premise for this assumption is that carbonaceous *Conotubus* has been reported from the Dengying Formation in South Shaanxi, China, and interpreted as precursor (ancestor) of *Cloudina* (Hua et al., 2007). Considering that *Cloudina* was interpreted as primarily organic in composition (Yang et al., 2020b), another interpretation about these carbonaceous specimens is that they may represent a taphomorph of *Cloudina* preserved without secondary mineralization. This potential interpretation generally calls for a further examination of the carbonaceous *Conotubus* from South Shaanxi.

Although Lin et al. (1986) suspected that *Conotubus* is related to annelids by comparing it with Cretaceous fossils *Diploconcha* Conrad, 1875, and *Longitubus* Howell, 1943, other studies considered it closely related to *Cloudina* (Hua et al., 2007; Cai et al., 2011), with an undetermined phylogenetic affinity. Thus, its phylogenetic affinity remains uncertain.

Discussion

Based on the detailed taxonomic description, we propose that the genus *Cloudina* consists of *Cloudina hartmannae* Germs, 1972, *Cloudina carinata*, Cortijo et al., 2010, and *Cloudina xuanjiangpingensis* Cai et al., 2017. We further suggest that the tubular remains in the type specimens of *Aulophycus lucianoi* may be compared to *Sinotubulites* or other taxa. Lectotypes of *Sinotubulites baimatuoensis* and *Conotubus hemiannulatus* are designated. *Cloudina waldei* from the Tamengo Formation, Corumbá Group in Southwest Brazil is tentatively assigned to *Sinotubulites baimatuoensis*. Moreover, *S. baimatuoensis* is reported from the Mooifontein Member of Nama Group in Aar Farm, Namibia.

Considering their narrow temporal range, broad spatial distribution, multiple taphomodes, and various sedimentary facies, Ediacaran tubular fossils have been proposed as index fossils for the late Ediacaran (Grant, 1990; Gaucher and Germs, 2009; Xiao et al., 2016; Adorno et al., 2017), although difficulties exist in biostratigraphic correlations because of their unresolved taxonomic status. Following the revision of the three taxa (*Cloudina*, *Sinotubulites*, and *Conotubus*), some of these tubular fossils are more acceptable for stratigraphic correlation and paleobiogeographic reconstruction (Fig. 11). The first appearance datum (FAD) of *Cloudina hartmannae* is considered approximately time-equivalent and has been applied as an index fossil for the late Ediacaran. Gaucher and Germs (2009) proposed a specific biozone based on the cloudinid appearances—the *Cloudina* Taxon Range Zone, ranging from >550–542 Ma for the Nama Group in Namibia, Ara Group in Oman, Corumbá Group in Brazil, and the Arroyo del Soldado Group in Uruguay. The coexistence of *Cloudina* with typical early Cambrian small shelly fossils, such as *Anabarites* and *Protohertzina* (Yang et al., 2016; Zhu et al., 2017; Cai et al., 2019), demonstrates that the taxon range zone extends to the early Cambrian. Later on, the *Cloudina-Namacalathus-Sinotubulites* Assemblage Zone (Zhu et al., 2017) was suggested, preceding the early Cambrian assemblage zone SSF I (*Anabarites trisulcatus-Protohertzina anabarica* Assemblage Zone). Also due to the range of *Cloudina* into early Cambrian strata, this assemblage zone requires a modification. Consequently, we redefine the terminal Ediacaran biozone as the *Cloudina hartmannae* Interval Zone based on species-level taxa. The zone is defined as the interval between the first appearance datum of *Cloudina hartmannae* and the first appearance datum of *Protohertzina anabarica* (i.e. the index fossil of the early Cambrian *Anabarites trisulcatus-Protohertzina anabarica* Assemblage Zone). The zone is also characterized by the co-occurrence of the species *Cloudina hartmannae*, *Sinotubulites baimatuoensis*, and *Namacalathus hermanastes* Grotzinger, Watters, and Knoll, 2000 (Warren et al., 2017). The age range of this biozone begins at ca. 550 Ma (Grotzinger et al., 1995) and ends at ca. 541 Ma, or 539 Ma with new data from Namibia (Linnemann et al., 2019). This zone is defined as an interval zone to avoid uncertainties with the range of Ediacaran tubular fossils into the Cambrian strata because there have been reports of the tubular fossils ranging into the basal Cambrian (Yang et al., 2016; Zhu et al., 2017; Cai et al., 2019). The definition of an interval zone must be seen as a compromise due to the rarity of other characteristic and widely distributed fauna in the Ediacaran, which might serve for a definition as an assemblage zone.

