New Finds of Skeletal Fossils in the Terminal Neoproterozoic of the Siberian Platform and Spain

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New finds of skeletal fossils in the terminal Neoproterozoic of the Siberian Platform and Spain

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A current paradigm accepts the presence of weakly biomineralized animals only, barely above a low metazoan grade of organization in the terminal Neoproterozoic (Ediacaran), and a later, early Cambrian burst of well skeletonized animals. Here we report new assemblages of primarily calcareous shelly fossils from upper Ediacaran (553–542 Ma) carbonates of Spain and Russia (Siberian Platform). The problematic organism *Cloudina* is found in the Yudoma Group of the southeastern Siberian Platform and different skeletal taxa have been discovered in the terminal Neoproterozoic of several provinces of Spain. New data on the morphology and microstructure of Ediacaran skeletal fossils *Cloudina* and *Namacalathus* indicate that the Neoproterozoic skeletal organisms were already reasonably advanced. In total, at least 15 skeletal metazoan genera are recorded worldwide within this interval. This number is comparable with that known for the basal early Cambrian. These data reveal that the terminal Neoproterozoic skeletal bloom was a real precursor of the Cambrian radiation. *Cloudina*, the oldest animal with a mineralised skeleton on the Siberian Platform, characterises the uppermost Ediacaran strata of the Ust'-Yudoma Formation. While in Siberia *Cloudina* co-occurs with small skeletal fossils of Cambrian aspect, in Spain *Cloudina*-bearing carbonates and other Ediacaran skeletal fossils alternate with strata containing rich terminal Neoproterozoic trace fossil assemblages. These finds treated together provide a possibility to correlate transitional Neoproterozoic–lower Cambrian strata around the world. Such a correlation concurs with available isotope and radiometric data and indicates that typical Ediacaran shelly fossils have not crossed the Precambrian–Cambrian boundary.

Key words: *Cloudina*, Ediacaran skeletal fossils, microstructure, extinction, Siberian Platform, Spain.

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Introduction

Several paradigms for the "Cambrian explosion" succeeded each other during the second half of the last century, from a complete refutation of any metazoan occurrence in the terminal Neoproterozoic, through an acceptance of soft-bodied multicellular organisms (vendobionts), to the recognition of true skeletonised metazoans. The first such skeletonised metazoans were described and figured as early as 1960 (Vologdin and Maslov 1960). However, *Cloudina* was the only well-known skeletal fossil from Ediacaran strata.

The situation changed at the beginning of the present century. New goblet-shaped (*Namacalathus*), coral-like (*Namapoikia*) and unnamed conical skeletal fossils were described from Namibia (Grotzinger et al. 2000; Wood et al. 2002), and a new and unusual cloudinid was discovered in central Spain (Cortijo et al. 2006, 2010). In addition, Ediacaran skeletal assemblages from China were redescribed in details and the identity of *Sinotubulites* and "*Chenella*" (the generic name itself is preoccupied) as skeletal fossils was confirmed (Hua et al. 2000a, b, 2005a; Chen et al. 2008).

Nonetheless, an understanding of Ediacaran being skeletal fossils as remains of weakly biomineralised animals only barely above a low metazoan grade of organisation, remained widespread in the scientific literature (e.g., Knoll 2003; Budd and Jensen 2004; Steiner et al. 2007; Brasier et al. 2011). Indeed, among four genera previously recognised in Ediacaran strata, i.e., *Cloudina*, *Sinotubulites*, *Namacalathus*, and *Namapoikia*, only the latter is described as a fossil possessing thick skeleton, albeit only of a cnidarian or poriferan grade of organisation.

Here we report new occurrences of skeletal fossils in upper

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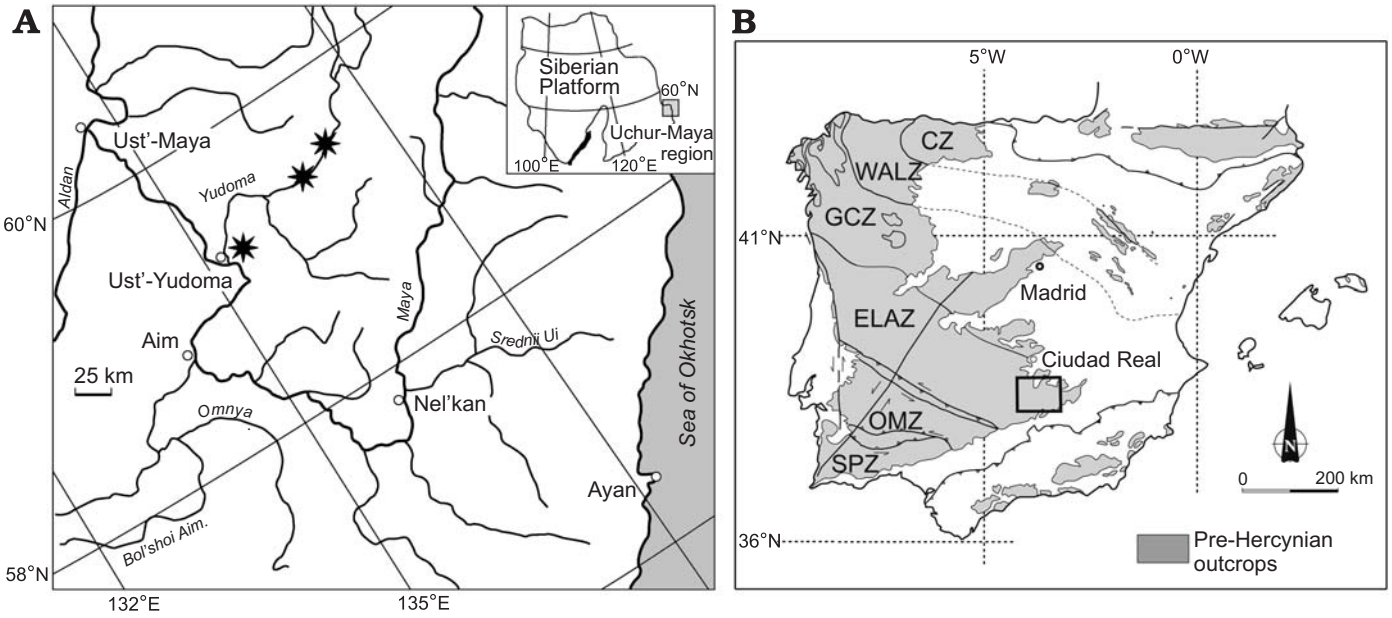

Fig. 1. Maps indicating studied localities. **A**. Map of Uchur-Maya region showing reference sections of the Yudoma River: 1, Nuuchchalakh; 2, Kyyry-Ytyga; 3, Ust'-Yudoma (*Suvorovella* and *Majaella* locality). Inset map indicates location within Siberian Platform. **B**. Pre-Hercynian outcrops and tectonostratigraphic zones of Iberian Peninsula. Valdelacasa, Ibor, Navalpino, and Abenójar anticlines are outlined. Zones: CZ, Cantabrian; ELAZ, East Lusitanian–Alcudian; GCZ, Galician–Castilian; OMZ, Ossa-Morena; SPZ South Portuguese; WALZ, West Asturian-Leonese.

Ediacaran carbonates of the Siberian Platform and Spain. These finds extend the record of the Ediacaran biomineralised taxa and increase the importance of such fossils as *Cloudina*, *Sinotubulites*, and *Chenmengella* (replacement name for *Chenella*) for subdivision and global correlation of Ediacaran strata as well as for understanding of evolutionary events during the terminal Neoproterozoic–Cambrian interval. Besides, the study of microstructure of *Cloudina* and *Namacalathus* specimens collected in their type localities from Namibia as well as on the Siberian Platform, in Spain, Oman, and Brazil, provides some innovative explanations for their biological affinities and for challenging re-evaluation of the Ediacaran skeletal world as a whole which was already comparatively diverse and derived by the end of this period.

Institutional abbreviations.—MPZ, Museo Paleontológico de la Universidad de Zaragoza, Spain; MNHN, Muséum Nationale d'Histoire Naturelle, Paris, France; PIN, Palaeontological Institute, Russian Academy of Sciences; SNIIGGiMS, Siberian Scientific-Researching Institute of Geology, Geophysics and Mineral Resources, Novosibirsk, Russia.

Occurrences of Ediacaran skeletal fossils on the Siberian Platform and in Spain

Siberian Platform.—The body fossils were poorly known in the terminal Neoproterozoic of the Siberian Platform. Among them should be noted problematic *Suvorovella* and *Majaella* from the Ust'-Yudoma Formation of the Maya River in the Uchur-Maya region (Vologdin and Maslov 1960), the Ediacaran fauna of the Khatyspyt Formation on the Olenëk Uplift (Sokolov 1985; Grazhdankin et al. 2008), and the problematic tubicolous *Cambrotubulus* from the Turkut Formation of the same region (Karlova 1987). Commonly, fragments of *Suvorovella* and *Majaella* from the Uchur-Maya region were erroneously referred to *Medusinites* and *Cyclomedusa* ex gr. *C. plana* Glaessner and Wade (Khomentovsky and Karlova 1993, 1994, 2002).

The Yudoma River transects the Uchur-Maya region forming the southeastern margin of the Siberian Platform (Fig. 1A). Here, in cliffs of the right Yudoma River bank about Nuuchchalakh Valley (opposite the Kurus Island) and 1.6 km downstream of the Ulakhan-Ytyga River mouth (the Kyyry-Ytyga Creek), key sections of the Yudoma Group outcrop (Semikhatov et al. 1970). The Yudoma Group unconformably overlies bluish-green thin-bedded fine-grained sandstone and siltstone of the Cryogenian Ust'-Kirbi Formation. Downstream, the Yudoma Group is conformably overlain by greenish- and rose-grey mudstone and wackestone of the Cambrian Pestrotsvet Formation. The Yudoma Group was subdivided in these sections by Semikhatov et al. (1970) into intervals 1 to 11 of a total thicknes of ca. 320 m (Fig. 2D). Of those strata, intervals 1 to 7 are represented mostly by various layers of sandstone and siltstone interbedded with subdued dolostone while intervals 8 to 11 encompass mostly dolostone beds.

