A diverse and exquisitely preserved organic-walled microfossil assemblage from the Meso–Neoproterozoic Mbuji-Mayi Supergroup (Democratic Republic of Congo) and implications for Proterozoic biostratigraphy

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ABSTRACT

A well preserved and diversified microfossil assemblage is reported from the Meso–Neoproterozoic Mbuji-Mayi Supergroup in the Kasai oriental Province, central part of Democratic Republic of Congo. A total of 49 taxa belonging to 27 genera were identified, including 11 species of unambiguous eukaryotes, 10 species of possible eukaryotes or prokaryotes and 28 species of probable bacteria. This assemblage is more diverse than previously reported but includes taxa reported in coeval worldwide assemblages. It is characterized by abundant sphaeromorphs, filamentous colonial aggregates and filamentous forms, as well as a relatively low diversity of acanthomorphs including the Late Mesoproterozoic and Early Neoproterozoic index fossil – *Trachyhystrichosphaera aimika* – reported for the first time in Central Africa. This species co-occurs with other taxa also reported for the first time in Africa: *Trachyhystrichosphaera botula*, *Jacutianema solubila*, *cf. Tappania* sp., *Valeria elongata* and numerous other taxa. Correlation with other geochronologically constrained successions that contain *Trachyhystrichosphaera* confirms *T. aimika* as promising index fossil to define the Late Mesoproterozoic–Early Neoproterozoic interval. The available biostratigraphic data enable to suggest a minimum Tonian age for the Mbuji-Mayi Supergroup. This age is consistent with the published and new geochronological data. Comparison with worldwide Proterozoic assemblages permits to define microfossil assemblages useful for biostratigraphy. This study significantly improves our understanding of the diversity of the Late Mesoproterozoic–Early Neoproterozoic biosphere, and in particular the diversification of early eukaryotes, preserved in the Democratic Republic of Congo rock record and more broadly in Africa where micropaleontological investigations are sparse.

1. Introduction

Proterozoic microfossils constitute a major source of paleontological information essential for understanding early life evolution. In particular, they document the evolution of biological innovations and patterns of diversification of early eukaryotes (e.g. Butterfield, 2015; Javaux, 2011; Javaux and Knoll, in review; Knoll, 2014) but are also helpful for biostratigraphic correlations and paleoenvironmental reconstruction of Proterozoic rocks (Butterfield and Chandler, 1992; Knoll, 2009; Knoll et al., 2006). To date, few paleontological investigations have been carried out in the Pre-Ediacaran Proterozoic of Africa. Prior to our new study

presented here, two early studies investigated the micropaleontology of the Mbuji-Mayi (former Bushimay) Supergroup in Democratic Republic of Congo (DRC) (Baudet, 1987; Maithy, 1975). They reported respectively 34 and 41 taxa of organic-walled microfossils. However, our taxonomic revision, based on more recent work on Precambrian organic-walled microfossils (Butterfield et al., 1994; Hofmann and Jackson, 1994; Sergeev et al., 1997; Sergeev, 2009; Yankauskas et al., 1989) suggests that many of these were synonymous. Other studies report few acritarchs in the Late Mesoproterozoic Taoudeni Basin of Mauritania (Amard, 1984, 1986; Lottaroli et al., 2009), mostly species of *Leiosphaeridia* and *Arctacellularia*, although a new study evidences a higher diversity and the occurrence of acanthomorphs (Beghin et al., in review). Baudet (1988) reported 20 microfossil taxa, especially sphaeromorphs, in the Mesoproterozoic Kavumwe Group of Burundi (Deblond et al., 2001; Fernandez-Alonso et al.,

2012). In the Neoproterozoic Kwahu Group of Ghana (>0.85 Ga Abetifi and Anyaboni formations), Couëffé and Vecoli (2011) reported 10 genera: *Leiosphaeridia*, *Pterospermopsimorpha*, *Synsphaeridium*, *Coneosphaera*, *Arctacellularia*, *Navifusa*, *Satka*, *Valeria*, *Trachysphaeridium* and putative *Trachyhystrichosphaera* (the latter is doubtful based on published illustration, where no processes are visible, cfr. their figure 6.8).

To improve our understanding of the Late Mesoproterozoic–Early Neoproterozoic biosphere evolution and especially the microfossil record of Central Africa, we studied the assemblage of organic-walled microfossils preserved in fine-grained siliciclastic rocks of the Meso–Neoproterozoic Mbuji-Mayi Supergroup, in the Sankuru-Mbuji-Mayi area, DRC (Figs. 1 and 2).

Our new study of a larger number of samples (263) from 5 drill cores, using a non-standard maceration protocol minimizing mechanical shocks, reveals an exceptionally diverse and well-preserved assemblage of 49 taxa of organic-walled microfossils. Among those, 22 taxa are reported for the first time in the assemblage but are known elsewhere. Comparison with coeval world-wide assemblages shows that the Mbuji-Mayi assemblage is more diverse but includes taxa known elsewhere except for one possible new taxon (unnamed acanthomorph), permitting to develop a worldwide biostratigraphy for the Late Mesoproterozoic–Early Neoproterozoic interval.

2. Geological setting, depositional environments and age of the Mbuji-Mayi Supergroup

The Mbuji-Mayi Supergroup is a sedimentary sequence unaffected by regional metamorphism (Raucq, 1957), deposited in the intracratonic failed-rift Sankuru-Mbuji-Mayi-Lomami-Lovoy Basin

(SMLL; Delpomdor and Préat, 2013; Delpomdor et al., 2013a,b) which extends from SE to NW between North Katanga and Kasai provinces. In the South-eastern part of the SMLL Basin (i.e. Northwest Katanga Province), the Mbuji-Mayi Supergroup overlies the Mesoproterozoic Kibaran Belt while in the North-western part of SMLL Basin, where we focused our work (i.e. Oriental Kasai Province), it rests unconformably upon the Archean Kasai Block (Fig. 1; Cahen and Mortelmans, 1947; Raucq, 1957, 1970). Amygdaloidal basaltic lavas overlie the Mbuji-Mayi Supergroup, at the confluence of Mbuji-Mayi and Sankuru rivers (Cahen et al., 1984). Lithostratigraphically, the Mbuji-Mayi Supergroup consists of two distinct successions; a lower siliciclastic sequence (~500 m thick) of the BI Group and an upper carbonate sequence (~1000 m thick) with stromatolitic build-ups and black shales of the BII Group (Figs. 2 and 3; Raucq, 1957, 1970). The sediments which formed the BI Group came from the Kibaran Belt, the Bangweulu and Kasai blocks. They indicate a detrital transport from the SE and/or E of SMLL Basin (Delpomdor et al., 2013a). The BI Group comprises six subgroups in ascending order: BIa, BIb, BIc, BId, BIE and BIe. The BIa is not represented in the Western part of the SMLL Basin (i.e. Sankuru-Mbuji-Mayi area), but has been observed in the South-eastern part, especially near Makululu and Kiandoki villages (Cahen and Mortelmans, 1947) and the BIE is only visible in the Kafuku Region. The BII Group, which comprises mostly transgressive carbonates, consists of five subgroups in ascending order: BIIa, BIIb, BIIc, BIId and BIIe. Detailed descriptions of these subgroups have been given in Raucq (1957, 1970) and updated (especially for the carbonates) in Delpomdor et al. (2013a, 2015).

A total of 11 microfacies are recognized from the BIe to BIIe subgroups showing that carbonates were deposited in a marine environment that evolved to evaporitic marine, lacustrine and
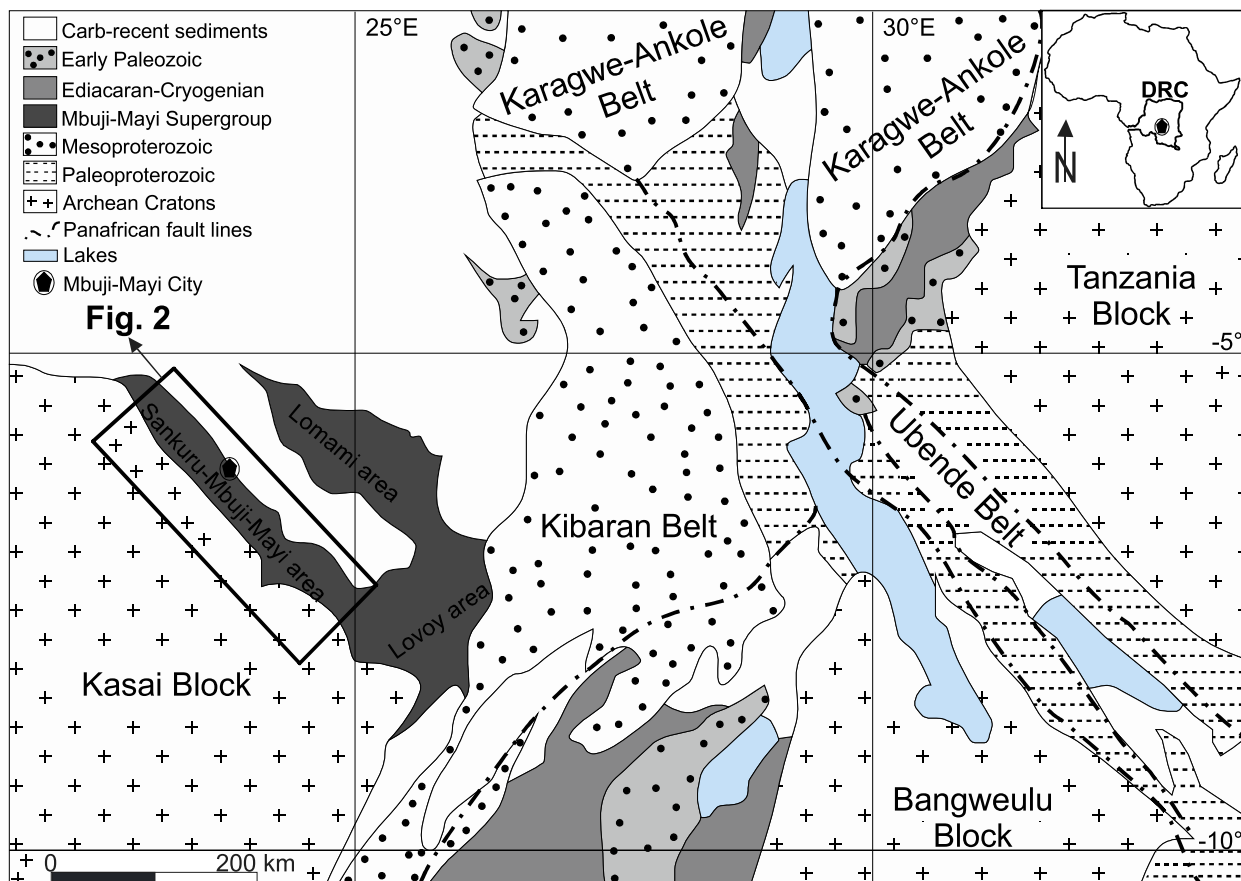