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.xgxd254hb.

References

Adorno, R.R., Carmo, D.A.d., Germs, G., Walde, D.H.G., Denezine, M., et al., 2017, *Cloudina lucianoi* (Beurlen & Sommer, 1957), Tamengo Formation, Ediacaran, Brazil: Taxonomy, analysis of stratigraphic distribution and biostratigraphy: Precambrian Research, v. 301, p. 19–35.

Adorno, R.R., Walde, D.H.G., Erdtmann, B.D., Denezine, M., Cortijo, I., Do Carmo, D.A., Giorgioni, M., Ramos, M.E.A.F., and Fazio, G., 2019, First occurrence of *Cloudina carinata* Cortijo et al., 2010 in South America, Tamengo Formation, Corumbá Group, upper Ediacaran of Midwestern: Estudios Geológicos, v. 75, e095. https://doi.org/10.3989/egeol.43587.550.

Becker-Kerber, B., and Pacheco, M.L.A.F., 2018, Comment on Adorno et al. (2017) "Cloudina lucianoi (Beurlen & Sommer, 1957), Tamengo Formation, Ediacaran, Brazil: Taxonomy, analysis of stratigraphic distribution and biostratigraphy": Precambrian Research, v. 317, p. 268–270.

Becker-Kerber, B., Pacheco, M.L.A.F., Rudnitzki, I.D., Galante, D., Rodrigues, F., and de Moraes Leme, J., 2017, Ecological interactions in *Cloudina* from the Ediacaran of Brazil: implications for the rise of animal biomineralization: Scientific Reports, v. 7, 5482. https://doi.org/10.1038/s41598-017-05753-8.

Becker-Kerber, B., da Silva, F.R., Borges Amorim, K., Liza Alves Forancelli Pacheco, M., and de Moraes Leme, J., 2019, Putting the cart before the horse: an example of how the lack of taphonomical approaches can mislead paleobiological inferences for the late Ediacaran: Precambrian Research, v. 332, 105385. https://doi.org/10.1016/j.precamres.2019.105385.

Bengtson, S., and Yue, Z., 1992, Predatorial borings in late Precambrian mineralized exoskeletons: Science, v. 257, p. 367–369.

Beurlen, K., and Sommer, F.W., 1957, Observac¸ões estratigráficas e paleontológicas sobreo calcário Corumbá: Boletim de Geologia e Mineralogia-DNPM, v. 168, p. 1–47.

Brain, C.K., 2001, Some observations on *Cloudina*, a terminal Proterozoic index fossil from Namibia: Journal of African Earth Sciences, v. 33, p. 475–480.

Cai, Y., and Hua, H., 2007, Pyritization in the Gaojiashan Biota: Chinese Science Bulletin, v. 52, p. 645–650.

Cai, Y., and Hua, H., 2008, Fossil diagenesis and weathering of pyritized fossils in the late Ediacaran Gaojiashan Biota in Ningqiang, Shaanxi: Acta Palaeontologica Sinica, v. 47, p. 214–221. [in Chinese with English abstract]

Cai, Y., Hua, H., Xiao, S., Schiffbauer, J.D., and Li, P., 2010, Biostratinomy of the late Ediacaran pyritized Gaojiashan Lagerstätte from southern Shaanxi, South China: importance of event deposits: Palaios, v. 25, p. 487–506.

Cai, Y., Schiffbauer, J.D., Hua, H., and Xiao, S., 2011, Morphology and paleoecology of the late Ediacaran tubular fossil *Conotubus hemiannulatus* from the Gaojiashan Lagerstätte of southern Shaanxi Province, South China: Precambrian Research, v. 191, p. 46–57.

Cai, Y., Hua, H., and Zhang, X., 2013, Tube construction and life mode of the late Ediacaran tubular fossil *Gaojiashania cyclus* from the Gaojiashan Lagerstätte: Precambrian Research, v. 224, p. 255–267.

Cai, Y., Xiao, S., Hua, H., and Yuan, X., 2015, New material of the biomineralizing tubular fossil *Sinotubulites* from the late Ediacaran Dengying Formation, South China: Precambrian Research, v. 261, p. 12–24.