According to Semikhatov et al. (1970), intervals 1–8 comprise the Lower Yudoma Subformation of the Yudoma Formation, whereas intervals 9–11 represent its Upper Yudoma Subformation. Khomentovsky et al. (1972) placed

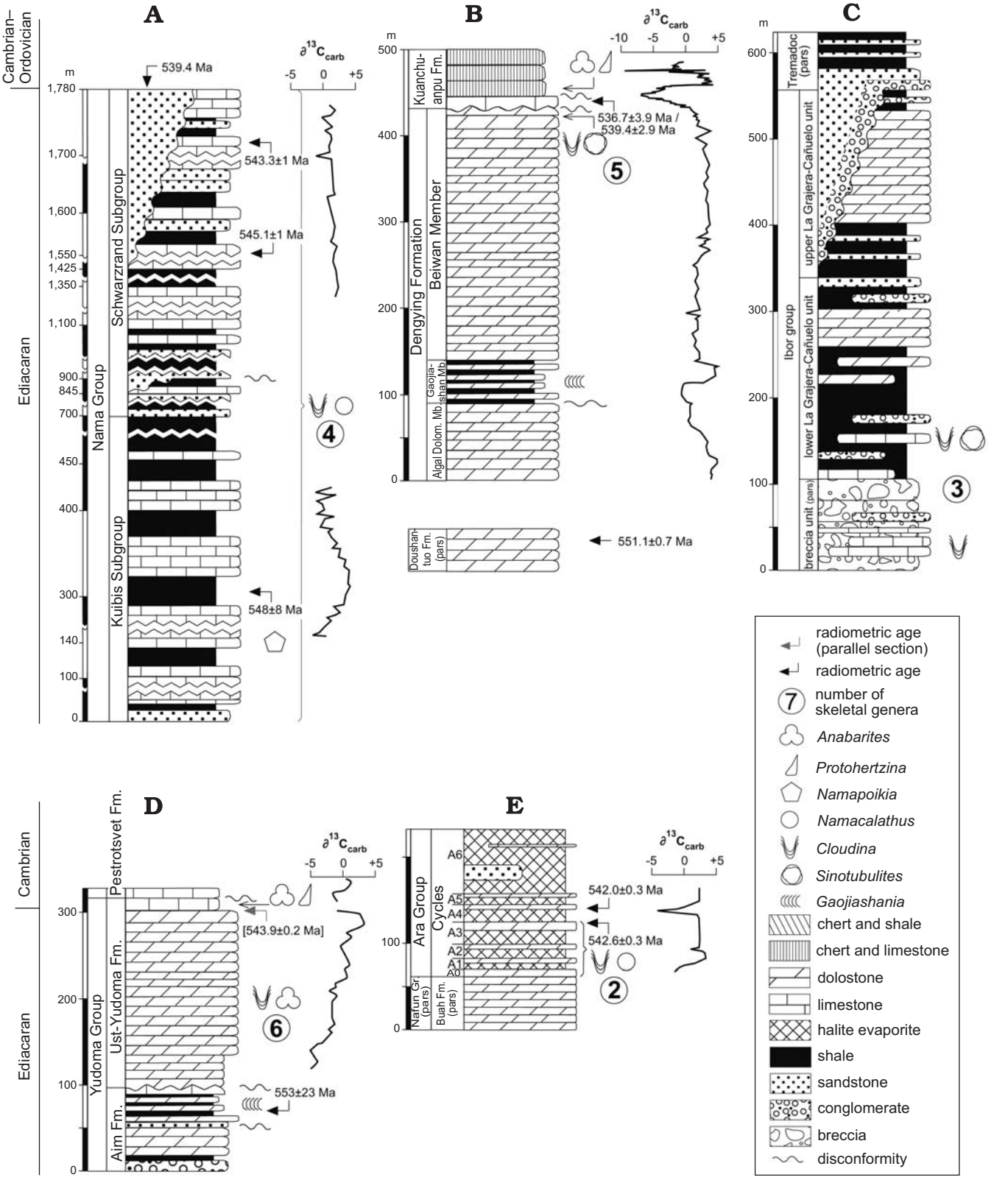

Fig. 2. Stratigraphic distribution of Ediacaran skeletal fossil assemblages from around the world. **A**. Zaris (Kuibis Subgroup) and Witputs (Schwarzrand Subgroup) subbasins, Nama Basin, Namibia (Grotzinger et al. 1995, 2000, 2005; Saylor et al. 1998; Wood et al. 2002). **B**. Yangtze Platform, southern Shaanxi, China (Hua et al. 2000b; Steiner et al. 2007; Zhu et al. 2007: lower C isotope curve; Ishikawa et al. 2008: upper C isotope curve; Pb/U radiometric data after Condon et al. 2005; Compston et al. 2008; Zhu et al. 2009). **C**. Abenójar (Abenójar Village and Tirteafuera River) Anticline, East Lusitanian–Alcudian Zone, central Spain (Ortega Girones and Sánchez Vizcaíno 1987). **D**. Yudoma River, Uchur-Maya region, Siberian Platform, Russia (C isotope data after Brasier et al. 1994; Podkovyrov and Davydov 1998; Pb-Pb radiometric data after Semikhatov et al. 2003). **E**. South Oman Salt Basin (Brasier et al. 2000; Amthor et al. 2003; Schröder and Grotzinger 2007). Abbreviations: Dolom., dolomite; Fm., formation; Gr., group; Mb., member.

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the Lower–Upper Subformation boundary at the base of the interval 4 judged by an apparent rhythm represented by intervals 4–11. The Upper and Lower "subformations" are now recognised as the Aim and Ust'-Yudoma formations of the Yudoma Group, and some researchers doubt in presence of the Aim Formation in the Nuuchchalakh section (Ioganson and Kropachev 1979; Shenfil' 1991; Semikhatov et al. 2003). However, a field correlation of the sections along the Yudoma, Maya, and Aim rivers does indicate an affinity of at least intervals 1–3 to the Aim Formation (Khomentovsky 1985). Moreover, the unconformity accentuated by deep erosional pockets in the topmost strata of the interval 8 and basal pebble conglomerate (pebbles consist of underlying black dolomudstone of the interval 8) observed by one of the present authors (AZ and Andrey Ivantsov during their field work of 1998) allows us to consider the interval 9 as the basal one of the Ust'-Yudoma Formation.

The fossils are found in the intervals 6, 10, and 11 of the Yudoma Group. The interval 6 (Aim Formation) is represented by an alternation of dark-grey thin-bedded siltstone and bluish-grey wavy-bedded dolomudstone bedding planes of which teem with *Gaojiashania annulocosta* Zhang, Li, and Dong, 1992 in the Nuuchchalakh section (Zhuravlev et al. 2009). In the interval 10 (Ust'-Yudoma Formation) consisting of light-grey sucrosic dolograinstone, commonly porous and cross-bedded, 108 m below the top of the Ust'-Yudoma Formation of the Kyyry-Ytyga section, *Cambrotubulus* cf. *C. decurvatus* Missarzhevsky, 1969, *Anabarites trisulcatus* Missarzhevsky, 1969, *A. grandis* Val'kov, 1982, *Jacutiochrea tristicha* (Missarzhevsky, 1969), and *Cloudina* ex gr. *C. riemkeae* Germs, 1972 are present (Fig. 3A, C–E). An undoubted Nemakit–Daldynian (lowermost Cambrian) skeletal assemblage appears in the uppermost 8 m of the Ust'-Yudoma Formation consisting of light-grey dolomitic limestone (interval 11 of the Kyyry-Ytyga section). The assemblage includes the protoconodonts *Protohertzina unguliformis* Missarzhevsky, 1973 as well as the anabaritids *Cambrotubulus decurvatus* Missarzhevsky, 1969, *Anabarites trisulcatus* Missarzhevsky, 1969, *A. tripartitus* Missarzhevsky, 1969, *A. latus* (Val'kov and Sysoev, 1970), *Longiochrea rugosa* Val'kov and Sysoev, 1970, *Lobiochrea* cf. *L. natella* Val'kov and Sysoev, 1970, and *Tiksitheca licis* Missarzhevsky, 1969. Earlier, only *Anabarites trisulcatus* Missarzhevsky, 1969 was mentioned at the same level of the Nuuchchalakh section (Khomentovsky 1985). Additionally, in the overlying basal 4.7 m of the Pestrotsvet Formation in the Kyyry-Ytyga section, protoconodonts *Fomitchella infundibuliformis* Missarzhevsky, 1969, anabaritids *Cambrotubulus decurvatus* Missarzhevsky, 1969, *Anabarites trisulcatus* Missarzhevsky, 1969, *A. tripartitus* Missarzhevsky, 1969, *A. latus* (Val'kov and Sysoev, 1970), *Longiochrea* cf. *L. rugosa* Val'kov and Sysoev, 1970, *Lobiochrea* cf. *L. natella* Val'kov and Sysoev, 1970, and *Tiksitheca* sp., hyolithelminths *Hyolithellus tenuis* Missarzhevsky, 1966, and *H.* ex gr. *H. vladimirovae* Missarzhevsky, 1966, halkieriids *Halkieria* sp., chancelloriids, as well as fragments of orthothecid and helcionelloid shells, are present.

At approximately the same level of the *Cloudina*-bearing interval 10 in the Yudoma Group stratotype in the Yudoma River mouth area (Maya River left bank), other problematic calcareous fossils occur, namely *Suvorovella* and *Majaella* (Khomentovsky 1985; Fig. 1A).

Other possible remains of skeletal Ediacaran animals have been noted together with the calcified microbes *Renalcis* and *Girvanella* as either "skeletal organisms resembling tabulatomorph corals" or calcified algae *Amganella* in dolostone typical of lower interval 10, which outcrops in the stratotype area of the Aim Formation (Nevolin et al. 1978; Shishkin and Stepanova 1978). These fossils are possibly related to modular skeletal corals discovered more recently in the Ediacaran Omkyk Member of the Nama Group in southern Namibia, together with *Cloudina* and other skeletal fossils (Grotzinger et al. 2000; Wood et al. 2002).

Spain.—In central Spain, terminal Neoproterozoic macrofossils are distributed in the Galician–Castilian and East Lusitanian–Alcudian tectonostratigraphic zones where vendotaenids, *Nimbia*, probable *Beltanelloides*, *Nemiana,* and *Tirasiana* and possible sabelliditids, as well as *Cloudina* and other shelly fossils, are found (Liñán et al. 1984, 2002; Palacios Medrano 1989; Vidal et al. 1994, 1999; Gámez Vintaned 1996; Fernández-Remolar 2001; Fernández Remolar et al. 2005; Cortijo et al. 2006, 2010; Zhuravlev et al. 2006; Jensen et al. 2007).

Cloudina and other Ediacaran skeletal fossils are found in two different tectonostratigraphic zones, the Galician–Castilian and East Lusitanian–Alcudian zones, where they are restricted to scarce thin carbonate units (e.g., Ibor Group and nivel de Fuentes) (Figs. 1B, 2C). The nivel de Fuentes is interpreted as megabreccias formed at the basin margin by seismic events during the Ediacaran–Cambrian interval (Santamaría Casanovas and Remacha Grau 1994).