Fig. 1. Tectonic setting synthesis of some Paleoproterozoic–Neoproterozoic Basins in Central Africa (Modified after Kadima et al., 2011 and references therein).
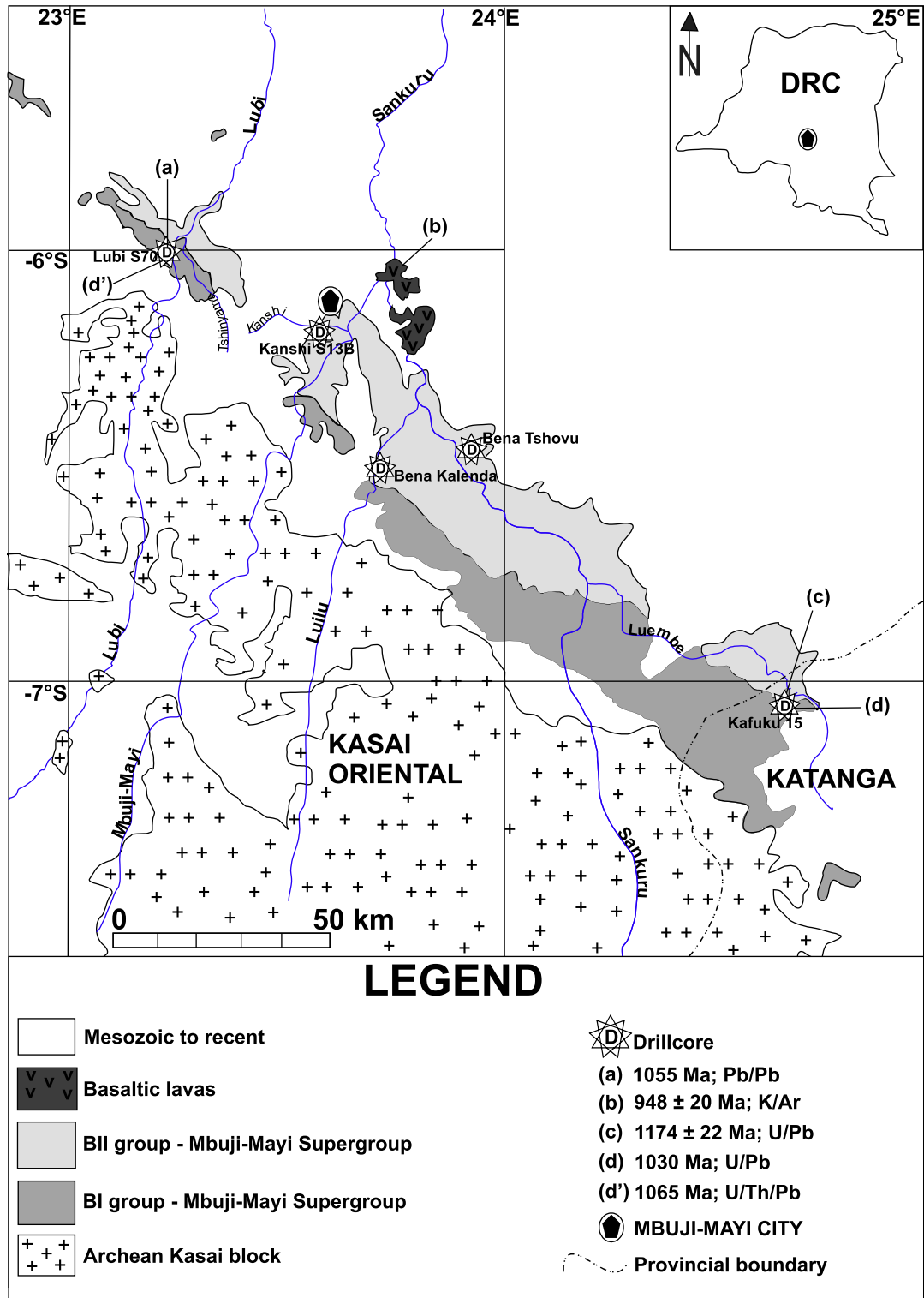
Fig. 2. Simplified geological map of the Mbuji-Mayi Supergroup in the Sankuru-Mbuji-Mayi region. Location of boreholes are indicated by white stars: Lubi S70; Kanshi S13B; Bena Kalenda; Bena Tshovu in eastern Kasai and Kafuku 15 in northwestern Katanga (Democratic Republic of Congo), modified from Delpomdor et al., 2013a. (See caption of Fig. 3 for references).

sabkha settings in the superficial parts of a ramp-system (Delpomdor et al., 2013b, 2015).

Syngenetic galena from three samples (two coming from BIe$_1$ Formation in Lubi and Senga-Senga valleys and the third from contact between BIIa and BIIb in Luembe Valley) gave a ^{207}Pb/^{206}Pb age of 1065, 1040 and 910 Ma respectively (Cahen, 1954; Holmes and Cahen, 1955; Raucq, 1957). The model age is about 1055 Ma (Cahen, 1974). Amygdaloidal basaltic lavas overlying the Mbuji-Mayi Supergroup at the Sankuru-Mbuji-Mayi confluence yielded an age of 948 ± 20 Ma (Cahen et al., 1984). Recently, Delpomdor et al. (2013a) reported a maximum age of 1174 ± 22 Ma, for the Mbuji-Mayi Supergroup deposit, established
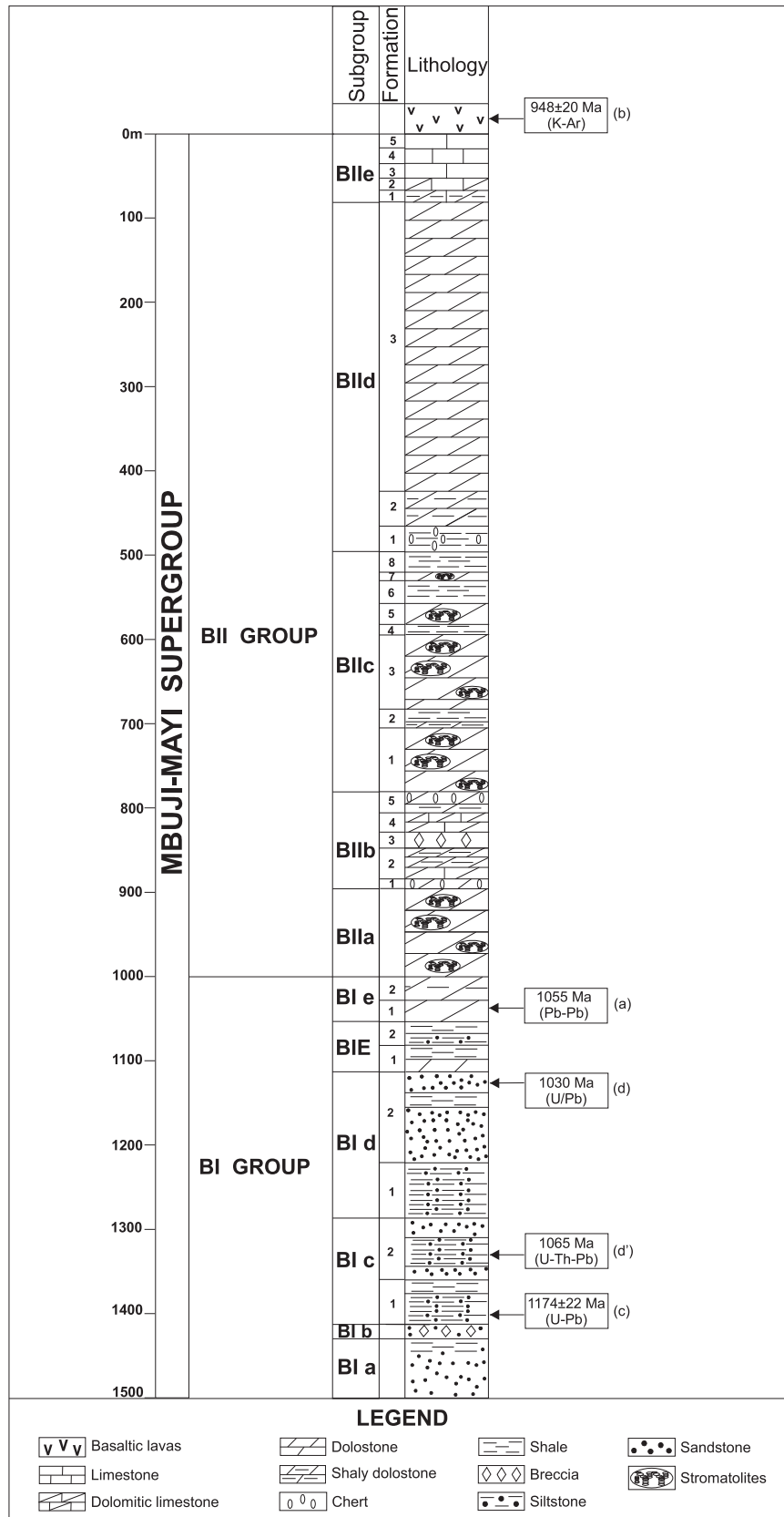
Fig. 3. Synthetic lithostratigraphy of Mbuji-Mayi Supergroup (modified from Raucq, 1957, 1970). Radiometric data from (a) Cahen (1974), (b) Cahen et al. (1984), (c) Delpomdor et al. (2013a), (d) and (d′) François et al. (2015 and *in preparation*).

by U-Pb methods on detrital zircon grains from the BId subgroup (in Kafuku 15 drill cores).