Cai, Y., Cortijo, I., Schiffbauer, J.D., and Hua, H., 2017, Taxonomy of the late Ediacaran index fossil *Cloudina* and a new similar taxon from South China: Precambrian Research, v. 298, p. 146–156.

Cai, Y., Xiao, S., Li, G., and Hua, H., 2019, Diverse biomineralizing animals in the terminal Ediacaran Period herald the Cambrian explosion: Geology, v. 47, p. 380–384.

Chen, M., and Wang, Y., 1977, Tubular animal fossils in the middle Denying Formation, upper Sinian, East Yangtze Gorge: Chinese Science Bulletin, v. 4–5, p. 219–221. [in Chinese]

Chen, M., Chen, Y., and Qian, Y., 1981, Some tubular fossils from Sinian–lower Cambrian boundary sequences, Yangtze Gorge: Bulletin of the Tianjin Institute of Geology and Mineral Resources, v. 3, p. 117–124. [in Chinese with English abstract]

Chen, X., Zhou, P., Zhang, B., Wei, K., and Zhang, M., 2016, Lithostratigraphy, biostratigraphy, sequence stratigraphy and carbon isotope chemostratigraphy of the upper Ediacarian in Yangtze Gorges and their significance for chronostratigraphy: Geology and Mineral Resources of South China, v. 32, p. 87–105. [in Chinese with English abstract]

Chen, Z., and Sun, W., 2001, Late Sinian (tubular) metazoan fossils: *Cloudina* and *Sinotubulites* from southern Shaanxi: Acta Micropalaeontologica Sinica, v. 18, p. 180–202. [in Chinese with English summary]

Chen, Z., Bengtson, S., Zhou, C.M., Hua, H., and Yue, Z., 2008, Tube structure and original composition of *Sinotubulites*: shelly fossils from the late Neoproterozoic in southern Shaanxi, China: Lethaia, v. 41, p. 37–45.

Conrad, T., 1875, Descriptions of New Genera and Species of Fossil Shells of North Carolina: Appendix, *in* Kerr, W.C., ed., Report of the Geological Survey of North Carolina: Raleigh, Josiah Turner, 12 p.

Conway Morris, S., Mattes, B., and Chen, M., 1990, The early skeletal organism *Cloudina*: new occurrences from Oman and possibly China: American Journal of Science, v. 290, p. 245–260.

Cortijo, I., Martí Mus, M., Jensen, S., and Palacios, T., 2010, A new species of *Cloudina* from the terminal Ediacaran of Spain: Precambrian Research, v. 176, p. 1–10.

Cortijo, I., Cai, Y., Hua, H., Schiffbauer, J.D., and Xiao, S., 2015a, Life history and autecology of an Ediacaran index fossil: development and dispersal of *Cloudina*: Gondwana Research, v. 28, p. 419–424.

Cortijo, I., Martí Mus, M., Jensen, S., and Palacios, T., 2015b, Late Ediacaran skeletal body fossil assemblage from the Navalpino anticline, central Spain: Precambrian Research, v. 267, p. 186–195.

Ding, Q., Xing, Y., Wang, Z., Yin, C., and Gao, L., 1993, Tubular and trace fossils from the Sinian Dengying Formation in the Miaohe-Liantuo area, Hubei Province: Geological Review, v. 39, p. 118–123.

Gaucher, C., and Germs, G.J.B., 2009, Skeletonised metazoans and protists, *in* Gaucher, C., Sial, A.N., Halverson, G.P., and Frimmel, H.E., eds., Neoproterozoic–Cambrian Tectonics, Global Change and Evolution: A Focus on Southwestern Gondwana: Amsterdam, Elsevier, p. 327–338.

Gaucher, C., Boggiani, P., Sprechmann, P., Sial, A., and Fairchild, T., 2003, Integrated correlation of the Vendian to Cambrian Arroyo del Soldado and Corumbá groups (Uruguay and Brazil): palaeogeographic, palaeoclimatic and palaeobiologic implications: Precambrian Research, v. 120, p. 241–278.

Germs, G., 1972, New shelly fossils from Nama Group, South West Africa: American Journal of Science, v. 272, p. 752–761.

Germs, G.J.B., 1983, Implications of a sedimentary facies and depositional environmental analysis of the Nama Group in South West Africa/Namibia: Geological Society of South Africa, v. 11, p. 89–114.

Germs, G.J.B., 1995, The Neoproterozoic of southwestern Africa, with emphasis on platform stratigraphy and paleontology: Precambrian Research, v. 73, p. 137–151.