Within the Galician–Castilian Zone of central Spain (Castilla-La Mancha), the Río Huso section (northern flank of the Valdelacasa Anticline) provides the most complete record of trace fossil assemblages for the terminal Neoproterozoic–lower Cambrian transition in Spain. The section is represented by the Greywacke Schist Complex, which is subdivided into the Domo Extremeño Group (Estenilla and Cíjara formations) and the Río Huso Group (nivel de Fuentes/Membrillar Olistostrome and Pusa Shale) (Palacios Medrano 1989; Vidal et al. 1994; Cortijo et al. 2010). The lowermost Estenilla Formation (with a thickness >800 m) consists of shale with sandstone and conglomerate interlayers. It contains trace fossils *Torrowangea rosei* Webby, 1970, *Phycodes* aff. *P. pedum* Seilacher, 1955, *Gordia* ichnosp., *Neonereites* aff. *N. uniserialis* Seilacher, 1960, *Bergaueria*? ichnosp., *Planolites* ichnosp., and *Helminthopsis* ichnosp., as well as *Nimbia occlusa* Fedonkin, 1980. The succeeding Cíjara Formation (175 m in thickness) is represented by shale and sandstone and contains a similar but less rich trace fossil assemblage. It is overlain with a sharp

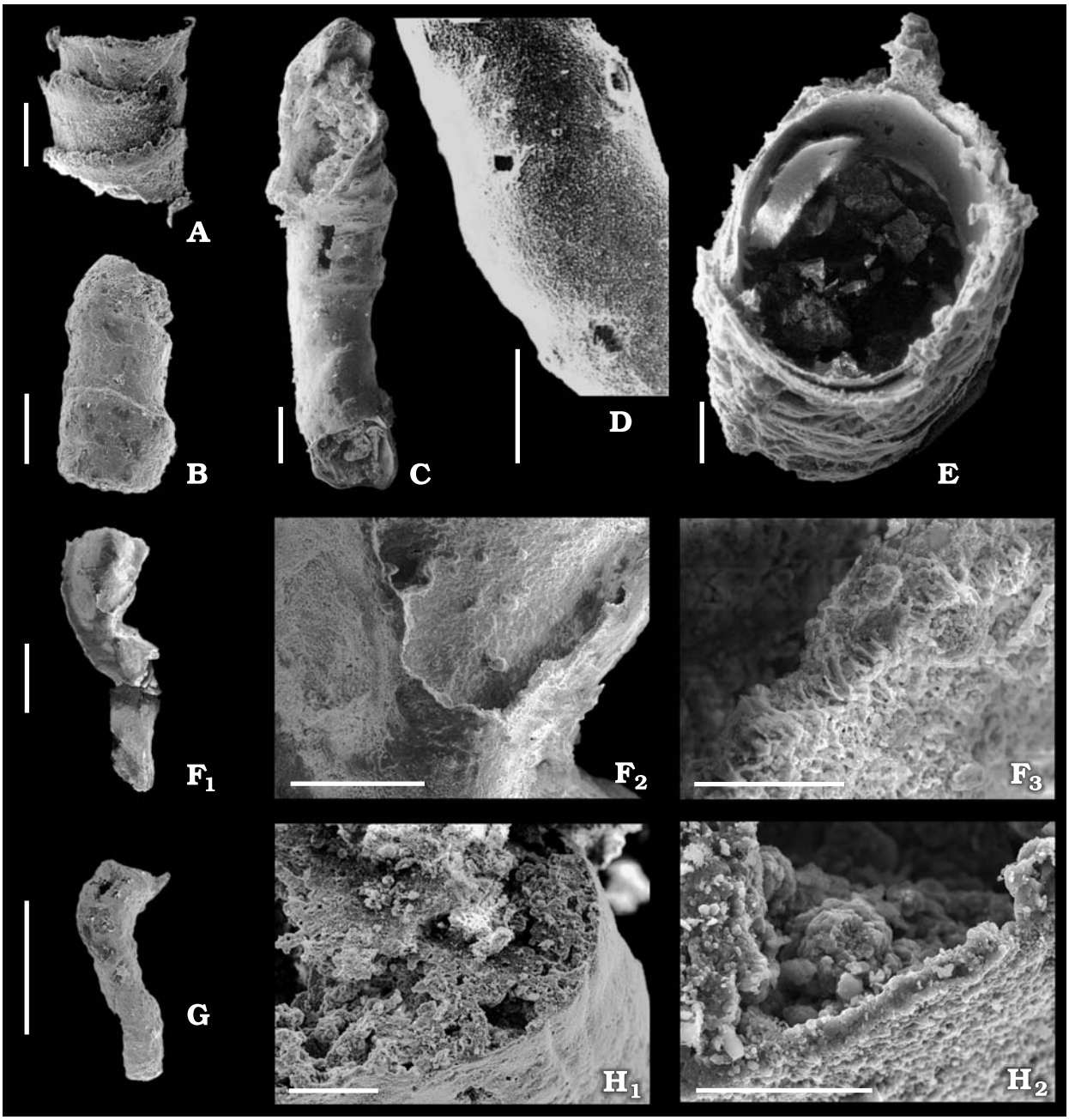

Fig. 3. SEM images of late Ediacaran *Cloudina*. **A**, **C**–**E**. *Cloudina* ex gr. *C. riemkeae* Germs, 1972; Kyyry-Ytyga (1.6 km downstream from Ulakhan-Ytyga Creek mouth), Yudoma River, right bank, Siberian Platform, Russia, Ust'-Yudoma Formation. **A**. SNIIGGiMS 1630/1, tube fragment with abraded shell wall. **C**. SNIIGGiMS 1630/2, fragment of tube with holes formed after microdolomite crystal dissolution. **D**. SNIIGGiMS 1630/3, detail of tube fragment with holes formed after microdolomite crystal dissolution. **E**. SNIIGGiMS 1630/4, tube nested funnels. **B**, **F**–**H**. *Cloudina* ex gr. *C. hartmanae* Germs, 1972; Tirteafuera River, Abenójar Anticline, East Lusitanian–Alcudian Zone, central Spain, lower La Grajera-Cañuelo unit, Ibor Group. **B**. MPZ 2007/3918, abraded tube fragment with imprints of mica crystals of the matrix. **F**. MPZ 2007/3919; F_1, tube fragment with wall preserved; F_2, detail of F_1; F_3, detail of F_1, wall microstructure. **G**. MPZ 2007/3920, abraded tube fragment. **H**. MPZ 2007/3921; H_1, tube fragment with wall preserved; H_2, detail of H_1 showing wall microstructure. Scale bars A, D, E, H_1 100 μm; B, C, F_2 300 μm; F_1, G 1 mm; F_3 50 μm; H_2 30 μm.

contact by the nivel de Fuentes (50 m in thickness), a carbonate olistostrome with *Cloudina* spp. Unusually large *Planolithes* ichnosp. is present in siliciclastic interlayers within the olistostrome (Brasier et al. 1979). *Torrowangea rosei* Webby, 1970, *Gordia* ichnosp., *Cochlichnus* ichnosp., and *Planolithes* ichnosp. occur in the basal strata of the Pusa Shale (Gámez Vintaned 1996). A much more diverse trace fossil assemblage of *Torrowangea rosei* Webby, 1970, *Phycodes pedum* Seilacher, 1955, *P.* aff. *P. pedum* Seilacher, 1955, *Gordia* ichnosp., *Neonereites uniserialis* Seilacher, 1960, *N.* aff. *N. uniserialis* Seilacher, 1960, *Helminthopsis* ichnosp., *Cochlichnus* ichnospp., *Monomorphichnus lineatus* Crimes, Legg, Marcos, and Arboleya, 1977, *Planolites montanus* Richter, 1937, *Bilinichnus* ichnosp., ichnosp. ex gr. *Scolicia*, *Treptichnus* ichnosp.,

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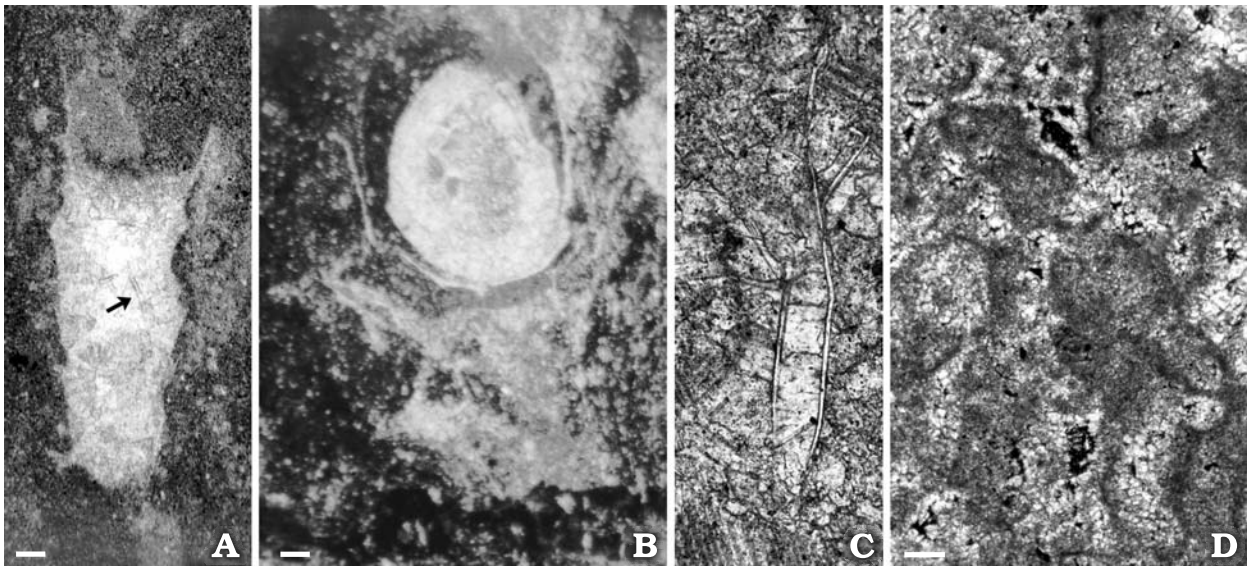

Fig. 4. Late Ediacaran calcareous fabrics from Ibor Group, Abenójar Anticline, East Lusitanian–Alcudian Zone, central Spain. **A**, **B**. *Cloudina* ex gr. *C. hartmanae* Germs, 1972, lower La Grajera-Cañuelo unit, Tirteafuera River. **A**. MPZ 2007/3923, longitudinal section showing wall fragments or bacterial microburrowing within skeleton (arrow). **B**. MPZ 2007/1465, oblique longitudinal section. **C**. MPZ 2009/496, longitudinal section of corolla-bearing "*Cloudina*" *carinata* Cortijo, Martí Mus, Jensen, and Palacios, 2010, lower La Grajera-Cañuelo unit, Tirteafuera River. **D**. MPZ 2007/3925, thrombolite structure, breccia unit "calizas de Abenójar", Abenójar. Scale bars 250 μm.

Belorhaphe ichnosp., *Dimorphichnu*s ichnosp., *Diplichnites* ichnosp., *Megagrapton* cf. *M. irregulare* Książkiewicz, 1968, *Psammichnites* ichnosp., and *Treptichnus bifurcus* Miller, 1889 appears 250 m above the base of this unit (Gámez Vintaned 1996).

Neither the lowermost trace fossil assemblage (Estenilla Formation) nor the basal Pusa Shale one contains any distinct Cambrian forms, but *Phycodes* aff. *P. pedum*, an ethological precursor of *P. pedum*, appears in those assemblages and also reaches the basal Cambrian ones (Gámez Vintaned 1996: fig. 9; Vidal et al. 1994: figs. 15c, d, 17e, f; similar traces have been figured by Jensen et al. 2000 from Namibia). Conversely, the upper Pusa Shale trace fossil assemblage includes the index ichnofossil *Phycodes pedum*, which is a Phanerozoic expression of increasing ethological complexity in sea bottom bioturbation across the Neoproterozoic–Cambrian boundary. Additionally, other ichnofossils of typical Cambrian patterns such as *Treptichnus* and *Psammichnites*, arthropod-produced scratch marks *Monomorphichnus*, *Diplichnites*, and *Dimorphichnus* (which are also unknown in Neoproterozoic rocks), and "primitive" forms of the graphoglyptids *Belorhaphe* and *Megagrapton* occur at the same level.