3. Materials and methods

3.1. Samples

In this study, five drill cores located within the Sankuru-Mbuji-Mayi area (western part of SMLL Basin) between Lubi and Luembe rivers (Fig. 2) were sampled. These drill cores were drilled in the 1950's and the cores are stored in the Department of Geology from the Royal Museum for Central Africa (RMCA) in Tervuren, Belgium. The studied drill cores were described by Wazilewski (1953) and Raucq (1957,1970), from NW to SE (Fig. 4; with depths and number of treated samples in brackets). The drill core Lubi S70 (in Lubi Valley, 349 m depth and 96 samples) consists of the base of Mbuji-Mayi Supergroup, i.e. from the base of BIIa Subgroup up to the top of BIb Subgroup and reaches the contact with the granitic basement of the Kasai Block. The drill core Kanshi S13B (425 m depth, 66 samples) located at 11.5 km on the west of the Kanshi and Mbuji-Mayi rivers confluence, crosses the BII Group, more precisely from the base of the BIId Subgroup to the top of the BIIb Subgroup. The drill core Bena Tshovu (60 m depth, 6 samples) intersects the middle of the BIId Subgroup. The drill core Bena Kalenda (91 m depth, 28 samples) crosses the bottom of the BIIb Subgroup. Finally the drill core Kafuku 15 (200 m depth, 67 samples) cuts through the base of the BIIa Subgroup up to BId Subgroup. Thus, a total of 263 shale and siltstone samples have been investigated for micropaleontology in this study.

3.2. Sample preparation and microscopy

Organic-walled microfossils were extracted from thinly laminated siltstone and light to dark grey shale samples using slow acid maceration techniques (Grey, 1999), involving the dissolution of the mineral rock matrix by use of concentrated HCl and HF, followed by hot HCl to remove neo-formed fluorides, rinsing with distilled water and decanting between each steps, with no centrifugation to minimize mechanical shocks. No oxidation was applied on organic residues. The macerates were filtered using 25 μm and 10 μm mesh-size filters for removal of fine-grained amorphous organic matter and facilitating taxonomic study of palynomorphs. For each sample, two slides of two size fractions (10–25 μm and >25 μm) were mounted permanently for optical microscopy study. Transmitted-light photomicrographs were acquired using an Axio Imager A1m microscope equipped with an AxioCam MRc5 digital camera (both Carl Zeiss, Germany). All specimens discussed here are deposited in the laboratory of Paleo biogeology-Paleopalynology-Paleobotany (PAL³), Department of Geology, UR GEOLOGY, at the University of Liege. Specimens illustrated are provided with a slide number followed by an England Finder coordinates. Maithy's original slides (MRAC collection, Tervuren) were also examined.

4. Diversity of the Mbuji-Mayi assemblage

As noted above, the former studies carried out on Mbuji-Mayi assemblage (Baudet, 1987 and Maithy, 1975) reported several species of acritarchs and filamentous forms. Several of these species were synonymized to others species in later studies (Butterfield et al., 1994; Hofmann and Jackson, 1994; Sergeev et al., 1997; Sergeev, 2009; Yankauskas et al., 1989) or in the present study, as discussed in the systematic paleontology section (in supplementary data).

Our new investigation shows that organic-walled microfossils from the Mbuji-Mayi Supergroup are characterized by abundant sphaeromorph acritarchs, filamentous colonial aggregates and filamentous forms with a relatively low diversity of acanthomorphs (spine-bearing acritarchs). A total of 49 taxa belonging to 27 genera are identified (Fig. 5), increasing the diversity relatively to previous reports, with some taxa reported for the first time in the Mbuji-Mayi Supergroup. On the basis of morphological features, we categorize the Mbuji-Mayi assemblage into three groups: (1) unambiguous eukaryotes, (2) possible eukaryotes or prokaryotes and (3) prokaryotes, probably bacteria.

(1) Unambiguous eukaryotes (11 species). – These include all acritarchs with processes that extend from vesicles walls (acanthomorphs): *Germinosphaera bispinosa* Mikhailova, 1986 (Fig. 6A–C); *Trachyhystrichosphaera aimika* Timofeev et al., 1976 (Fig. 6D–L); *Trachyhystrichosphaera botula* Tang et al., 2013 (Fig. 6M–O), and an unnamed form (Fig. 6P and Q); acritarch with neck-like expansions ?cf. *Tappania* sp. (Figs. 6R and 7A, B); acritarchs with ornamented walls: *Lophosphaeridium granulatum* Maithy, 1975 (Fig. 7C–E), *Valeria elongata* Nagovitsin, 2009 (Fig. 7F and G) and *Valeria lophostriata* Yankauskas, 1982 (Fig. 7H); disphaeromorphs (vesicle enclosing another vesicle): *Pterospermopsimorpha insolita* Timofeev, 1969 (Fig. 7I–L) and *Pterospermopsimorpha pileiformis* Timofeev, 1966 (Fig. 7M and N); and the multicellular *Jacutianema solubila* Timofeev and Hermann, 1979 (Fig. 7O–R) interpreted as the Gongrosira-phase of a vaucheriacean xanthophyte (Butterfield, 2004) or an undetermined eukaryote (Butterfield, 2015). All these microfossils show a level of morphological complexity, combining wall ornamentation or processes expanding from the wall surface, recalcitrant composition and large size, or large cell size and multicellularity, a combination unknown in prokaryotes to date (Javaux et al., 2003).

(2) Possible eukaryotes or prokaryotes (10 species). – Here, are included large smooth-walled vesicles that do not preserve enough characters to place them unambiguously among eukaryotes and could as well be prokaryotic. Sphaeromorphs with recalcitrant organic walls and occasional excystment structures by partial or medial split include several species of *Leiosphaeridia* (Fig. 8A–I). Older populations from the Mesoproterozoic Roper Group (Australia) have been shown to possess multilayered walls considered as a diagnostic criteria for eukaryotes when combined with large size, excystment structures, and recalcitrant composition (Javaux et al., 2004), however these observations cannot be expanded to all leiospheres without time-consuming ultrastructural analyzes, since *Leiosphaeridia* spp. are probably polyphyletic. The species reported here include: *Leiosphaeridia crassa* Naumova, 1949 (Fig. 8A–C); *Leiosphaeridia jacutica* Timofeev, 1966 (Fig. 8D); *Leiosphaeridia minutissima* Naumova, 1949 (Fig. 8E); *Leiosphaeridia tenuissima* Eisenack, 1958 (Fig. 8F); *Leiosphaeridia ternata* Timofeev, 1966 (Fig. 8G) and *Leiosphaeridia* sp. (Fig. 8H and I). Other species that could be eukaryotic or prokaryotic include relatively large single oval vesicles such as *Navifusa actinomorpha* Maithy, 1975 (Fig. 8J and K) and *Navifusa majensis* Pyatiletov, 1980 (Fig. 8L), large vesicles with smaller attached vesicles *Coneosphaera* sp. (Fig. 8M and N), vesicles forming multicellular chains *Arctacellularia tetragonala* Maithy, 1975 (Figs. 8O–R, 9A–J and 10) previously interpreted as putative fungi at different stages of their life cycle (Hermann and Podkovyrov, 2008).