Glaessner, M., 1976, Early Phanerozoic annelid worms and their geological and biological significance: Journal of the Geological Society, v. 132, p. 259–275.

Grant, S., 1990, Shell structure and distribution of *Cloudina*, a potential index fossil for the terminal Proterozoic: American Journal of Science, v. 290-A, p. 261–294.

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

Grotzinger, J.P., Watters, W.A., and Knoll, A.H., 2000, Calcified metazoans in thrombolite-stromatolite reefs of the terminal Proterozoic Nama Group, Namibia: Paleobiology, v. 26, p. 334–359.

Hagadorn, J.W., and Waggoner, B., 2000, Ediacaran fossils from the southwestern Great Basin, United States: Journal of Paleontology, v. 74, p. 349–359.

Hahn, G., and Pflug, H., 1985, Die Cloudinidae n. fam., Kalk-Röhren aus dem Vendium und Unter-Kambrium: Senckenbergiana Lethaea, v. 65, p. 413–431.

Han, J., Cai, Y., Schiffbauer, J.D., Hua, H., Wang, X., Yang, X., Uesugi, K., Komiya, T., and Sun, J., 2017, A *Cloudina*-like fossil with evidence of asexual reproduction from the lowest Cambrian, South China: Geological Magazine, v. 154, p. 1294–1305.

Hodgin, E.B., Nelson, L.L., Wall, C.J., Barrón-Díaz, A.J., Webb, L.C., Schmitz, M.D., Fike, D.A., Hagadorn, J.W., and Smith, E.F., 2020, A link between rift-related volcanism and end-Ediacaran extinction? Integrated chemostratigraphy, biostratigraphy, and U-Pb geochronology from Sonora, Mexico: Geology, v. 49, p. 115–119.

Hofmann, H.J., and Mountjoy, E.W., 2001, *Namacalathus-Cloudina a*ssemblage in Neoproterozoic Miette Group (Byng Formation), British Columbia: Canada's oldest shelly fossils: Geology, v. 29, p. 1091–1094.

Howell, B.F., 1943, *Hamulus*, "*Falcula*," and Other Cretaceous Tubicola of New Jersey: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 95, p. 139–166.

Hua, H., Zhang, L., Zhang, Z., and Wang, J., 2000a, New fossil evidences from latest Neoproterozoic Gaojiashan Biota, South Shaanxi: Acta Palaeontologica Sinica, v. 39, p. 381–390. [in Chinese with English summary].

Hua, H., Zhang, L., Zhang, Z., and Wang, J., 2000b, Fossil evidences of latest Neoproterozoic Gaojiashan Biota and their characteristics: Acta Palaeontologica Sinica, v. 39, p. 507–515.

Hua, H., Pratt, B.R., and Zhang, L., 2003a, Borings in *Cloudina* shells: complex predator-prey dynamics in the terminal Neoproterozoic: Palaios, v. 18, p. 454–459.

Hua, H., Zhang, L., and Chen, Z., 2003b, Microbially mediated phosphatization in the late Sinian skeletal fossils, southern Shaanxi: Acta Palaeontologica Sinica, v. 42, p. 189–199. [in Chinese with English summary].

Hua, H., Chen, Z., Yuan, X., Zhang, L., and Xiao, S., 2005, Skeletogenesis and asexual reproduction in the earliest biomineralizing animal *Cloudina*: Geology, v. 33, p. 277–280.

Hua, H., Chen, Z., and Yuan, X., 2007, The advent of mineralized skeletons in Neoproterozoic Metazoa—new fossil evidence from the Gaojiashan Fauna: Geological Journal, v. 42, p. 263–279.

ICZN, 1999, International Code of Zoological Nomenclature, 4th Edition: London, International Trust for Zoological Nomenclature, 306 p.

Kontorovich, A.E., Varlamov, A.I., Grazhdankin, D.V., Karlova, G.A., Klets, A.G., et al., 2008, A section of Vendian in the east of West Siberian Plate (based on data from the Borehole Vostok 3): Russian Geology and Geophysics, v. 49, p. 932–939.

Li, Y., Ding, L., Zhang, l., Dong, J., and Chen, H., 1992, Description of fossils, *in* Ding, L., Zhang, l., Li, Y., and Dong, J., eds., The study of the late Sinian–early Cambrian biota from the northern margin of Yangtze Platform: Beijing, Scientific and Technical Documents Publishing House, p. 80–112.