In Robledo del Mazo (a locality east of the Río Huso section, northern flank of the Valdelacasa Anticline, Toledo Mountains), the middle, microlaminated interval of the Pusa Shale yields phosphatised skeletal fossils among which *Cloudina* has also been listed (Palacios et al. 1999). However, restudy of this fossil material demonstrates that it is a cross section of an unidentified tubicolous shell.

Additionally, within the Galician–Castilian Zone, *Cloudina* ex gr. *C. hartmanae* Germs, 1972 ("microorganismos tubulares" in Palacios Medrano 1989: pl. 16; *Cloudina* sp. in Grant 1990: fig. 7C, D; *C. hartmannae* in Vidal et al. 1994: fig. 12A, B) is recognised on the southern flank of the Valdelacasa Anticline where a *Cloudina*-bearing carbonate unit of the Membrillar Olistostrome is sandwiched between mudstone beds containing *Nimbia occlusa* Fedonkin, 1980 and *Tirasiana* (Fedonkin in Palacios Medrano 1989). As well, *Cloudina* sp. has been discovered in the Pastores carbonates to the southwest of Salamanca (Vidal et al. 1994; Rodrígez Alonso et al. 1995). The siliciclastic rocks embracing these carbonates are conglomerate, sandstone, and sandstone-black shale alternations deposited by debris flows, high- and low-concentration turbidity currents, submarine slides in slope and base-of-slope environments. Finds of *Cloudina* are restricted to limestone-breccia interbeds. Such breccia layers gradationally change into underlying and overlying sandstone beds, suggesting a secondary brecciation through load and fluidisation processes. The $^{87}Sr/^{86}Sr$ (0.70845–0.70853) and $\delta^{13}C$ (>-4.6‰) values shown by these carbonates are probably primary or slightly modified (Valladares et al. 2006).

In the East Lusitanian–Alcudian Zone of central Spain (Castilla-La Mancha), terminal Neoproterozoic fossiliferous carbonates of the Ibor Group outcrop, from west to east, in the Ibor, Navalpino, and Abenójar anticlines (Figs. 1B, 2C). A calcareous fossil listed by Vidal et al. (1994: fig. 12E) as "*Cloudina hartmannae*" from carbonates of the Ibor Anticline bears prominent corollas with hollow longitudinal ribs and thereby differs from all other Ediacaran shelly fossils (Cortijo et al. 2006, 2010; Zhuravlev et al. 2006; Fig. 4C). *Cloudina* ex gr. *C. hartmanae* Germs, 1972 is noted from Ibor Group wackestone outcropping in the Navalpino Anticline (*Cloudina* sp. in Vidal et al. 1994: fig. 12C). Abenójar outcrops (Abenójar Village and Tirteafuera River) are repre-

sented by Ibor Group oolitic and thrombolitic limestone (Fig. 4D). A calcareous fossil, cited as *Cloudina* sp. from the breccia unit (Fig. 2C) of these localities (Vidal et al. 1994: fig. 12D; calizas de Abenójar), has a polygonal cross-section like that of "*Cloudina*" *carinata* Cortijo et al. (2010). Up the succession, tubicolous phosphatised steinkerns of *Cloudina* ex gr. *C. hartmanae* Germs, 1972 and *Sinotubulites* sp. have been etched from the lower La Grajera-Cañuelo unit of the Tirteafuera River (Figs. 3B, F–H, 5A, B), while calcareous tubes of *Cloudina* ex gr. *C. hartmanae* are recognised in thin sections of a thrombolite from the same locality (Fig. 4A, B). Simple trace fossils of *Cochlichnus* and *Planolites* ichnogenera and vendotaenid filaments are abundant in shales.

Ediacaran shelly fossils and the terminal Neoproterozoic biostratigraphy

New finds outlined above confirm that, despite of the problems with the affinities of *Cloudina* and other Ediacaran skeletal fossils, they seem to be very useful for subdivision and wide correlation of terminal Neoproterozoic strata. The presence of *Cloudina* in an assemblage with *Anabarites* allows us to consider the interval 10 of the Ust'-Yudoma Formation on the Yudoma River to be uppermost Ediacaran. A correlation of Uchur-Maya sections with those of the Olenëk Uplift suggests that the uppermost Ust'-Yudoma Formation (interval 11 bearing *Anabarites–Protohertzina* assemblage) is coeval with the lower Kessyuse Formation containing an assemblage of the *Anabarites trisulcatus* Zone (Khomentovsky and Karlova 1994, 2002), while the lower Ust'-Yudoma Formation (intervals 9–10) is coeval with the Turkut Formation where scarce "*Cambrotubulus*" (?*Chenmengella*) tubes have been recorded (Karlova 1987). This suggests that the beds with *Gaojiashania* (upper Aim Formation) are coeval with the Khatyspyt Formation of the Olenëk Uplift where typical Ediacaran fossils are present (Sokolov 1985; Grazhdankin et al. 2008; Zhuravlev et al. 2009). If the correlation of Nuuchchalakh and Kyyry-Ytyga sections is correct, the *Gaojiashania* beds are underlain by strata of 553±23 Ma as determined by Semikhatov et al. (2003) who applied Pb-Pb radiometric analysis to the less altered limestones from the lower Kyyry-Ytyga section.

A similar succession of terminal Neoproterozoic–early Cambrian fossil assemblages is observed in South China. In this region, an assemblage of diverse fossils including *Paracharnia* and *Gaojiashania* (middle Dengying Formation) is succeeded by *Cloudina–Sinotubulites* assemblage (upper Dengying Formation), which in turn is succeeded by the lowermost Meishucunian (= upper Nemakit–Daldynian) *Anabarites trisulcatus–Protohertzina anabarica* small shelly fossil assemblage and coeval trace fossils of Cambrian aspect (overlying Kuanchuanpu Formation) (Chen et al. 1981; Ding et al. 1992; Hua et al. 2000a, b; Li et al. 2005; Weber et al. 2007; Cai et al. 2010). The Dengying Formation is underlain by the Doushantuo Formation containing in its topmost part an ash bed of 551±0.7 Ma according to U-Pb dating (Condon et al. 2005). The complete skeletal assemblage of the Beiwan Member (upper Dengyin Formation) thus consists of *Cloudina sinensis* Zhang, Li, and Dong in Ding et al. 1992, *Sinotubulites baimatuoensis* Chen, Chen, and Qian, 1981, *Qinella levis* Zhang, Li, and Dong in Ding et al. 1992, *Chenmengella laevis* (Zhang, Li, and Dong in Ding et al. 1992), *C. costata* (Zhang, Li, and Dong in Ding et al. 1992), *Protolagena limbata* Zhang and Li, 1991 including its possible synonyms, several species of *Conotubus* Zhang, Li, and Dong in Ding et al. 1992, and a new fossil figured by Steiner et al. (2007: fig. 2L) as "*Cloudina* cf. *hartmannae*". The latter fossil does not possess an eccentrically nested stock of funnel-like segments, but rather a cornute thick-walled annulated shell. *Qinella* cannot be a synonym of *Sinotubulites* (cf. Chen and Sun 2001) as its type species bears longitudinal ribs on its surface and its tube consists of thick, loosely-spaced layers.

These records of *Cloudina* allow us to tie together transitional terminal Neoproterozoic–lower Cambrian strata of the South China and Siberian platforms and the Altay Sayan Foldbelt including West Siberian Plate (Kheraskova and Samygin 1992; Bagmet 1994; Dyatlova and Sycheva 1999; Kontorovich et al. 2008; AZ personal observations) as well as of Namibia, Brazil, Oman, Mexico, the western United States, and Canada (Germs 1972; McMenamin 1985; Signor et al. 1987; Zaine and Fairchild 1987; Conway Morris et al. 1990; Grant 1990; Hofmann and Mountjoy 2001).

Sinotubulites is identified in Mexico and the western United States (McMenamin 1985; Signor et al. 1987). It should be noted that fragments figured by Signor et al. (1987: fig. 5.3, 5.4) from the lower Deep Spring Formation of eastern California and western Nevada as *Coleoloides inyoensis* Signor, Mount, and Onken, 1987 (= *Coleoloides* sp. in Signor et al. 1983: fig. 3A) probably belong to *Cloudina dunfee* (Signor et al. 1987), because they are not finely and regularly sculptured by spiral ridges as it is in the *Coleoloides* shells but rather bear deeply incised and irregularly spaced spiral grooves. Such a pattern is observed on *Cloudina* steinkerns (Fig. 3B). Also, in addition to a distinct size difference, *Salanytheca*? sp. from the same American localities (Signor et al. 1983: fig. 3C, 1987: fig. 5.2) appears to differ from typical *Salanytheca* in the absence of a regular ornament, and is more similar to *Cloudina* in having a shell structure consisting of eccentrically nested funnel-like segments. It matches the size range of typical *Cloudina* (Grant 1990). Another problematic skeletal fossil, *Wyattia reedensis* Taylor, 1966, is restricted to the underlying upper Reed Dolomite (Taylor 1966). *Wyattia* might be a senior synonym of *Cloudina*, but unfortunately it has been described from thin sections lacking diagnostic features. The assemblage of the La Ciénega Formation fossils from Sonora, Mexico is more diverse and includes *Sinotubulites cienegensis* McMenamin (1985), *Chenmengella* sp. (= *Cambrotubulus* cf. *C. decurvatus* in

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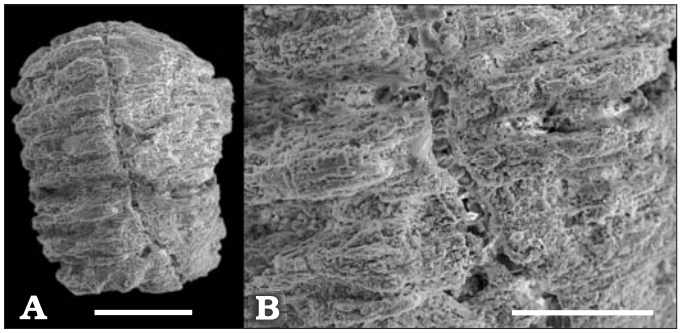

Fig. 5. Late Ediacaran *Sinotubulites* sp. MPZ 2007/3922; Tirteafuera River, Abenójar Anticline, East Lusitanian–Alcudian Zone, central Spain; Ibor Group. **A**. Tube inner mold fragment with a longitudinal crack. **B**. Detail of A. Scale bars A 200 μm; B 100 μm. Both SEM images.

McMenamin 1985: fig. 5.1, 5.4), and *Qinella* sp. (= circothecid hyolith in McMenamin 1985: 1423, fig. 5.3).

The status of fossils recorded under the names "*Cloudina*" and *Acuticloudina* from Argentina, Antarctica, and Uruguay (Yochelson and Herrera 1974; Yochelson and Stump 1977; Gaucher and Sprechmann 1999; Gaucher et al. 2003) requires further study. Some of these objects could indeed be Ediacaran skeletal biomineralised fossils but are unlikely to be cloudinids.

Previously, *Namacalathus* was not distinguished among *Cloudina* fragments in the Nama Group and was interpreted as deformed *Cloudina* shells (e.g., Grant 1990: fig. 8B). *Namacalathus hermanastes* is now recognised in the Ediacaran Byng Formation (Miette Group) of western Canada, the Birba Formation (Ara Group, Huqf Supergroup) of Oman (Hofmann and Mountjoy 2001; Amthor et al. 2003), the Kotodzha and Raiga formations of the West Siberian Plate, Russia (Kontorovich et al. 2008), the Kuibus and Schwarzrand subgroups (Nama Group) of Namibia.