(3) Prokaryotes, probably bacteria (28 species). – This category captures all remaining microfossils with simple organization and occurring in filamentous colonial aggregates, or filamentous and coccoidal forms: *Chlorogloeaopsis kanshiensis* Maithy, 1975 (Fig. 9K) and *Chlorogloeaopsis zairensis* Maithy, 1975 (Fig. 9L); *Polysphaeroides filliformis* Hermann in Timofeev et al., 1976 (Fig. 9M–R); *Glomovertella miroedikhia* Hermann in Hermann and Podkovyrov, 2008 (Fig. 11A and B); *Obruchevella valdaica* Shepeleva, 1974
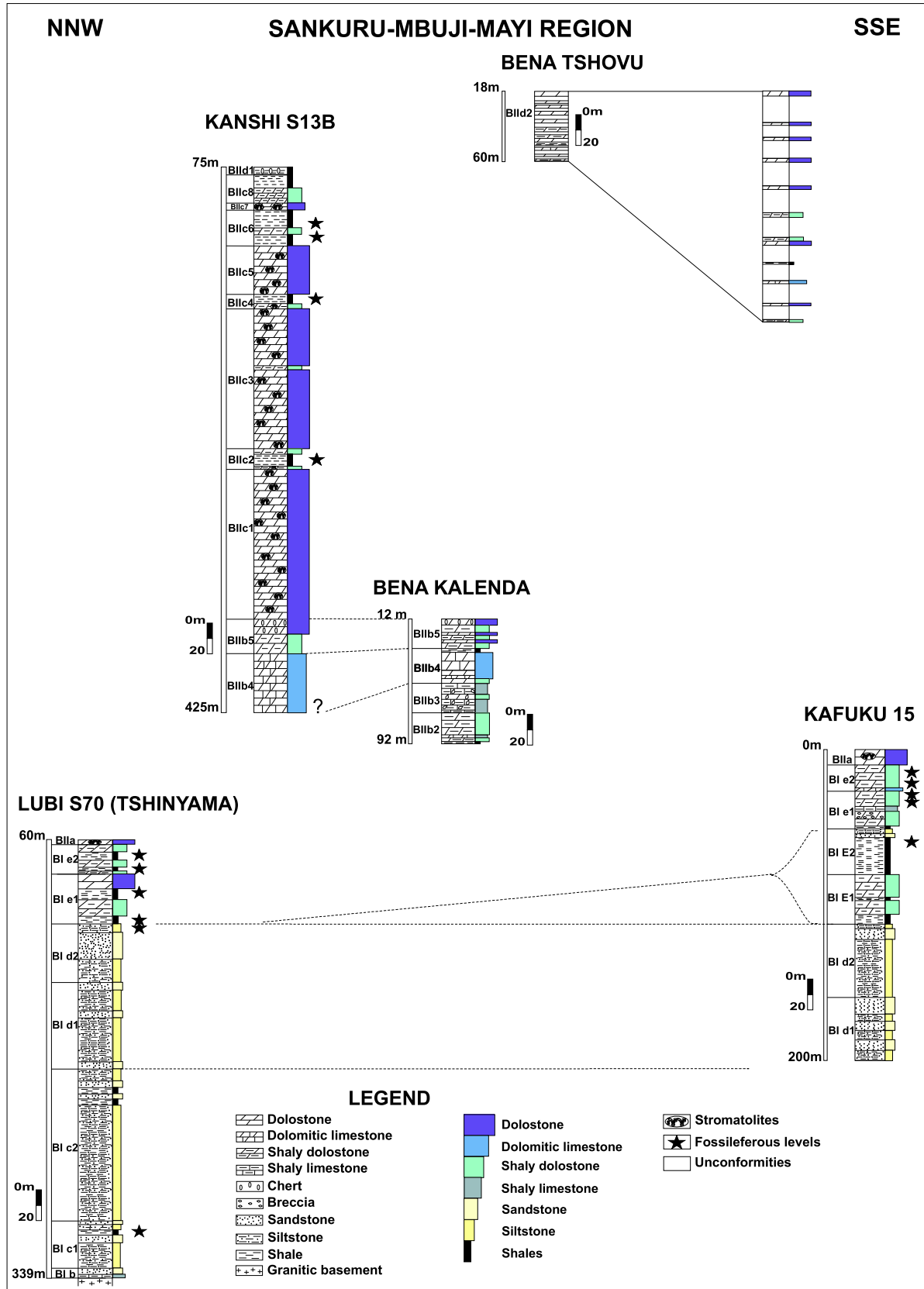
Fig. 4. Detailed lithology of studied drill cores with indication of fossiliferous levels. Unconformities are exclusively present in Bena Tshovu drill core. Modified from Delpomdor et al. (2013a) and Raucq (1970).

LUBI S70	KAFUKU 15	KANSHI S13B	TAXA **R**are (1-9) **C**ommon (10-50) **A**bondant (> 50)		
R A C A A A C C C C C C A C R A A A A C A	 R A A C C C C C C C A A A A C	A A A R A A C R C C A A A A A R C C C C C C C R C C A C R C A A A A A A C A R R R R C R C R R R	1 *Arctacellularia tetragonala* 2 *Chlorogloeaopsis kanshiensis* 3 *Chlorogloeaopsis zairensis* 4 *Coneosphaera* sp. 5 *Eomicrocystis elegans* 6 *Eomicrocystis malgica* 7 *Fabiformis baffinensis* 8 *Germinosphaera bispinosa* 9 *Glomovertella miroedikhia* 10 *Jacutianema solubila* 11 *Leiosphaeridia crassa* 12 *Leiosphaeridia jacutica* 13 *Leiosphaeridia minutissima* 14 *Leiosphaeridia* sp. 15 *Leiosphaeridia tenuissima* 16 *Leiosphaeridia ternata* 17 *Lophosphaeridium granulatum* 18 *Myxococcoides minor* 19 *Navifusa actinomorpha* 20 *Navifusa majensis* 21 *Obruchevella valdaica* 22 *Opaque filament* 23 *Ostiana microcystis* 24 *Palaeolyngbya catenata* 25 *Pellicularia tenera* 26 *Polysphaeroides filliformis* 27 *Polytrichoides lineatus* 28 *Pterospermopsimorpha insolita* 29 *Pterospermopsimorpha pileiformis* 30 *Rugosoopsis tenuis* 31 *Siphonophycus kestron* 32 *Siphonophycus punctatus* 33 *Siphonophycus robustum* 34 *Siphonophycus septatum* 35 *Siphonophycus solidum* 36 *Siphonophycus typicum* 37 *Spumosina rubiginosa* 38 *Symplassosphaeridium* spp. 39 *Synsphaeridium* spp. 40 ?cf. *Tappania* sp. 41 *Tortunema magna* 42 *Tortunema patomica* 43 *Tortunema wernadskii* 44 *Trachyhystrichosphaera aimika* 45 *Trachyhystrichosphaera botula* 46 *Trachytrichoides ovalis* 47 Unnamed form 48 *Valeria elongata* 49 *Valeria lophostriata*		

Fig. 5. The taxonomic composition of Mbuji-Mayi assemblage and their distribution relative to studied drill cores.