Liang, D., Cai, Y., Nolan, M., and Xiao, S., 2020, The terminal Ediacaran tubular fossil *Cloudina* in the Yangtze Gorges area of South China: Precambrian Research, v. 351, 105931. https://doi.org/10.1016/j.precamres.2020.105931.

Lin, S., Zhang, Y., Tao, X., Wang, M., and Zhang, L., 1986, Body and trace fossils of Metazoa and algal macrofossils from the upper Sinian Gaojiashan Formation in southern Shaanxi: Geology of Shaanxi, v. 4, p. 9–17.

Linnemann, U., Ovtcharova, M., Schaltegger, U., Gärtner, A., Hautmann, M., et al., 2019, New high-resolution age data from the Ediacaran-Cambrian boundary indicate rapid, ecologically driven onset of the Cambrian explosion: Terra Nova, v. 31, p. 49–58.

McMenamin, M.A.S., 1985, Basal Cambrian small shelly fossils from the La Ciénega Formation, northwestern Sonora, Mexico: Journal of Paleontology, v. 59, p. 1414–1425.

Mehra, A., and Maloof, A., 2018, Multiscale approach reveals that *Cloudina* aggregates are detritus and not in situ reef constructions: Proceedings of the National academy of Sciences, v. 115, p. E2519–E2527.

Min, X., Hong, H., Yaoping, C., and Bo, S., 2019a, Asexual reproduction of tubular fossils in the terminal Neoproterozoic Dengying Formation, South China: Precambrian Research, v. 322, p. 18–23.

Min, X., Hua, H., Liu, L., Sun, B., Cui, Z., and Jiang, T., 2019b, Phosphatized *Epiphyton* from the terminal Neoproterozoic and its significance: Precambrian Research, v. 331, 105358. https://doi.org/10.1016/j.precamres.2019.105358.

Mount, J.F., Gevirtzman, D.A., and Signer, P.W., III, 1983, Precambrian–Cambrian transition problem in western North America: Part I. Tommotian fauna in the southwestern Great Basin and its implications for the base of the Cambrian System: Geology, v. 11, p. 224–226.

Pacheco, M.L., Leme, J., and Machado, A., 2011, Taphonomic analysis and geometric modelling for the reconstitution of the Ediacaran metazoan *Corumbella werneri* Hahn et al. 1982 (Tamengo Formation, Corumbá Basin, Brazil): Journal of Taphonomy, v. 9, p. 269–283.

Penny, A.M., Wood, R., Curtis, A., Bowyer, F., Tostevin, R., and Hoffman, K.H., 2014, Ediacaran metazoan reefs from the Nama Group, Namibia: Science, v. 344, p. 1504–1506.

Penny, A.M., Wood, R.A., Zhuravlev, A.Y., Curtis, A., Bowyer, F., and Tostevin, R., 2017, Intraspecific variation in an Ediacaran skeletal metazoan: *Namacalathus* from the Nama Group, Namibia: Geobiology, v. 15, p. 81–93.

Pruss, S.B., Blättler, C.L., Macdonald, F.A., and Higgins, J.A., 2018, Calcium isotope evidence that the earliest metazoan biomineralizers formed aragonite shells: Geology, v. 46, p. 763–766.

Schiffbauer, J.D., Selly, T., Jacquet, S.M., Merz, R.A., Nelson, L.L., Strange, M.A., Cai, Y., and Smith, E.F., 2020, Discovery of bilaterian-type throughguts in cloudinomorphs from the terminal Ediacaran Period: Nature Communications, v. 11, 205. https://doi.org/10.1038/s41467-019-13882-z.

Selly, T., Schiffbauer, J.D., Jacquet, S.M., Smith, E.F., Nelson, L.L., et al., 2020, A new cloudinid fossil assemblage from the terminal Ediacaran of Nevada, USA: Journal of Systematic Palaeontology, v. 18, p. 357–379.

Shore, A., and Wood, R., 2021, Environmental and diagenetic controls on the morphology and calcification of the Ediacaran metazoan *Cloudina*: Scientific Reports, v. 11, 12341. https://doi.org/10.1038/s41598-021-90768-5.

Shore, A., Wood, R., Curtis, A., and Bowyer, F., 2020, Multiple branching and attachment structures in cloudinomorphs, Nama Group, Namibia: Geology, v. 48, p. 877–881.