A correlation of some of these regions is supported by chemostratigraphic (stable isotope) data: a continuous positive carbon isotope excursion interval (within $\delta^{13}C$ limits of +1‰ to +2‰) is observed at the level of *Cloudina* occurrences in dolostone of the Nuuchchalakh section and in the "nivel de Fuentes" (Río Huso Group) in Spain (Strauss et al. 1995; Podkovyrov and Davydov 1998) as well as in the upper Dengying Formation (Beiwan Member, southern Shaanxi) and at levels with *Cloudina* in Oman, Namibia, and the Great Basin of the United States (Pelechaty 1998; Shields 1999; Yang et al. 1999; Corsetti and Hagadorn 2000, 2003; Amthor et al. 2003; Condon et al. 2005; Fig. 2A, B, D, E). Additionally, a close primary Sr-isotope ratio trend (within limits of 0.70829–0.70844) is observed in the Kyry-Ytyga section at levels below the first occurrences of *Cloudina* (Semikhatov et al. 2003), as well as at the levels characterised by Ediacaran faunas in sections of the Nama Group in Namibia, Huqf Supergroup in Oman, and Dengying Formation in South China (Burns et al. 1994; Saylor et al. 1998; Yang et al. 1999; Shields 1999). Above the *Cloudina* level, the notorious negative carbon isotope drop (from 0 – +2‰ down to -4 – -7‰ and back again) approaching the Ediacaran–Cambrian boundary is observed in Siberia, Oman, South China, and the Great Basin at least (Podkovyrov and Davydov 1998; Amthor et al. 2003; Corsetti and Hagadorn 2003; Semikhatov et al. 2004; Zhu et al. 2007; Ishikawa et al. 2008; Fig. 2B, D, E).

Globally, the first appearance of the earliest Cambrian *Phycodes pedum* trace fossil assemblage occurs just above this deep negative $\delta^{13}C$ excursion in numerous mixed carbonate siliciclastic systems such as the Mackenzie Mountains, Canada (Narbonne et al. 1994), the Great Basin (Corsetti and Hagadorn 2003), the Olenök Uplift, northern Siberian Platform (Knoll et al. 1995), the Zavkhan Basin, Mongolia (Brasier et al. 1996), and South China (Weber et al. 2007; Zhu et al. 2007).

It is important to note that in the Spanish sections the assemblages of *Cloudina, Sinotubulites*, and other Ediacaran skeletal fossils always precede the *Monomorphichnus lineatus–Phycodes pedum* trace fossil assemblage defining the lower Cambrian boundary (Gámez Vintaned 1996). A similar succession of Ediacaran to basal Cambrian fossil assemblages is known in the Great Basin of the United States, Mexico, and South China (Hagadorn and Waggoner 2000; Corsetti and Hagadorn 2003; Sour-Tovar et al. 2007; Weber et al. 2007). Unfortunately, the preservation of fossil attributed to cf. *Cloudina* from the lowermost Wood Canyon Formation of the Great Basin, as well as its morphological features, do not allow us to be sure in its affinities: it does not display any sinuosity and branching despite its significant length (up to 35 mm).

Recent finds of somewhat complex infaunal burrowing fossils in the upper Spitskop Member (Urusis Formation, Schwarzrand Subgroup, Nama Group) further decrease the gap between possible position of the Ediacaran–lower Cambrian boundary and the level yielding the latest *Cloudina* in southern Namibia (Jensen et al. 2000; Jensen and Runnegar 2005). According to radiometric data in this region, *Cloudina* existed already from 548.8±1 Ma (Grotzinger et al. 1995; Narbonne et al. 1997). The upper limit of *Cloudina* distribution in Oman, according to Brasier et al. (2000), is constrained to the uppermost Ara Group, which is overlain by the Fara Formation with ignimbrites of 544.5±3.3 Ma U-Pb zircon age. However, Amthor et al. (2003) framed its latest occurrences between Birba Formation volcanic ash beds of 542.6±0.3 Ma and 542.0±0.3 Ma U-Pb zircon age (Fig. 2E). In any case, *Cloudina* precedes the *Phycodes pedum* trace fossil assemblage in Namibia, too. These observations agree broadly with the revised early Cambrian time scale based on volcanic ash zircon U-Pb isotope data of Compston et al. (2008) and Zhu et al. (2009), who estimated the lower Meishucunian Stage (lowermost Cambrian) boundary as 539.4± 2.9 Ma and 536.7±3.9 Ma, respectively (Fig. 2B).

Thus, on the Siberian Platform the upper, *Purella antiqua* Zone of the Nemakit–Daldynian Stage and the upper part of the lower, *Anabarites trisulcatus* Zone, bearing *Anabarites–Protohertzina* assemblage and lacking *Cloudina*, is probably

also Cambrian. Khomentovsky and Karlova (2005) suggested that the lowermost part of the *Anabarites trisulcatus* Zone of the Nemakit–Daldynian Stage may be attributed to a separate *Cambrotubulus* Zone characterised by *Cambrotubulus* sp., *Anabarites* sp., *Chancelloria* sp., and *Protospongia* sp. It is very probable that these authors mistook *Chenmengella* fragments for *Cambrotubulus* and those of *Namacalathus*-like goblet-shaped fossil for *Chancelloria*. Thus, their "*Cambrotubulus*" Zone embraces the *Cloudina–Anabarites* assemblage determinated now in the lowermost Nemakit–Daldynian strata on the Yudoma River (Fig. 2D). The equivalent of the global Precambrian–Cambrian boundary, established in eastern Newfoundland, in Siberia is restricted to the lowermost Nemakit–Daldynian Stage rather than to the base of the Tommotian Stage as the lower part of the *Anabarites trisulcatus* Zone, containing *Cloudina–Anabarites* assemblage, is definitely Ediacaran.

Biomineralisation and inferred affinities of Ediacaran shelly fossils

The new Siberian finds extend a stratigraphic distribution of some anabaritids into the Ediacaran strata. Thus, a current list of Ediacaran fossils with calcareous mineralised skeletons is (in order of their appearance in literature) as follows: *Suvorovella* Vologdin and Maslov, 1960; *Majaella* Vologdin and Maslov, 1960; *Wyattia* Taylor, 1966; three anabaritid genera (*Cambrotubulus* Missarzhevsky in Rozanov et al. 1969; *Anabarites* Missarzhevsky in Voronova and Missarzhevsky 1969; *Jacutiochrea* Val'kov and Sysoev, 1970); *Cloudina* Germs 1972 (= *Nevadatubulus* Signor, Mount, and Onken, 1987); *Sinotubulites* Chen, Chen, and Qian, 1981; *Qinella* Zhang, Li, and Dong in Ding et al. 1992; *Protolagena* Zhang and Li, 1991; *Chenmengella* nom. nov. (pro *Chenella* Zhang, Li, and Dong in Ding et al. 1992); *Namacalathus* Grotzinger, Watters, and Knoll, 2000; *Namapoikia* Wood, Grotzinger, and Dickson, 2002; a new cloudinid of Cortijo et al. (2006, 2010), possible *Platysolenites* co-occurring with the *Cloudina–Namacalathus* assemblage on the West Siberian Plate (Kontorovich et al. 2008: fig. 3g), and at least two more new genera still undescribed.

One of these genera has been previously reported from Namibia as a "tube-shaped thin-walled fossil" by Grotzinger et al. (2000: 346, fig. 14C–E). It possesses a subspherical basal part and a distal tubular part closed at the base. Also, so-called "isolated central spines of *Chancelloria*", which are commonly mentioned from the lowermost Nemakit– Daldynian part of the Ust'-Yudoma Formation on the southern Siberian Platforms (e.g., Khomentovsky and Karlova 2005: 24), may belong to the same genus. One such specimen is, probably, pictured by Vologdin and Maslov (1960: fig. 1o) as "hyolithoides(?)" from the Yudoma River locality containing *Suvorovella* and *Majaella*. Another cornute thick-walled shelly fossil with transverse ridges is figured by Steiner et al. (2007: fig. 2L) from South Chinese Ediacaran strata and referred by the authors to "*Cloudina* cf. *hartmannae"*. Some further problematic forms are figured and informally described from Ediacaran strata of the Dengying Formation of South China and one of them, a "stout tube with closed base and weak annulation", is likely to be a skeletal fossil (Hua et al. 2005a: pl. 1: 5). Ediacaran silica clusters from southwestern Mongolia, which were though to be hexactinellide sponge hexacts (Brasier et al. 1997), were subsequently re-interpreted as abiogenic arsenopyrite crystals (Antcliffe et al. 2011). Besides, the age determination of these finds is based on a fragmentary carbon and strontium isotope record from what is a very tectonically complex area with a highly controversial interpretation of the lithostratigraphic succession (Esakova and Zhegallo 1996; Khomentovsky and Gibsher 1996). Thus, the stratigraphic position of strata yielding these spicules requires further age constraint.

It should be noted that "*Cloudina*" *carinata* Cortijo, Palacios, Jensen, and Martí Mus, 2010 shows a longitudinal subdivision rather than any kind of budding, possesses transverse corollas and prominent external longitudinal crests, and displays an apparent absence of any transverse structures within its tube and articulation and imbrication of successive funnels rather than their eccentric nesting and fusion (Cortijo et al. 2010). Some of these differences are obvious in longitudinal sections of both typical *Cloudina* and "*Cloudina*" *carinata* (Fig. 4A, C) and cast doubt on an interpretation of this new fossil as *Cloudina*, especially the type of asexual reproduction which is a feature of familial or higher taxonomic levels (e.g., Marfenin 1993).

The primary compositions of Ediacaran shells were aragonite and high-Mg calcite (Grant 1990; Fedorov and Zhuravlev 1993; Grotzinger et al. 2000; Chen and Sun 2001; Zhuravlev and Wood 2008). Among them, *Namapoikia*, anabaritids, and possibly *Sinotubulites* and *Protolagena* were primarily aragonitic (Wood et al. 2002; Kouchinsky and Bengtson 2002; Chen et al. 2008; Cai et al. 2010). Skeletons of *Cloudina* either bear microdolomite crystals or are preferentially overgrown by euhedral calcite, or show both these features indicative of high-Mg calcite original composition (Fig. 3C, D). A preferential dolomitisation of *Cloudina* tubes is also established in the Nama Group of Namibia (Grant 1990), the Birba Formation of Oman (Conway Morris et al. 1990), the Dengying Formation of South China (Hua et al. 2005b, 2007), and the Reed Formation and the overlying lower member of the Deep Spring Formation at several localities in eastern California and western Nevada (Domke et al. 2009). In Oman specimens, the *Cloudina* tube walls are selectively formed of very finely crystalline dolomite which is believed to be a direct replacement of the original calcium carbonate; epitaxial overgrowths of the wall by radially arranged dolomite is common, and the spaces between segments are often filled by a coarser dolomite spar (Conway Morris et al. 1990).