(Fig. 11C); Opaque filament (possibly pyritized *Siphonophycus* sp, but this remains to be evidenced, Fig. 11D); *Palaeolyngbya catenata* Hermann, 1974 (Fig. 11E and F); *Pellicularia tenera* Yankauskas, 1980 (Fig. 11G); *Polytrichoides lineatus* Hermann, 1974 (Fig. 11H); *Rugosoopsis tenuis* Timofeev and Hermann, 1979 (Fig. 11I–K); *Siphonophycus kestron* Schopf, 1968 (Fig. 11L); *Siphonophycus*
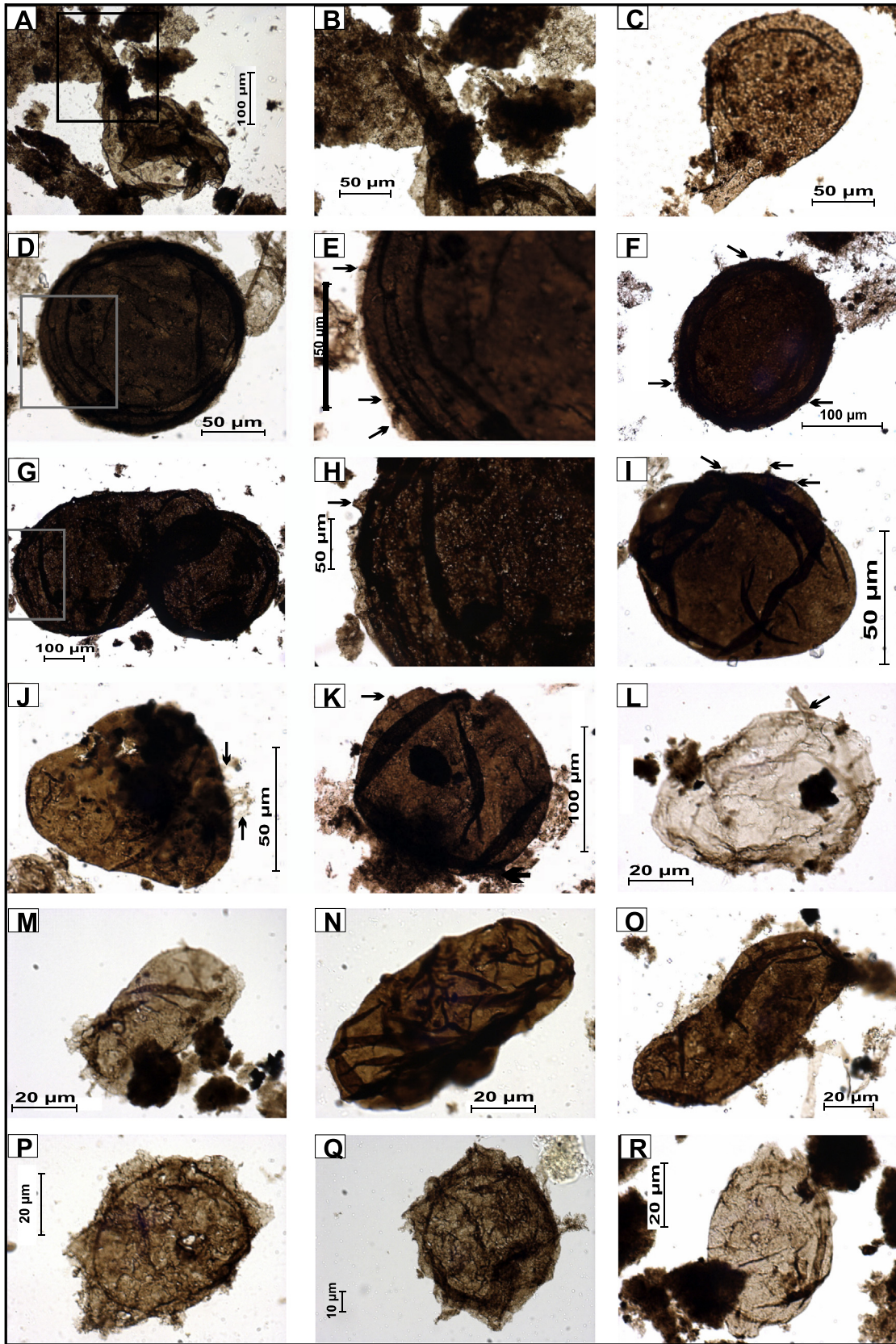
Fig. 6. (A–C) *Germinosphaera bispinosa,* (A) specimen 65066/W-44-1 and (B) magnification of box area in A; (C) *Germinosphaera bispinosa*, specimen 65066/Z-57-1. (D–L) *Trachyhystrichosphaera aimika*, with processes at the arrows (D) specimen 65078/G-44-1; (E) magnification of box area in D; (F) specimen 65084/S-56-4; (G) specimen 71270/ V-32-3; (H) magnification of box area in G; (I) specimen 65078/S-41-4; (J) specimen 65092/P-40-3; (K) specimen 65092/W-37-1; (L) specimen 65058/P-42-3. (M–O) *Trachyhystrichosphaera botula*, (M) specimen 65059/V-58-1; (N) specimen 65084/O-45-3; (O) specimen 65092/L-30-4. (P and Q) Unnamed form, specimens 65092/B-54-2 and 65096/C-56-2 respectively. (R) ?cf. *Tappania* sp., specimen 65061/Q-34-1; (R) specimen.
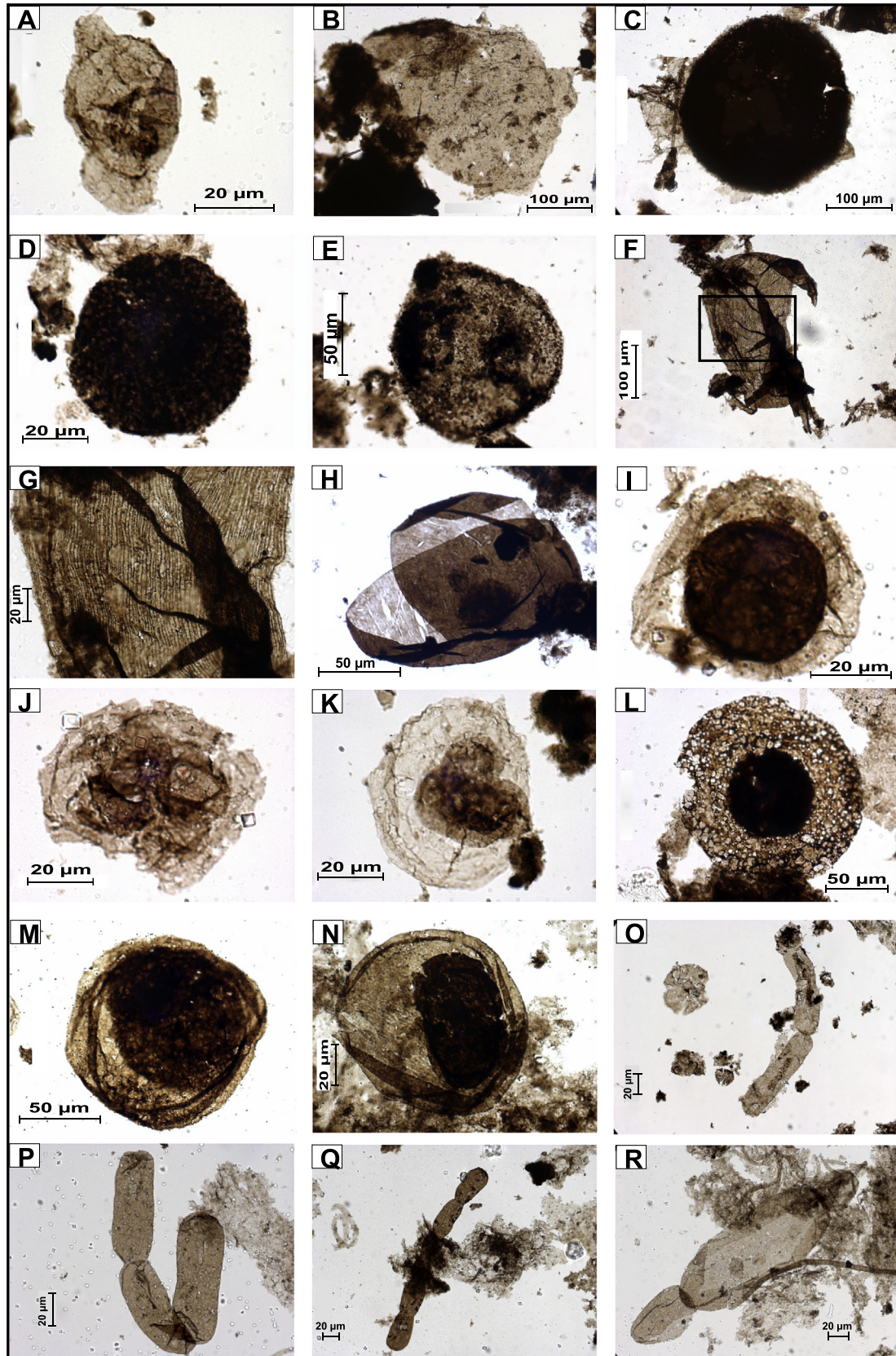
Fig. 7. (A and B) ?cf. *Tappania* sp., specimens 65065/J-29-3 and 65066/J-40-4 respectively. (C–E) *Lophosphaeridium granulatum*, specimens 65078/P-29-2, 65255/R-48-2 and 65062/F-59-4 respectively. (F and G) *Valeria elongata*, (F) specimen 65066/T-39-1, with longitudinal striations and (G) magnification of box area in F. (H) *Valeria lophostriata*, specimen 71707/J-51-2, with concentric striations on inner side of the wall. (I–L) *Pterospermopsimorpha insolita*, (I) specimen 65092/F-38-4; (J) and (K) dividing specimens, 65078/G-58-4; 65087/L-49-2 respectively; (L) specimen with perforations, probably caused by mineral dissolution during extraction process, 65086/J-34-3. (M and N) *P. pileiformis* specimens 65080/N-36-4 and 65080/S-32-1 respectively. (O–R) *Jacutianema solubila*, (O) and (P) botuliform cells in pair or triad, specimens 65083/U-60-4 and 65080/E-33-1 respectively; (Q) specimen 65078/O-28-2, linear chain showing incomplete division; (R) specimen 65080/Q-39-1, sausage-shaped cells with associated thin-walled vesicles.
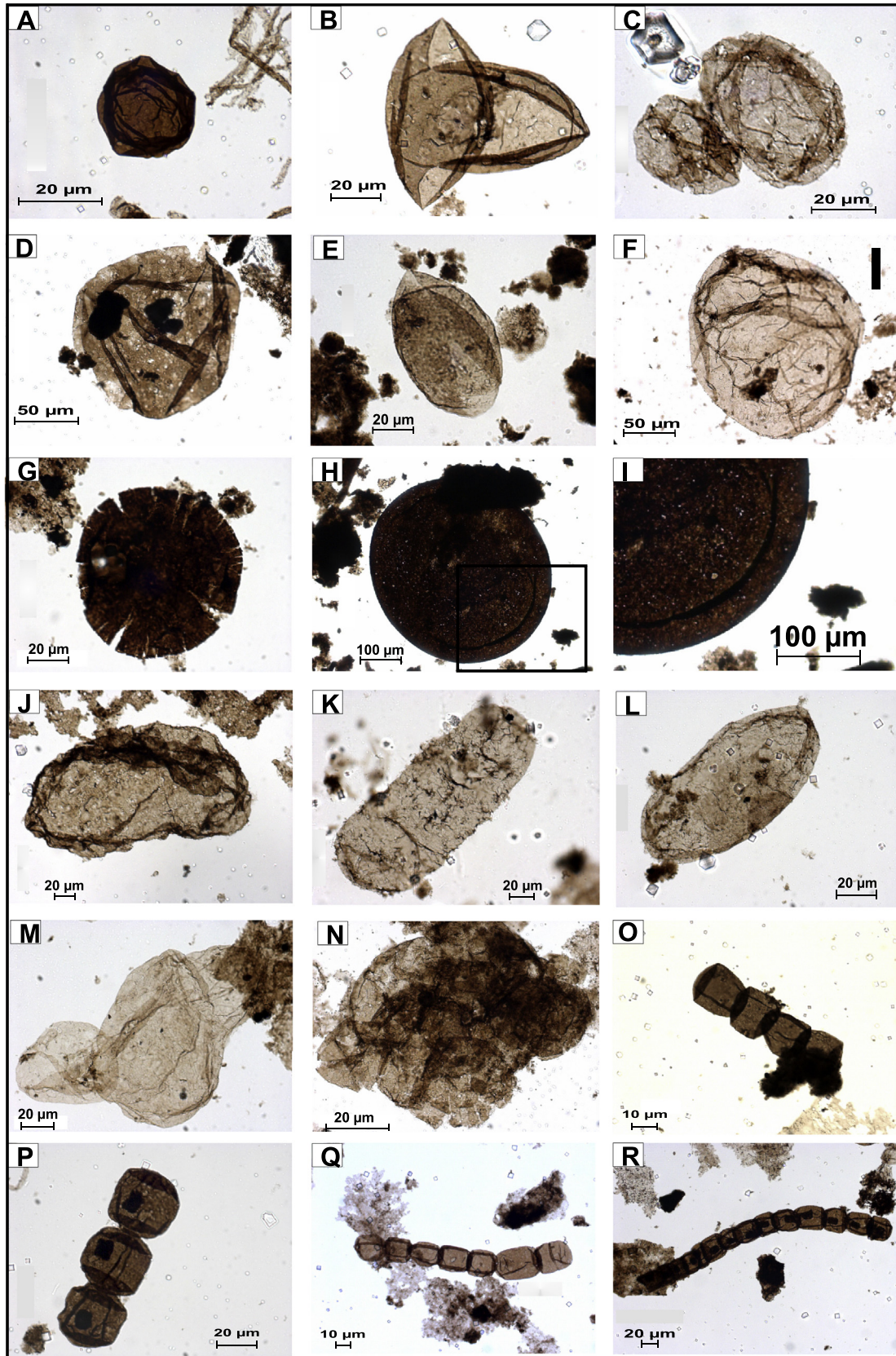
Fig. 8. (A–C) *Leiosphaeridia crassa*, (A) specimen 65078/R-59-2; (B) specimen 65078/F-55-1, with excystment structure by medial split and (C) two joined vesicles, specimens 65078/J-55-1; (D) *L. jacutica,* specimen 65058/O-43-2; (E) *L. minutissima*, specimen 65063/D-32-2; (F) *L. tenuissima*, specimen 65064/S-26-2; (G) *L. ternata*, specimen 65088/P-36-2; (H and I) *Leiosphaeridia* sp. with concentric peripheral folding and tiny pores on more opaque wall, (H) specimen 71270/H-32-3 and (I) magnification of box area in H. (J and K) *Navifusa actinomorpha*, (J) specimen 65078/R-49-2; (K) specimen 67082/B-36-3. (L) *N. majensis*, specimen 65078/F-54-1. (M and N) *Coneosphaera* sp., specimens 65084/E-48-3 showing a stage of cell-division and 65080/O-39-4. (O–R) *Arctacellularia tetragonala*, (O) specimen 65078/N-49-3 with ellipsoidal cells; (P) specimen 65078/M-53-3 showing a development of cells shape from ellipsoidal to barrel-shaped; (Q) specimen 65078/F-54-2; (R) specimen 65078/H-50-4.
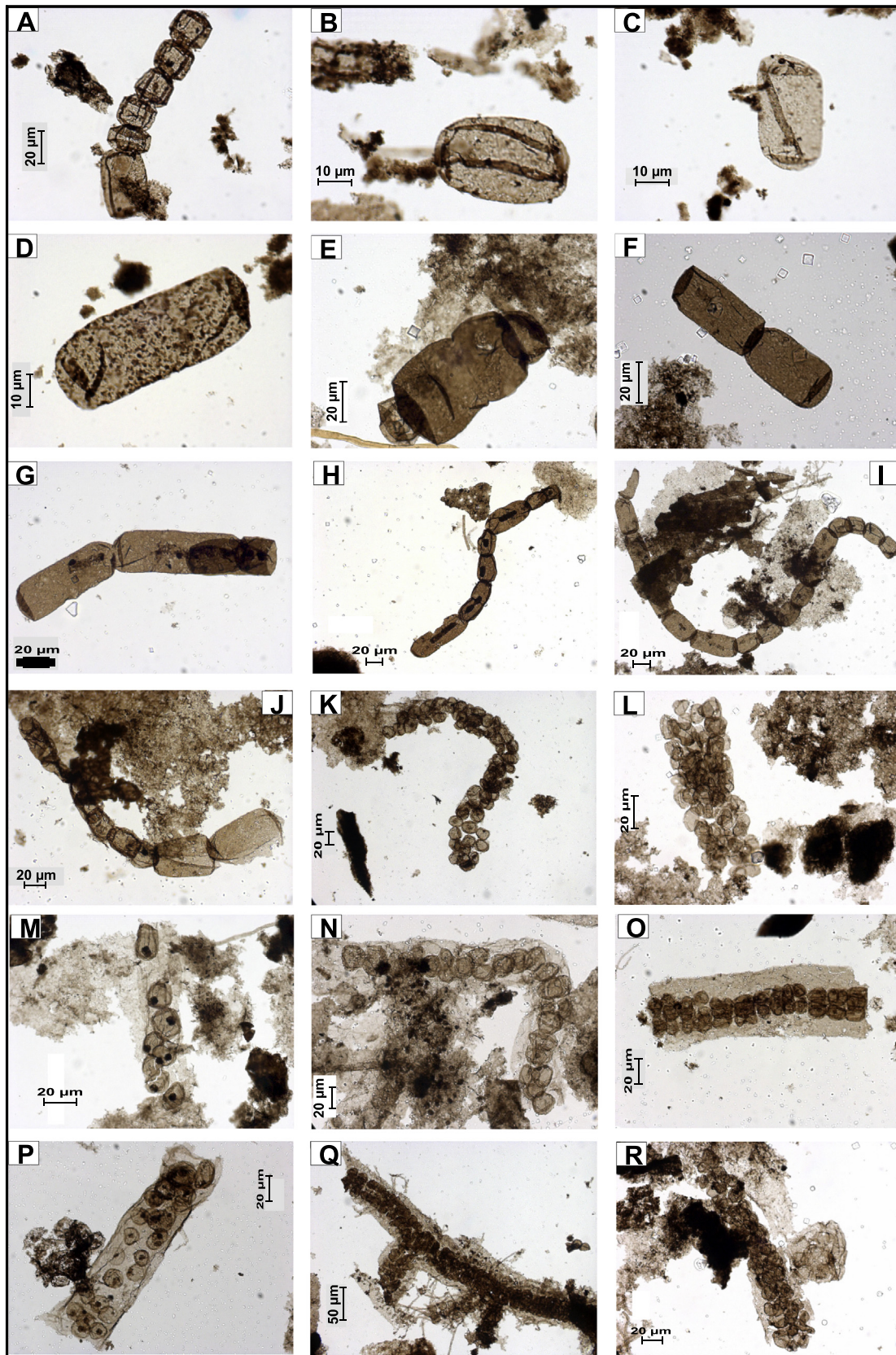
Fig. 9. (A–J) *Arctacellularia tetragonala*, (A) specimen 65091/X-58-4 with barrel-shaped cell in one of ends; (B–D) single vesicle, previously regarded as *A. kelleri*, specimens 65067/O-60-1, 65065/J-34-3 and 65067/H-39-3 respectively; (E) barrel-shaped vesicle with small vesicles in ends, specimen 65078/V-51-4; (F and G) dyads of cylindrical vesicles, specimens 65078/G-58-3 and 65078/Q-52-2 respectively; (H–J) chains of several barrel-shaped and ellipsoidal vesicles with or without dark inclusion, specimens 65078/N-53-4, 65078/H-47-1 and 65086/C-29-4 respectively. (K) *Chlorogloeaopsis kanshiensis*, specimen 65080/P-52-4. (L) *Chlorogloeaopsis zairensis*, specimen 65078/N-60-3. (M–R) *Polysphaeroides filliformis*, (M and N) cells in one row, specimens 65081/G-53-465080/X-31-3 respectively; (O) specimen 65080/N-48-3; (P) cells irregularly distributed in sheath, specimen 65080/E-53-3; (Q) branched specimen 65080/L-52-3 and (R) specimen 65078/P-57-3, with sheath more degraded and less conspicuous.