Signor, P.W., McMenamin, M.A.S., Gevirtzman, D.A., and Mount, J.F., 1983, Two new pre-trilobite faunas from western North America: Nature, v. 303, p. 415–418.

Signor, P.W., Mount, J.F., and Onken, B.R., 1987, A pre-trilobite shelly fauna from the White-Inyo region of eastern California and western Nevada: Journal of Paleontology, v. 61, p. 425–438.

Smith, E.F., Nelson, L.L., Strange, M.A., Eyster, A.E., Rowland, S.M., Schrag, D.P., and Macdonald, F.A., 2016, The end of the Ediacaran: two new exceptionally preserved body fossil assemblages from Mount Dunfee, Nevada, USA: Geology, v. 44, p. 911–914.

Smith, E.F., Nelson, L.L., Tweedt, S.M., Zeng, H., and Workman, J.B., 2017, A cosmopolitan late Ediacaran biotic assemblage: new fossils from Nevada and Namibia support a global biostratigraphic link: Proceedings of the Royal Society B: Biological Sciences, v. 284, 20170934. https://doi.org/10.1098/rspb.2017.0934.

Sokolov, B.S., 1965, The most ancient early Cambrian deposits and sabelliditids, *in* Sokolov, B.S., ed., All-Union Symposium on Paleontology of Precambrian and Early Cambrian: Novosibirsk, Akad Nauk SSSR, p. 78–91. [in Russian]

Sour-Tovar, F., Hagadorn, J.W., and Huitrón-Rubio, T., 2007, Ediacaran and Cambrian index fossils from Sonora, Mexico: Palaeontology, v. 50, p. 169–175.

Steiner, M., Li, G., Qian, Y., Zhu, M., and Erdtmann, B.D., 2007, Neoproterozoic to early Cambrian small shelly fossil assemblages and a revised biostratigraphic correlation of the Yangtze Platform (China): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 254, p. 67–99.

Sun, B., Hua, H., and Cai, Y., 2012, Morphology and palaeoecology of the late Ediacaran tubular fossil *Sinotubulites*: Acta Palaeontologica Sinica, v. 51, p. 107–113.

Taylor, M.E., 1966, Precambrian mollusc-like fossils from Inyo County, California: Science, v. 153, p. 198–201.

Terleev, A.A., Postnikov, A.A., Tokarev, D.A., Sosnovskaya, O.V., and Bagmet, G.N., 2011, *Cloudina-Namacalathus-Korilophyton* association in the Vendian of the Altay-Sayan Foldbelt (Siberia), *in* Neoproterozoic Sedimentary Basins: Stratigraphy, Feodynamics and Petroleum Potential: Proceedings of the International Conference (Novosibirsk, 30 July–02 August, 2011), p. 96–98.

Torsvik, T.H., and Cocks, L.R.M., 2013, New global palaeogeographical reconstructions for the early Palaeozoic and their generation, *in* Harper, D.A.T., and Servais, T., eds., Early Palaeozoic Biogeography and Palaeogeography: Geological Society, London, Memoirs, v. 38, p. 5–24.

Vinn, O., and Zatoń, M., 2012, Inconsistencies in proposed annelid affinities of early biomineralized organism *Cloudina* (Ediacaran): structural and ontogenetic evidences: Carnets de Géologie, v. 2012/03 (CG2012_A03), p. 39–47.

Walde, D.H.G., do Carmo, D.A., Guimarães, E.M., Vieira, L.C., Erdtmann, B.-D., Sanchez, E.A.M, Adorno, R.R., and Tobias, T.C., 2015, New aspects of Neoproterozoic–Cambrian transition in the Corumbá region (state of Mato Grosso do Sul, Brazil): Annales de Paléontologie, v. 101, p. 213–224.

Walde, D.H.-G., Weber, B., Erdtmann, B.-D., and Steiner, M., 2019, Taphonomy of *Corumbella werneri* from the Ediacaran of Brazil: sinotubulitid tube or conulariid test?: Alcheringa, v. 43, p. 335–350.

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

Warren, L., Pacheco, M., Fairchild, T.R., Simões, M., Riccomini, C., Boggiani, P.C., and Cáceres, A.A., 2012, The dawn of animal skeletogenesis: ultrastructural analysis of the Ediacaran metazoan *Corumbella werneri*: Geology, v. 40, p. 691–694.