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Cloudina microstructure was studied under SEM on specimens from Namibia, Brazil, and Oman and *Namacalathus* microstructure was observed on slabs from its type locality. Each of these specimens as well as comparative lower Cambrian cribricyath material has been processed under scanning electron microscope and under transmitted light in ultrathin sections, prepared by the method elaborated by Lafuste (1970). Of those specimens, the Namibian sample set is especially interesting because here in the same slab, *Namapoikia* skeletons are built by a coarse calcite mosaic, *Cloudina* tubes are micritised, and *Namacalathus* skeleton consists of bladelike calcite crystals which are parallel to the wall surface. Relative quality of preservation of different precipitates in the same sample is indicative for an aragonite primary composition if coarse spar mosaic fills molds, generally irregularly cross-cutting original structure; for high-Mg calcite incipient microstructure if skeletal fabrics are preserved despite of micritisation and spar-filled molds with microdolomite; and for low-Mg calcite original composition if skeletal fabrics did not undergone significant alternations (James and Klappa 1983; Zhuravlev and Wood 2008; Porter 2010). Thus, following these mineralogical criteria, *Namapoikia* represents a skeletal structure of primary aragonitic composition, *Cloudina* tubes were originally composed of Mg-calcite, while *Namacalathus* skeletons lack any features of diagenetic alternation. A distribution of epitaxial synsedimentary early marine cements developing in optical continuity with skeletal elements further supports these suggestion: bladed equant calcite is typical of *Namacalathus* skeletons; fibrous primary high-Mg calciteis developed on *Cloudina* tubes; and neomorphosed aragonite botryoids of acicular crystals infill void space in *Namapoikia* thickets (Grant 1990; Grotzinger et al. 2000; Wood et al. 2002).

It is necessary to point out, that despite differences in preservation (dolomitic in Oman and Namibia, calcitic in Brazil, and phosphatic in Spain and China), *Cloudina* bears a similar skeletal microstructure in terms of microcrystal size and arrangement. These peculiarities are indicative of a low diagenetic alternation of its skeleton in these regions. The *Cloudina* tube consists of extremely thin (8–12 μm thick) primary layers fusing to form a thicker secondary lamina (up to 60 μm thick) (Fig. 6C, D). An individual layer thickness is equal to the size of individual crystals. Crystals are digitated in outlines, slightly elongated along the layer thickness, and oriented normally to the layer surface. The interlayer space is sealed by elongated crystals (40–60 μm in length) which are initiated at the inner surface of the primary layer and are in optical continuity with its crystals (Fig. $6D_1$, D_2, D_5, C_3). The remainder of the tube space is usually occupied by coarse calcite mosaic and/or sediment similar to the hosting sediment. Two stages of tube formation are inferred: the biologically controlled formation of primary layer and periodic mineralisation of the interlayer space where the primary layer served as a template controlling crystal orientation. Interestingly, the same microstructure pattern is preserved in phosphatised specimens from the Tirteafuera River locality in Spain (Fig. $3F_3$) and from the Dengying Formation of South China (Feng et al. 2003: fig. 1a, b). Specimens from Namibia, studied under cathodoluminescence, possess thicker elements (8–50 μm, mostly 10–25 μm thick), but the variation in thickness appears to result from further dolomitisation (Grant 1990).

Cloudina is definitely not related to early Cambrian cribricyaths, with which it was compared (e.g., Germs 1972; Glaessner 1976; Khomentovsky and Karlova 1993) and differs from the latter in both growth pattern and microstructure. Cribricyaths possess a continuous, non-segmented, bilaterally symmetrical, hornlike skeleton, twisted along its growth direction, with a distinct continuous, although eccentric inner wall in the majority of species. Their microstrusture is homogenous microgranular comprising isometric microgranules 2 μm in size (Fig. 6B). In general, the *Cloudina* microstructural pattern resembles that of sabellid polychaetans. Tubes of sabellids consist of an extremely thin organic film separating outer and inner aragonitic layers (ca. 25–60 μm thick) composed of spherulits each of which comprises a bundle of needle-shaped crystallites forming primitive irregular prisms (Vinn et al. 2008: text-fig. 1D, F). However, if such an organic film was present in the *Cloudina* tube wall it would be replaced by a coarse calcite mosaic rather than by microgranules, and the elongated crystals growing on them do not form spherulitic aggregates (Fig. $6D_1$, D_2).

Thus, the more advanced serpulid (Annelida) affiliation of *Cloudina* suggested by Glaessner (1976) and Hua et al. (2005b) should be discounted on the microstructure data at least. No annelid builds a tube of such an odd construction, possessing a "hemispherical basal end" and tabulae (e.g., Vinn 2005). As a serpulid secretes its tube by precipitating calcium carbonate in a pair of anterolateral subcollar glands, suspending the resulting crystals in a fluid organic matrix, and moulding this slurry onto the anterior tube margin (Hedley 1958; Neff 1971; Pernet 2001), their microstructure pattern is in no ways resembling that of *Cloudina*. Hua et al.'s (2005b) data on asexual reproduction of *Cloudina* do not prove its annelid affinities either, because cnidarians demonstrate much more diverse variation in asexual development than it was listed by Hua et al. (2005b; e.g., Marfenin 1993). The pattern of asexual reproduction of *Cloudina* observed by Hua et al. (2005b: fig. 1K–R) matches well to intercalar budding of cnidarians but not to serpulid budding with a bud tube development at the surface of the parental one but not inside it (Pernet 2001).

SEM study of the cross-section of a *Namacalathus* skeleton from its type area (Kuibis Subgroup, Zaris Subbasin, Namibia) revealed a microstructure composed of elongate parallel bladelike calcite crystals (laths), drastically different from the microgranular microstructure of *Cloudina* and void-filled skeletons of *Namapoikia* from the same locality (Fig. 6A). This observation accords well with an inference regarding the composition of the *Namacalathus* skeleton by Grotzinger et al. (2000), who noted common preferential

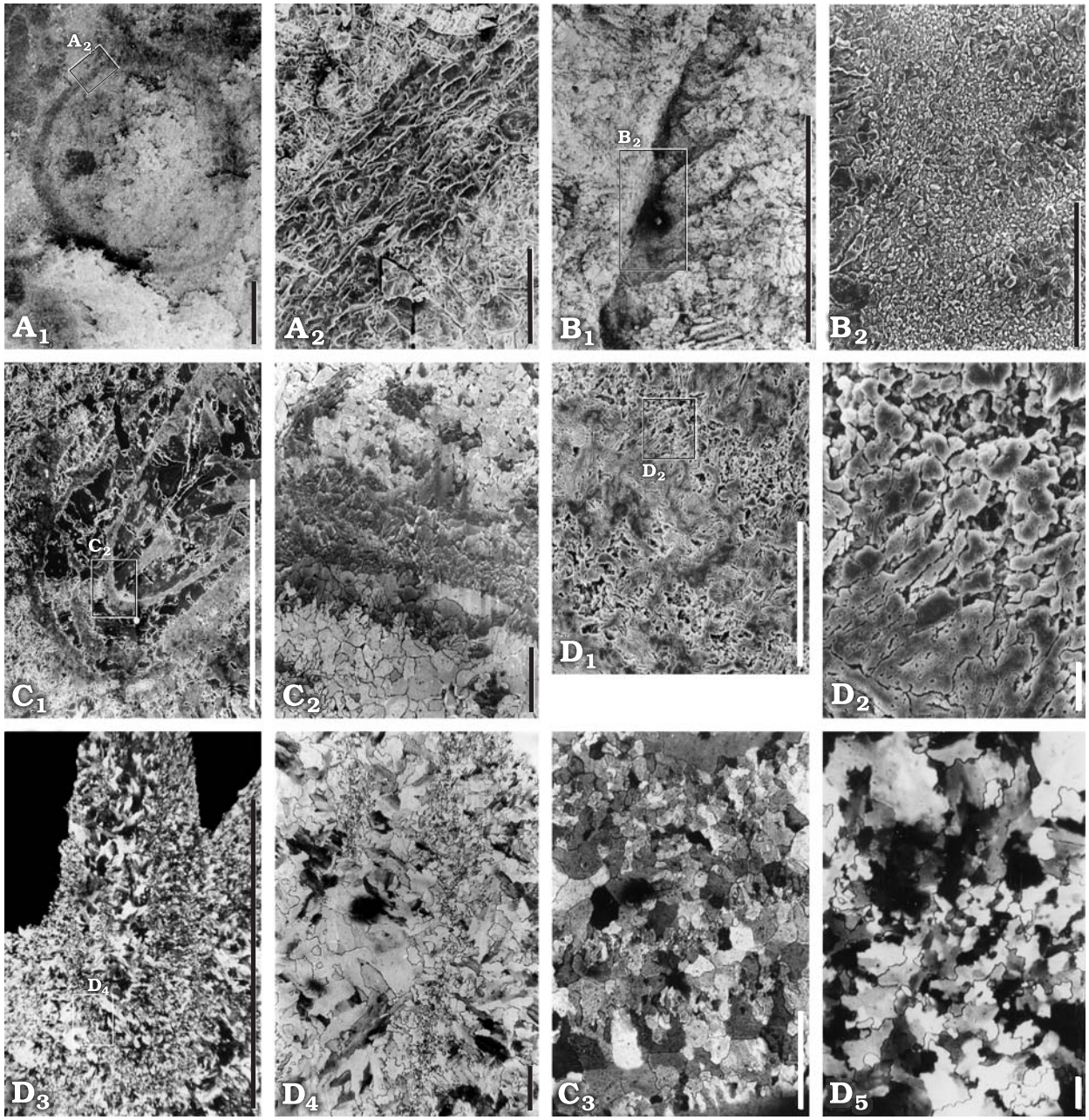

Fig. 6. Microstructure of late Ediacaran and early Cambrian microfossils. **A**. *Namacalathus hermanastes* Grotzinger, Watters, and Knoll, 2000, Kuibis Subgroup, Nama Group, Upper Ediacaran, Zaris Subbasin, Namibia; MNHN Ca 370-1; A_1, cross-section of stem; A_2, detail of A_1 showing blade-like elongate parallel crystals (laths) of calcite. **B**. Cribricyath *Szecyathus cylindrucus* Vologdin, 1957, Usa Formation, Botoman Stage, Lower Cambrian, Batenevskiy Range, Altay Sayan Foldbelt, Russia; MNHN Ca 194; B_1, detail of skeleton outer wall; B_2, detail of B_1 (rectangle) showing microgranular microstructure. **C**. *Cloudina hartmanae* Germs, 1972, Birba Formation, Ara Group, Upper Ediacaran, Oman; MNHN Ca 361; C_1, oblique longitudinal section; C_2, detail of C_1; C_3, oblique longitudinal ultrathin section, crossed nicols. **D**. *Cloudina hartmanae* Germs, 1972, Birba Formation, Ara Group, Upper Ediacaran, Oman; MNHN Ca 360; D_1, longitudinal section showing two primary skeletal layers; D_2, detail of D_1 showing secondary elongated crystals initiated at primary layer surface; D_3, longitudinal ultrathin section showing several primary layers, crossed nicols; D_4, detail of D_3, transmitted light; D_5, detail of D_4, crossed nicols. Scale bars A_1, B_1, C_1, D_3 1 mm; A_2, B_2, C_2, D_1, D_4 100 μm; C_3, D_2, D_5 10 μm.

overgrowths of shells by euhedral calcite crystals. This microstructure very much resembles a foliated calcite microstructure of some mollusc, brachiopod, and bryozoan skeletons (e.g., Taylor and Weedon 2000: fig. 5; Kobayashi and Samata 2006: fig. 6; Checa et al. 2007: fig. 1). Both foliated calcite and aragonite microstructures are restricted to phyla that are united in the Lophotrochozoa clade of the Bilateria (e.g., Adoutte et al. 2000). Such a platy structure implies that the skeleton of *Namacalathus* was enveloped by an organic matrix and that these species bore a group of genes which encoded for organic matrix responsible for the formation of such a microstructure.