punctatus Maithy, 1975 (Fig. 11M); *Siphonophycus robustum* (Fig. 11N.r) and *Siphonophycus septatum* Schopf, 1968 (Fig. 11N. s); *Siphonophycus solidum* Golub, 1979 (Fig. 11O); *Siphonophycus typicum* Hermann, 1974 (Fig. 11N.t); *Tortunema magna* Tynni and Donner, 1980 (Fig. 11P); *Tortunema patomica* Kolosov, 1982 (Fig. 11Q); *Tortunema wernadskii* Shepeleva, 1960 (Figs. 11R, 12A); *Trachytrichoides ovalis* Hermann *in* Timofeev et al., 1976 (Fig. 12B and C); *Eomicrocystis elegans* Golovenok and Belova, 1984 (Fig. 12D and E); *Eomicrocystis malgica* Golovenok and Belova, 1985 (Fig. 12F); *Fabiformis baffinensis* Hofmann *in* Hofmann and Jackson, 1994 (Fig. 12G and H); *Myxococcoides minor* Schopf, 1968 (Fig. 12I); *Ostiana microcystis* Hermann *in* Timofeev et al., 1976 (Fig. 12J); *Spumosina rubiginosa* Andreeva, 1966 (Fig. 12K); *Symplassosphaeridium* spp. (Fig. 12L) and *Synsphaeridium* spp. (Fig. 12M). All these species are present in the Kanshi S13B drill core while both the Lubi S70 and Kafuku 15 cores contain respectively 22 and 16 taxa. No microfossils were recovered from the (mostly carbonate) Bena Kalenda and Bena Tshovu drill cores. The fossiliferous formations are, from bottom to top: BIc_1, BId_2 (clastic facies with interbedded shales); BIE_2, BIe_1, BIe_2 (essentially homogenous dolo-mudstones and dolo-laminites with interbedded shales); $BIIc_2$, $BIIc_4$ and $BIIc_6$ (dark grey/brown shales). The richest level, in terms of diversity and abundance, is located in the Kanshi S13B drill core ($BIIc_6$ Formation) between 111 and 122.9 m depth. The color of the microfossils and particulate organic matter in the investigated samples varies from light brown to dark brown, even to black for most samples from the Kafuku 15 drill core. Difference in diversity and abundance of recovered microfossils (Fig. 13) in these drill cores are probably more related to differences in facies and diagenetic alteration, the Lubi S70 and Kafuku 15 sedimentary rocks representing very shallow environments with signs of emersion (mudcraks, gypsum/anhydrite layers), that have been interpreted as lacustrine and sabkha environments in supratidal zone (Delpomdor et al., 2013b, 2015). However, new geochronology is ongoing to better constrain the age of the BI and BII groups (previously dated between ∼1174 and 948 Ma) and test if the difference in diversity and abundance could be related to stratigraphy rather than ecology and preservation (François et al., 2015). The highest diversity, abundance and better preservation of organic materials including microfossils, occur in subtidal to intertidal marine shales deposited between stromatolitic carbonates preserved in the Kanshi S13B drill core (upper part of Mbuji-Mayi Supergroup).