Warren, L.V., Quaglio, F., Riccomini, C., Simões, M.G., Poiré, D.G., Stríkis, N.M., Anelli, L.E., and Strikis, P.C., 2014, The puzzle assembled: Ediacaran guide fossil *Cloudina* reveals an old proto-Gondwana seaway: Geology, v. 42, p. 391–394.

Warren, L.V., Quaglio, F., Simões, M.G., Gaucher, C., Riccomini, C., Poiré, D.G., Freitas, B.T., Boggiani, P.C., and Sial, A.N., 2017, -*Cloudina-Corumbella-Namacalathus* association from the Itapucumi Group, Paraguay: increasing ecosystem complexity and tiering at the end of the Ediacaran: Precambrian Research, v. 298, p. 79–87.

Wood, R., 2018, Exploring the drivers of early biomineralization: Emerging Topics in Life Sciences, v. 2, p. 201–212.

Wood, R., Curtis, A., Penny, A., Zhuravlev, A.Y., Curtis-Walcott, S., Iipinge, S., and Bowyer, F., 2017a, Flexible and responsive growth strategy of the Ediacaran skeletal *Cloudina* from the Nama Group, Namibia: Geology, v. 45, p. 259–262.

Wood, R., Ivantsov, A.Y., and Zhuravlev, A.Y., 2017b, First macrobiota biomineralization was environmentally triggered: Proceedings of the Royal Society B: Biological Sciences, v. 284, 20170059. https://doi.org/10.1098/rspb.2017.0059.

Wood, R.A., Zhuravlev, A.Y., Sukhov, S.S., Zhu, M., and Zhao, F., 2017c, Demise of Ediacaran dolomitic seas marks widespread biomineralization on the Siberian Platform: Geology, v. 45, p. 27–30.

Xiao, S., Narbonne, G.M., Zhou, C., Laflamme, M., Grazhdankin, D.V., Moczydlowska-Vidal, M., and Cui, H., 2016, Toward an Ediacaran time scale: problems, protocols, and prospects: Episodes, v. 39, p. 540–555.

Yang, B., Steiner, M., Zhu, M., Li, G., Liu, J., and Liu, P., 2016, Transitional Ediacaran–Cambrian small skeletal fossil assemblages from South China and Kazakhstan: implications for chronostratigraphy and metazoan evolution: Precambrian Research, v. 285, p. 202–215.

Yang, B., Shang, X., Steiner, M., and Liu, P., 2020a, Ediacaran tubular fossils from the Shennongjia area, Hubei Province and their stratigraphic significance: Journal of Stratigraphy, v. 44, p. 448–454. [in Chinese with English abstract]

Yang, B., Steiner, M., Schiffbauer, J.D., Selly, T., Wu, X., Zhang, C. and Liu, P., 2020b, Ultrastructure of Ediacaran cloudinids suggests diverse taphonomic histories and affinities with non-biomineralized annelids: Scientific Reports, v. 10, 535. https://doi.org/10.1038/s41598-019-56317-x.

Yochelson, E.L., and Herrera, H.E., 1974, Un fossil enigmatico del Cambrico Inferior de Argentina: Ameghiniana, v. 11, p. 283–294.

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

Zaine, M.F., and Fairchild, T.R., 1987, Novas considerações sobre os fósseis da Formação Tamengo, Grupo Corumbá, SW do Brasil: X Congresso Brasileiro de Paleontologia, Rio de Janeiro, 19–25 Juhlo, 1987, p. 797–807.

Zhang, L., 1986, A discovery and preliminary study of the late stage of late Gaojiashan biota from Sinian in Ningqiang County, Shaanxi: Bulletin of the Xi'an Institute of Geology and Mineral Resources, Chinese Academy of Geological Sciences, v. 13, p. 67–88. [in Chinese with English abstract]

Zhang, L., and Hua, H., 2000, Late Sinian tubular shell fossils and their significance: Acta Palaeontologica Sinica, v. 39, p. 326–333. [in Chinese with English summary]

Zhu, M., Zhuravlev, A.Y., Wood, R.A., Zhao, F., and Sukhov, S.S., 2017, A deep root for the Cambrian explosion: implications of new bio- and chemostratigraphy from the Siberian Platform: Geology, v. 45, p. 459–462.

Zhuravlev, A.Y., Linan, E., Vintaned, J.A.G., Debrenne, F., and Fedorov, A.B., 2012, New finds of skeletal fossils in the terminal Neoproterozoic of the Siberian Platform and Spain: Acta Palaeontologica Polonica, v. 57, p. 205–224.

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