The *Protolagena* skeleton has not been studied in details yet but probably it had a calcareous test, as indicated by the

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lack of flattening, its multilaminate micritic wall, and traces of aragonite in the wall as revealed by Raman microspectroscopic analysis (Zhang 1994; Cai et al. 2010). *Chenmengella* and *Qinella* tubes are phosphatic although this is probably secondary (Hua et al. 2003b, 2007; Cai and Hua 2007; this paper). However, conical tubes of *Conotubus* Zhang, Li, and Dong in Ding et al. 1992 from the Ediacaran of South China probably had a primary organic composition which is inferred due to their pyritisation and flattening (Cai et al. 2010). It is interesting to note that in a cross-section, preserved among Vologdin and Maslov's (1960: fig. 1e) type collection (PIN no. 1766/1000; Zhuravlev 2001) from the Ust'-Yudoma Formation of the Yudoma River, nominal *Majaella* resembles "foliose calcified metaphytes" described by Grant et al. (1991) from the Urusis Formation of the Nama Group in southern Namibia. However, the highly advanced skeletal structure of the Siberian fossil, consisting of a central cone with multiple fine concentric wrinkles and a flat peripheral ring with rhombic surface pattern, has no comparable morphology among calcified algae. Its general outlook rather reveals some similarities with "quilted" soft-bodied vendobionts, although it does not closely fit the morphology of any of them.

Steiner et al. (2007: 73) perhaps express a common view on the nature of Ediacaran fossils noting that it is doubtful if any true biomineralised shelly organisms were present in Neoproterozoic and *Namacalathus* even is interpreted as an unmineralised organism covered with a tufa-like encrustation (Brasier et al. 2011: 552). Such a definition is hardly applicable to organisms like *Suvorovella*, *Majaella*, and *Namapoikia*. Similarly, it is not the case for *Namacalathus* with its unique morphology. *Namacalathus* is the most advanced Neoproterozoic skeletal animal, which according to its microstructure is probably related to a lophotrochozoan stem group although it does not resemble morphologically even the earliest Cambrian molluscs and brachiopods.

Ediacaran shelly fossils and terminal Neoproterozoic extinction event

The Ediacaran skeletal fauna formed a totally new ecosystem, the metazoan-moderated reefal ecosystem, immediately after its introduction onto carbonate shelves (Grotzinger et al. 2005; Wood et al. 2005). Although these reefs were mostly thrombolites, they were true three-dimensional edifices that provided significant opportunity for further diversification. These skeletal fauna followed the distribution of available carbonate substrates without any distinct palaeogeographic pattern. In this respect it was similar to concurrent Ediacaran soft-bodied faunas, which were sensitive to environmental factors and changed their distribution in response to shifting habitat pattern rather than geographic barriers, as has been shown by Grazhdankin (2004; Fig. 7). Thus, the Ediacaran diversification was mostly the factor of growth of beta-diversity (taxonomic differentiation between communities) similar to that observed within early Cambrian reef communities (Zhuravlev and Naimark 2005).

The morphology of Ediacaran skeletal fossils is varied and not simple. In this respect they resemble famous Ediacaran vendobionts which also lack any close descendents if any at all. Similarly, apart from the anabaritids, the Ediacaran skeletal fauna vanished almost completely at the beginning of the Cambrian (ca. 541 Ma). However, the anabaritids were subjected to the same fate shortly thereafter, during the mid–early Cambrian (Botoman) mass-extinction event (Zhuravlev and Wood 1996). Some primitive trace fossil producers, *Gaojiashania–Palaeopascichnus*-group of organisms, the soft vendotaenid algae, the tubicolous organic-walled sabelliditids, and even some possible calcified cyanobacteria (*Gemma*, *Korilophyton*) disappeared approximately at the same time or at the very beginning of the early Cambrian.

It is not easy to determine whether the end-Ediacaran extinction was a global event (so-called Kotlin crisis; Brasier 1995) or a step-wise replacement of an old biota by a new one. Some authors have speculated on the various extrinsic factors which could have caused a global extinction of the entire Ediacaran biota. Among such factors an infamous asteroid impact causing mass phytoplankton mortality (Hsu et al. 1985); and widespread development of oxygen-deficient shallow marine environments either due to regression led to a massive release of methane-hydrates stored in marine sediments (Kimura and Watanabe 2001) or to upward expansion of anoxic water masses (Amthor et al. 2003; Schröder and Grotzinger 2007) were proposed. All these suggestions are mostly based on the presence of a pronounced negative stable carbon isotope shift abutting the Ediacaran–Cambrian boundary in many regions.

More recent data indicate a multiplicity of such $\delta^{13}C$ excursions (Kouchinsky et al. 2005; Ishikawa et al. 2008) but an absence of any coeval enrichment in redox-sensitive trace elements (Fike and Grotzinger 2008). As well, a gradual decrease and stepwise recovery pattern of this excursion seems to be inconsistent with the overturn of stratified ocean and melting of methane hydrate, which should result in sharp shift (Ishikawa et al. 2008). These latter and better biostratigraphically constrained isotope data are consistent with a continuous diversification of Early Cambrian biota across these shifts, and in many sections the latest Ediacaran elements co-occur with the earliest representants of early Cambrian fauna (e.g., *Cloudina* with anabaritids on the Siberian Platform; *Cloudina* with probable *Platysolenites* on the West Siberian Plate, Kontorovich et al. 2008; vendotaeniids with complex trace fossils in Spain, Vidal et al. 1994; vendobionts with trace fossils of Phanerozoic aspect in Namibia, Jensen and Runnegar 2005). Judging from radiometric dating, Grazhdankin (2004) suggested that a whole typical Ediacaran soft-bodied community (*Tribrachidium, Dickinsonia*) had still survived about 541±4 Ma in Ukraine (Mogilev Formation). Although claims for a

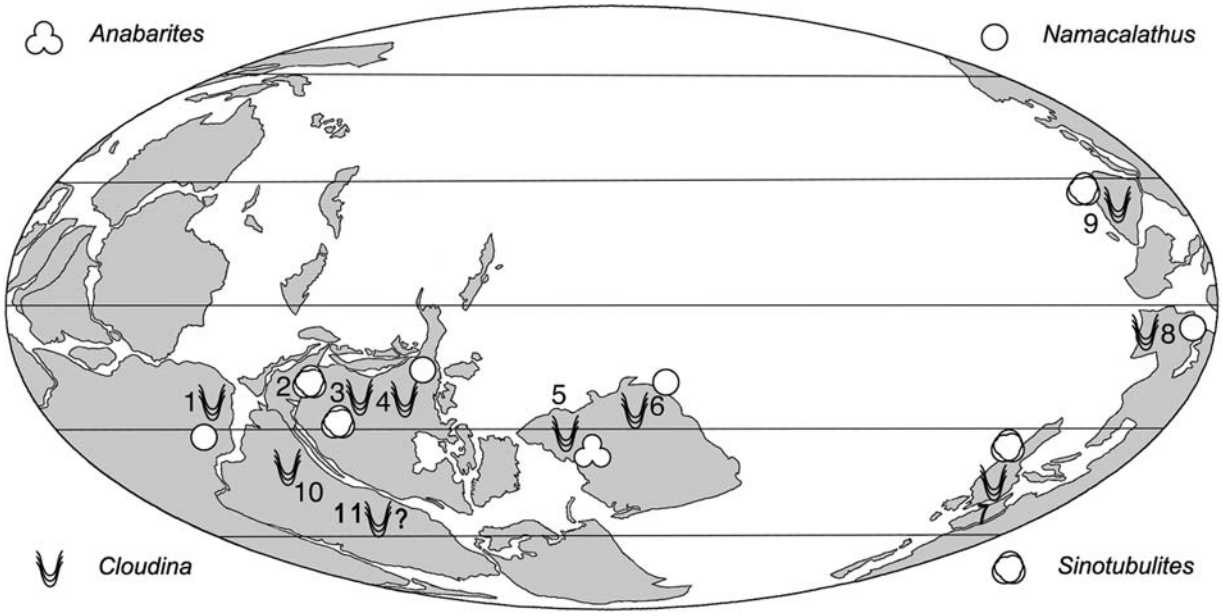

Fig. 7. Global reconstruction of late Ediacaran continental positions, simplified from Smith (2001), and indicating areas where carbonate deposits and principal skeletal fossil assemblages occur (symbols). 1, Kuibis and Schwarzrand subgroups, Namibia; 2, La Ciénega Formation, Sonora, Mexico; 3, upper Reed Dolomite and lower Deep Spring Formation, California and Nevada, USA; 4, Byng Formation, British Columbia, Canada; 5, Ust'-Yudoma Formation, Yakutia, Russia; 6, Zabit and Ungut formations, Eastern Sayan; Belka and Karchit formations, Mountain Shoria; Tarzhul Formation, Kuznetsky Alatau, Altay Sayan Foldbelt; Kotodzha and Raiga formations, West Siberian Plate, Russia; 7, Río Huso and Ibor groups, Castilla-La Mancha, Spain; 8, Birba Formation, Oman; 9, Beiwan and Baimatuo members, Dengying Formation, Hubei and Shaanxi, China; 10, Tamengo Formation, Corumbá Group, Mato Grosso do Sul, Brazil; 11, Yerbal Formation, Arroyo del Soldado Group, Uruguay.

discovery of Cambrian "Ediacaran" fossils are not uncommon (Conway Morris 1993; Crimes et al. 1995; Jensen et al. 1998; Hagadorn et al. 2000; Lin et al. 2006; Shu et al. 2006), none of them, even frondlike *Stromatoveris* described by Shu et al. (2006) from the Chengjiang Lagerstätte of China, possesses features typical of Ediacaran vendobionts whose peculiar organisation is supported by uniquely preserved specimens and by a growth pattern analysis (Zhuravlev 1993; Grazhdankin 2004; Narbonne 2004; Xiao et al. 2005; Ivantsov and Naimark 2007; Antcliffe and Brasier 2008).

Even if we accept the entire set of Cambrian fossils which have at one time or another been interpreted as Ediacaran survivors, their total number would be absolutely negligible in comparison with the overall number of fossils representing the Cambrian biota at any datum plane during the Cambrian interval. Ediacaran organisms, both skeletal and soft-bodied, disappeared, and their extinction was complete although not abrupt. The more advanced Early Cambrian fauna replaced the Ediacaran fauna due to increasing predator pressure as well as by a devastation of environments, because vendobionts depended firmly on microbial films (Seilacher and Pflüger 1994). The evidences for boreholes penetrating Ediacaran skeletons are still equivocal but the number of known predators at the very beginning of the early Cambrian epoch is sufficient to make them responsible for the elimination of the vendobionts (Zhuravlev and Riding 2001).

The Ediacaran–Cambrian biotic replacement has not happened at one stroke, but rather during a short interval of about 5 m.y. Strata of 545 Ma age contain pure Ediacaran biota whereas those of 540 Ma age almost completely lack such fossils. Perhaps this was the most remarkable biotic replacement in the history of life.