5. Biostratigraphic implications

As seen above, the Mbuji-Mayi assemblage is exceptionally diversified (49 taxa) and well-preserved. All of these microfossils (except one taxon) are known from different coeval Late Mesoproterozoic and Early Neoproterozoic assemblages worldwide (Fig. 14), although not all species are reported in every assemblage. Similar assemblages occur in Eurasia: the possible Tonian Lower Vychegda Formation (Lower assemblage) in Russia (Vorob'eva et al., 2009a); the Tonian Chichkan Formation in Kazakhstan (Sergeev and Schopf, 2010); the Tonian Miroedikha Formation, the Latest Mesoproterozoic Suukhaya Tunguska Formation and Lakhanda Group in Siberia (Hermann, 1990; Hermann and Podkovyrov, 2007, 2008; Knoll et al., 1995; Petrov and Semikhatov, 1997; Semikhatov et al., 2000; Sergeev et al., 1997; Yankauskas et al., 1989); the Mesoproterozoic Dzhelindukon Formation, Yurubchen Formation (Nagovitsin, 2009; Nagovitsin et al., 2010 and references therein) and Kotuikan Formation in Siberia (Vorob'eva et al., 2015); the Mesoproterozoic Sarda Formation of the Bahraich Group, Ganga Basin, in India (Prasad and Asher, 2001); the Tonian Gouhou Formation (Tang et al., 2015), Liulaobei Formation and Dongjia Formation
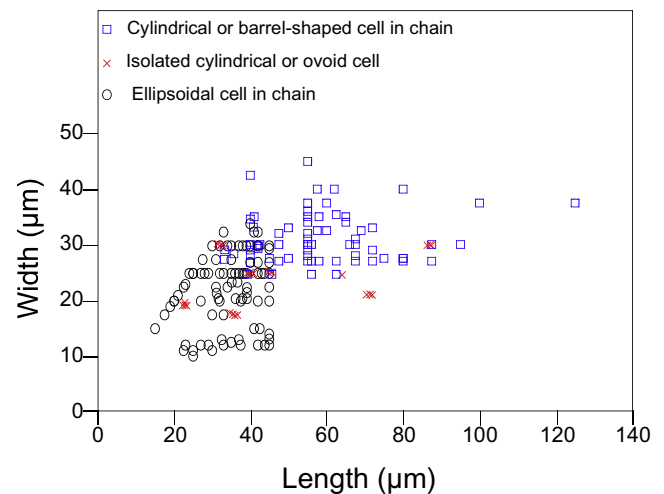

Fig. 10. Size distribution of *Arctacellularia* showing that ellipsoidal and barrel-shaped cells (that may occur within the same chain of cells) also overlap in diameter range, therefore suggesting they represent a single species (*A. tetragonala*) at different stage of development and displaying a variable cellular morphology.

in North China (Tang et al., 2013; Yin and Guan, 1999); the Tonian Svanbergfjellet Formation in Spitsbergen (Butterfield et al., 1994). In North America, taxa common with the Mbuji-Mayi assemblage occur in the Tonian Uinta Mountain Group and Chuar Group in USA (Nagy and Porter, 2005; Porter et al., 2003; Vidal and Ford, 1985); the Tonian Wynniatt Formation (Butterfield, 2005a,b; Butterfield and Rainbird, 1998); the Latest Mesoproterozoic Lone Land Formation (Samuelsson and Butterfield, 2001) and Bylot Supergroup (Hofmann and Jackson, 1994), all three in Canada. In Australia, some of the taxa are reported in the Tonian Kanpa Formation and Hussar Formation (Hill et al., 2000), the Alinya Formation (Zang, 1995) and Bitter Springs Formation (Schopf, 1968; Schopf and Blacic, 1971); and the Mesoproterozoic Roper Group (Javaux et al., 2001; Javaux and Knoll, in press). Similarities also occur with assemblages in the Mesoproterozoic Thule Supergroup, Greenland (Samuelsson et al., 1999) and Sao Francisco Craton, Brazil (Simonetti and Fairchild, 2000).

The Mbuji-Mayi assemblage is particular due to the association of taxa which are until now typical of Tonian of Asia (*Trachyhystrichosphaera botula* in the Liulaobei Formation) and the Mesoproterozoic–Early Neoproterozoic of East European Platform (*G. miroedikhia*, *Polysphaeroides filliformis*, *V. elongata*) with other ubiquist taxa (i.e. *V. lophostriata*, *J. solubila*, *A. tetragonala*, *P. insolita*, *P. pileiformis*, *T. aimika*, ?cf. *Tappania plana*, *G. bispinosa*, *S. rubiginosa*, *L. crassa*, *L. minutissima*, *L. jacutica*, *L. tenuissima*, *L. ternata*, *Tortunema* spp., *Siphonophycus* spp. and others). *J. solubila* shows several morphotypes (Figs. 7P–R, 8A) similar to those only reported in the Tonian Svanbergfjellet Formation of Spitsbergen (Butterfield, 2004) and the El Mreiti Formation in Mauritania (Beghin et al., in review; this species is reported in several other locations but the variability is rarely reported) and *A. tetragonala* also displays a range of morphologies unreported elsewhere (Fig. 9D–H). There are also other differences between the Mbuji-Mayi and other contemporaneous assemblages: *Kildinosphaera verrucata* Vidal *in* Vidal and Knoll, 1983, *Simia* spp. and *Satka* spp. are absent in the Mbuji-Mayi assemblage, while an unnamed acanthomorph species has not been reported elsewhere so far.

All of the assemblages cited above range from the Late Mesoproterozoic to the Tonian, constraining the Mbuji-Mayi microfossil assemblage to this time range. This is consistent with geochronological data on the minimum age of the Mbuji-Mayi Supergroup, 948 ± 20 Ma from basaltic lavas (U-Pb age; Cahen et al., 1984), as well as new geochronological datings between ca.
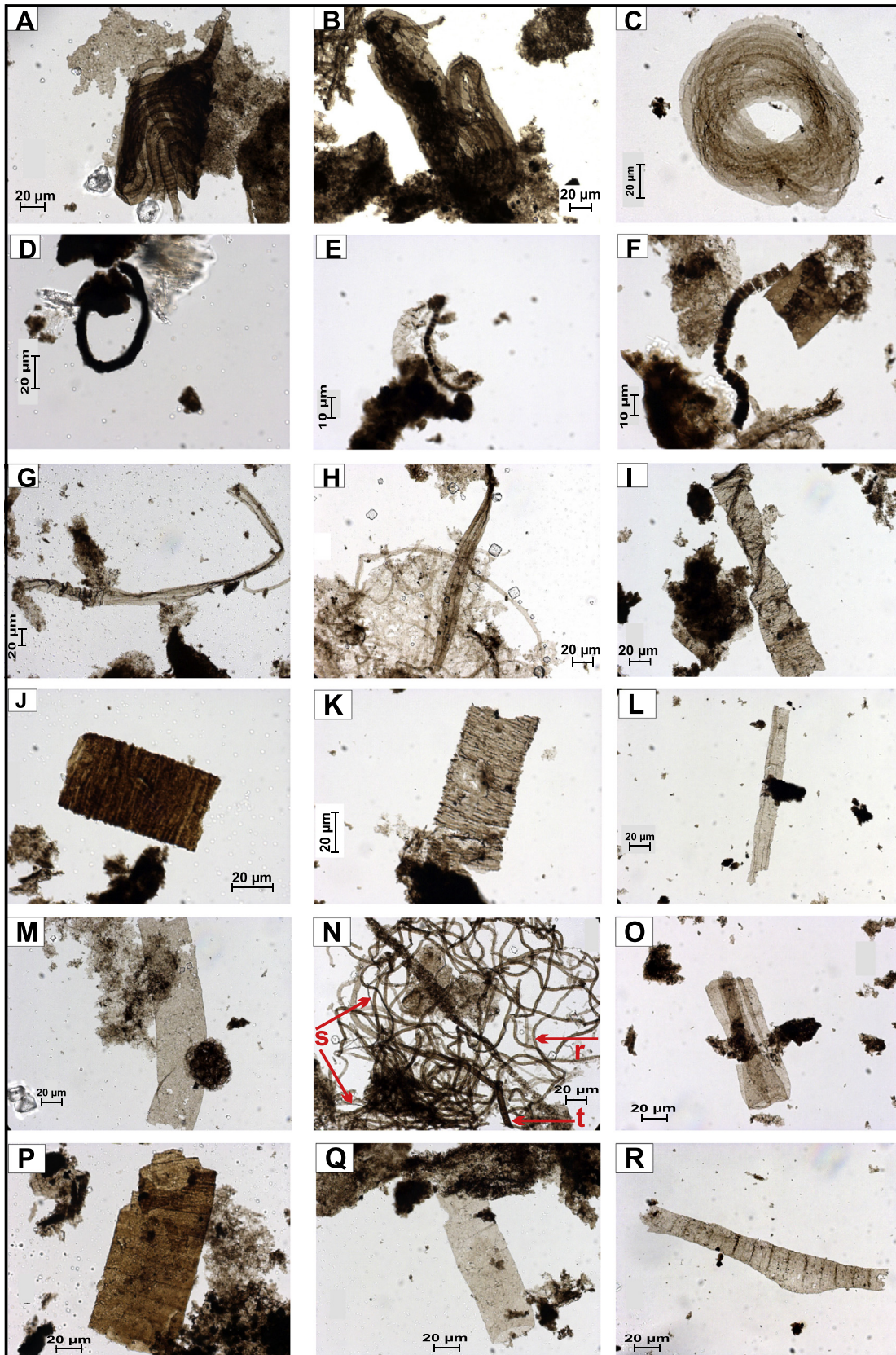
Fig. 11. (A and B) *Glomovertella miroedikhia*, specimens 65078/U-38-1 and 65092/J-50-1 respectively. (C) *Obruchevella valdaica*, specimen 65271/W-40-3. (D) Opaque filament, specimen 65058/V-46-2. (E and F) *Palaeolyngbya catenata*, specimens 65059/H-57-4 and 65081/Y-32-1 respectively. (G) *Pellicularia tenera*, specimen 65054/F-29-2. (H) *Polytrichoides lineatus*, specimen 65078/V-60-3. (I–K) *Rugosoopsis tenuis*, (I) specimen 65064/P-35-1; (J) specimen 65064/N-30-3 with a thicker inner tubular sheath and (K) specimen 65065/R-37-4. (L) *Siphonophycus kestron*, specimen 65065/V-40-4. (M) *Siphonophycus punctatus*, specimen 65078/U-48-3. (N) Microbial mat consisting of *Siphonophycus robustum*, denoted by arrow marked with "r" *S. septatum* denoted by arrow marked with "s" and *S. typicum*, denoted by arrow marked with "t", specimen 65078/T-59-1. (O) *Siphonophycus solidum*, specimen 65067/Y-60-2. (P) *Tortunema magna*, specimen 65092/S-36-2. (Q) *Tortunema patomica*, specimen 65064/X-41-3. (R) *Tortunema wernadskii*, specimen 65065/X-59-4.
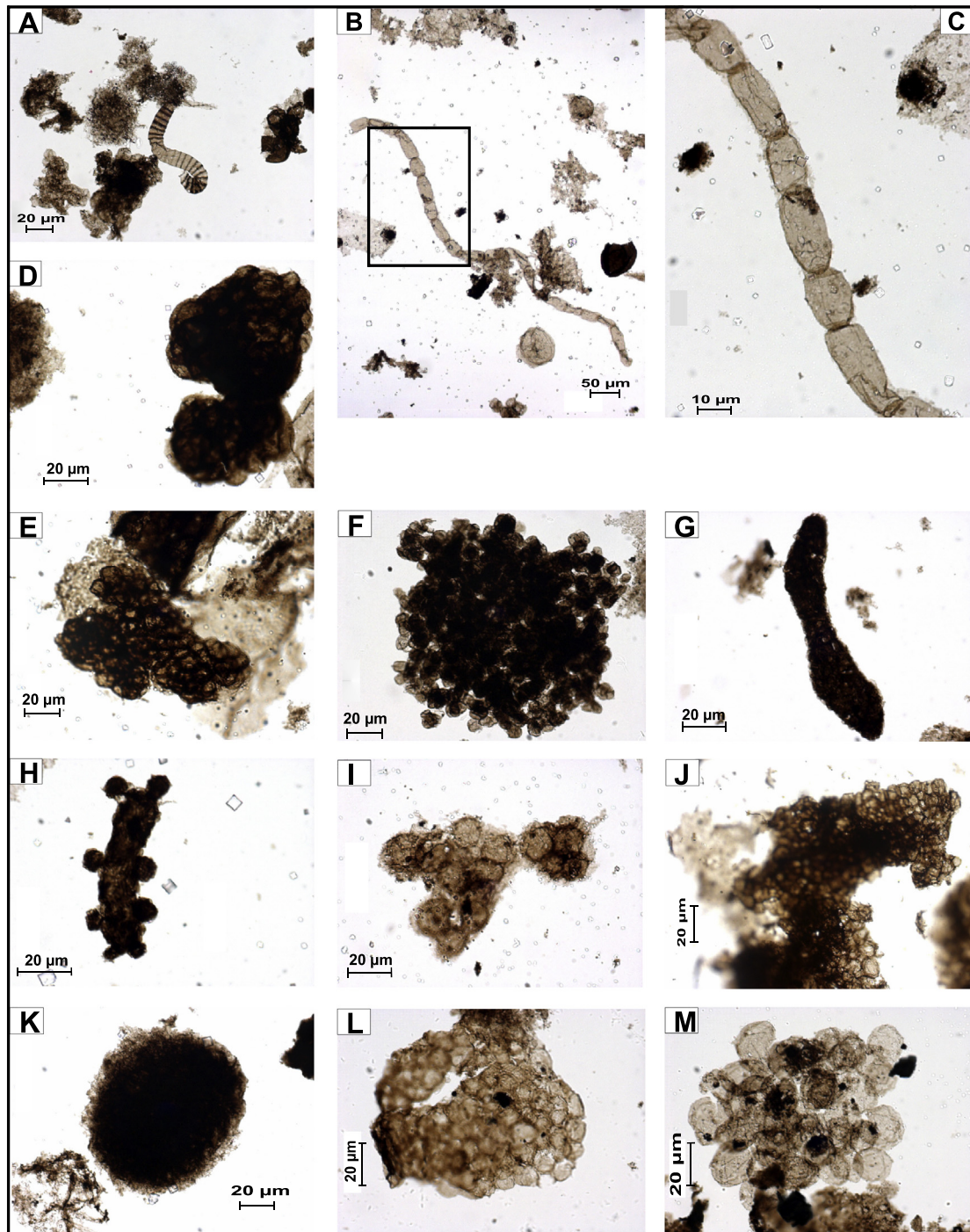
Fig. 12. (A) *Tortunema wernadskii,* specimen 65079/C-45-2. (B and C) *Trachytrichoides ovalis,* (B) specimen 65078/H-56-4; (C) magnification of box area in B. (D and E) *Eomicrocystis elegans*, specimens 65078/K-48-3, 65086/C-38-1 respectively. (F) *Eomicrocystis malgica*, specimen 65271/V-50-2. (G and H) *Fabiformis baffinensis*, specimens 65079/O-27-3 and 65078/K-49-2 respectively. (I) *Myxococcoides minor*, specimen 65080/F-46-4. (J) *Ostiana microcystis*, specimen 65086/W-26-1. (K) *Spumosina rubiginosa*, specimen 65078/T-50-1. (L) *Symplassosphaeridium* spp., specimen 65385/Q-51-4. (M) *Synsphaeridium* spp., specimen 65064/O-48-3.