Systematic palaeontology

Phyllum indet.

Family Cloudinidae Hanh and Pflug, 1985

Genus *Cloudina* Germs, 1972

Type species: *Cloudina hartmanae* Germs, 1972; Namibia, Schlip, Driedoornvlakte farm, Zaris Subbasin, Nama Group, Kuibis Subgroup, Schwarzkalk Limestone Member, upper Ediacaran (Germs 1972: 753–755, pl. 1: 1, holotype).

Remarks.—The original spelling of the species name "*C. hartmannae*" has been corrected to "*C. hartmanae*" by Glaessner (1976: 266) because the species was named after professor Olga Hartman (Germs 1972: 755).

Cloudina ex gr. *C. riemkeae* Germs, 1972

Fig. 3A, C–E.

Material.—Five etched specimens from the Kyyry-Ytyga locality, Yudoma River right bank, Yakutia-Sakha Republic, Russia (southeastern Siberian Platform); interval 10, Ust'-Yudoma Formation, Yudoma Group, upper Ediacaran.

Description.—Tubicolous, gently curving, sinuous, narrowly conical calcareous microfossil (up to 3 mm in length) consist-

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ing of eccentrically nested apically slightly flaring funnel-like segments (up to 10 segments per 1 mm of tube length). Segment width is relatively consistent and ranges from 0.20 mm (in its narrower lower part) to 0.25 mm in the same specimen, usually gradually increasing with increased length. The largest observed segment width is 0.50 mm. The tube inner surface is smooth. The primary composition of tubes is high-Mg calcite according to its present dolomitic composition and the presence of square holes probably formed after microdolomite crystal dissolution (Fig. 3D).

Remarks.—In its size range and relatively regular tube shape, Siberian *Cloudina* resembles *Cloudina riemkeae* Germs, 1972 from the Nama Group of Namibia and *C. dunfeei* Signor, Mount, and Onken, 1987 (Signor et al. 1987: 4.1–4.14; = *Coleolella* sp. in Signor et al. 1983: fig. 3B) from the lower Deep Spring Formation in the White-Inyo Mountains of eastern California and Esmeralda County of western Nevada, USA, thus confirming Grant's (1990) opinion on the synonymy of *Nevadatubulus* and *Cloudina*. However, differences in preservation of the material do not allow us to attribute our new specimens unequivocally to the Namibian species.

Among the last but not the least problems related to *Cloudina* is the question of predatory borings in its shells leading to far-reaching reconstructions of Neoproterozoic trophic webs and the basic phenomena caused the Cambrian explosive radiation. A number of such boring is discovered on *Cloudina* tubes from South China and Namibia (Bengtson and Yue 1992; Brain 2001; Hua et al. 2003a). Despite the presence of some holes, the Siberian material points to another interpretation. Some tubes bear square holes rather than rounded ones (Fig. 3C, D) and even small fragments (0.8 × 0.3 mm) display three or more holes (Fig. 3A, D). Such structures are probably formed as a result of diagenetic dissolution of microdolomite crystals which formed at the tube surface due to its primary high-Mg calcite composition. Further diagenetic processes led to infilling of the holes in such a way that they finally became rounded in outline and resemble unsuccessful incomplete borings (Fig. 3D). Circular pits similar in both size and shape to Precambrian "borings" appeared on the calcareous cuticle of crustaceans during bacterial degradation (Hof and Briggs 1997). No correlation between shell diameter and hole diameter was observed by Hua et al. (2003a) in *Cloudina*, and *Sinotubulites* from the same locality lacked any holes completely, probably, due to a differing primary mineralogy.

Cloudina ex gr. *C. hartmanae* Germs, 1972

Figs. 3B, F–H, 4A, B.

1989 "microorganismos tubulares"; Palacios Medrano 1989: pl. 16.
1990 *Cloudina* sp.; Grant 1990: fig. 7C, D.
1994 *Cloudina hartmannae* [sic] Germs, 1972; Vidal et al. 1994: fig. 12A, B.
1994 *Cloudina* sp.; Vidal et al. 1994: fig. 12C.

Material.—Two thin sections with six fossils and five etched fragmentary steinkerns from the Tirteafuera River locality, Abenójar Anticline, East Lusitanian–Alcudian Zone, central Spain; lower La Grajera-Cañuelo unit, Ibor Group, upper Ediacaran. As well, the same species is present in Ibor Group outcrops of the Navalpino Anticline, East Lusitanian–Alcudian Zone and in the Río Huso Group of the Río Huso section, northern flank of the Valdelacasa Anticline, Galician–Castilian Zone; central Spain (Grant 1990; Vidal et al. 1994).

Description.—Tubicolous calcareous microfossils consisting of apically slightly flaring funnel-like segments (up to 2.8 mm in diameter) eccentrically placed within each other and imparting an irregular polygonal shape to the cross-section. The tube length is over 4.2 mm. The wall thickness is ca. 0.08 mm. The wall is replaced by fine transparent sparry calcite mosaic whereas the tube cavity is sealed by coarse transparent sparry calcite beneath a possible tabula and by sediment above the tabula. Beneath the tabula, within sparry calcite mosaic, some rodlike, slightly curved transparent structures are preserved which can be either broken wall fragments (the thickness is the same) or bacterial borings (Fig. 4A).

Remarks.—Etched fossils from Spain were studied as gold-coated samples under scanning electronic microscope (SEM) Jeol JSM 6400 at the Servicio de Microscopía Electrónica, Universidad de Zaragoza in both secondary electron emission and backscattering regimes.

By its morphology and size range, this fossil is close to *Cloudina hartmanae* Germs, 1972 from the Nama Group of Namibia.

Hua et al. (2005b) discounted a presence of any tabula ("transverse cross wall") within *Cloudina* tubes. At the same time they demonstrated a "hemispherical basal end" (Hua et al. 2005b: fig. 1A, B, F; also see Chen and Sun 2001: pl. 1: 6–13, pl. 2: 4–6). Also, a longitudinal section of a *Cloudina* ex gr. *C. hartmanae* tube in our material shows that lower funnel-like tube segments are occupied by sparry calcite while the uppermost ones contain sediment only (Fig. 4A). Thus, the character of sediment and marine cement infilling indicates that some continuous transverse structures are present in tubes of this species at least. In any case, these are not tabulae typical of tubicolous polychaetes. The latter secrete tabulae, possibly in response to damage of the posterior end of the tube, but such tabulae bear an apparent perforation to accommodate tufts of chaetae on the worm's posterior abdominal segment (Hedley 1958). The presence of both "hemispherical basal end" and tabulae favours a microconchid lophophorate affiliation for this fossil. However, microconchids possess much more elaborated microstructure and perforated shells (Taylor and Vinn 2006).

Family indet.

Genus *Sinotubulites* Chen, Chen, and Qian, 1981

Type species: *Sinotubulites baimatuoensis* Chen, Chen, and Qian, 1981; China, western Hubei Province, Yangtze Platform, Dengying Formation, Baimatuo Member, upper Ediacaran (Chen et al. 1981: 119–120, pl. 1: 1, 2, holotype).

Sinotubulites sp.

Fig. 5A, B.

Material.—Two etched fragments of inner molds from the Tirteafuera River locality, Abenójar Anticline, East Lusitanian–Alcudian Zone, central Spain; lower La Grajera-Cañuelo unit, Ibor Group; upper Ediacaran.

Description.—Phosphatised multilayered tubicolous microfossil with thick wall and sharp transverse surface sculpture of steep discontinues irregular intercalating wavy wrinkles. The largest fragment is 0.4 mm wide and ca. 1.0 mm long. Wrinkle density is ca. 20 wrinkles per 1 mm.

Remarks.—This fossil is morphologically close to *Sinotubulites shaanxiensis* Zhang, Li, and Dong in Ding et al. 1992 from the Gaojiashan Member of the Dengying Formation of the Shaanxi Province, South China published by Chen and Sun (2001: pl. 3: 6, 7). However, the fragmentary preservation of our specimen precludes detailed comparison.

Genus *Chenmengella* A. Zhuravlev, Liñán, and Gámez Vintaned nov.

Etymology: In honour of Professor Chen Meng'e, one of the discoverers of the Ediacaran skeletal fauna, and in order to modify the original generic name (*Chenella*).

Type and only species: *Chenella laevis* Zhang, Li, and Dong in Ding et al., 1992; China, southern Shaanxi Province, Yangtze Platform, Dengying Formation, Beiwan Member, upper Ediacaran (Ding et al. 1992: 89, pl. 14: 3, holotype).

Diagnosis.—Cylindrical to weakly tapering, straight to slightly and irregularly curved, primarily calcareous tubicolous microfossil with circular to slightly oval cross-section and thin single-layered wall. Both wall surfaces are smooth.

Remarks.—The generic name is preoccupied by a foraminifer *Chenella* Miklukho-Maklay, 1959 and is thus replaced here (see Miklukho-Maklay 1959).

Although *Chenmengella* (= *Chenella*) until now has been described only from South China (Ding et al. 1992; Hua et al. 2000a, b; Zhang and Hua 2000) it is probably one of the most widespread Ediacaran skeletal fossils. It occurs in the La Ciénega Formation of northwestern Sonora, Mexico (*Cambrotubulus* cf. *C. decurvatus* Missarzhevsky, 1969 and ?*C.* cf. *C. decurvatus* in McMenamin, 1985: figs. 5.1, 5.4) and in the Turkut Formation on the northern Siberian Platform (*Cambrotubulus decurvatus* Karlova, 1987: fig. 1). Possibly, *Cambrotubulus decurvatus* commonly listed from the lowermost Nemakit–Daldynian part of the Ust'-Yudoma Formation on the southern Siberian Platforms (e.g., Khomentovsky and Karlova, 2005: 24) belongs to the same genus. By comparison with *Cambrotubulus*, *Chenmengella* lacks the thriradial symmetry of a cross-section and possesses straight to irregularly curved cylindrical tubes rather than regularly curved narrow conical shells.

In its morphology and dimensions, two other species of *Chenmengella* are similar to *Chenmengella laevis* (Zhang, Li, and Dong in Ding et al. 1992) from the Beiwan Member of the Dengying Formation of Shaanxi Province, South China. The species *Chenmengella canaliculata* Zhang et al. (Ding et al. 1992: pl. 14: 10; Hua et al. 2000a: pl. 2: 9; Zhang and Hua 2000: pl. 1: 4) differs from the type species by the presence of a brittle fracture following the tube length, probably merely indicating a fragility of such thin-walled tubes. Similarly, Steiner et al. (2007) noted that in the case of *C. canaliculata*, a single specimen existed only which exhibits a longitudinal furrow and dumbbell-shaped cross-section, both resulting from compaction. In turn, *Chenmengella regularis* Zhang and Hua, 2000 (Hua et al. 2000a: pl. 1: 2, 2000b: pl. 2: 11; McCall 2006: fig. 149.11) does not show any distinct feature other than a slightly different curvature of the longest tube fragments. As well, all these species co-occur in the same locality and are thus treated here as subjective synonyms.

Stratigraphic and geographic range.—Upper Ediacaran; Yangtze Platform (China), Siberian Platform (Russia) and Laurentia (Mexico).

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