1030 and 1065 Ma and obtained on diagenetic monazites and xenotimes coming from Lubi S70 and Kafuku 15 drill cores (François et al., *in prep).*

In addition, the Mbuji-Mayi assemblage includes a relatively low diversity of acanthomorphs that are distinct from the well-known Ediacaran Complex Acanthomorph Palynoflora or ECAP (Grey, 2005; Moczydłowska, 2005; Moczydłowska and Nagovitsin, 2012; Sergeev et al., 2011; Vorob'eva et al., 2009a). Nevertheless more than half (14 taxa) of the lowermost Vychegda assemblage including *T. aimika* (Vorob'eva et al., 2009a,b) also

occurs in the Mbuji-Mayi assemblage (Fig. 14) but these are ubiquitous.

Most of the Mbuji-Mayi microfossils are stratigraphically extremely long-ranging and thus, they are of a limited biostratigraphic value. In particular, *V. lophostriata* and *Leiosphaeridia* spp. are known since the late Paleoproterozoic, the Changzhougou Formation, North China (Lamb et al., 2009; Peng et al., 2009) and the Mallapunyah Formation, Australia (Javaux et al., 2004). Simple leiospheres occur in even older rocks, such as the Archean Moodies Group, South Africa (Javaux et al., 2010) and the Paleoproterozoic
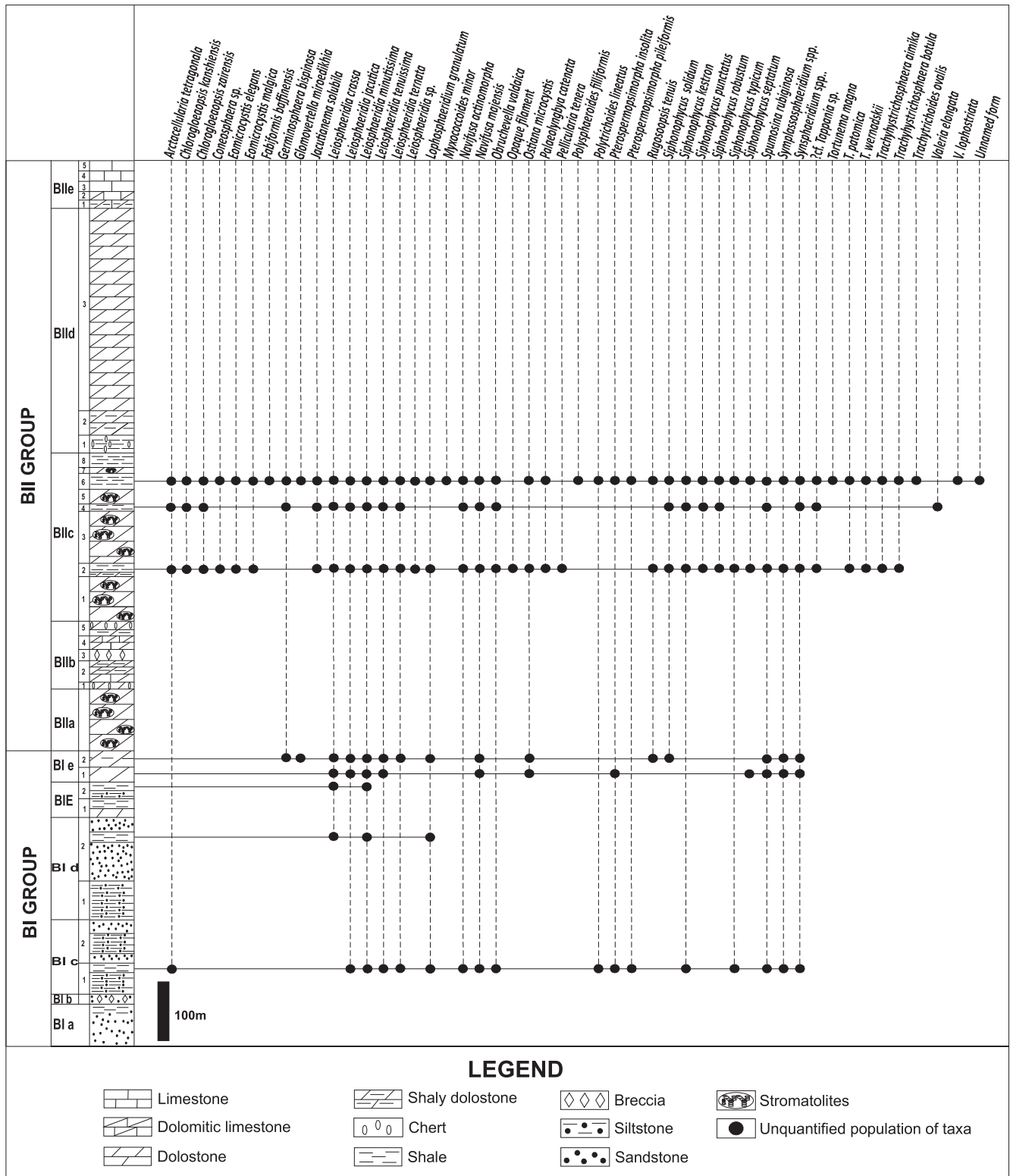
Fig. 13. Chart showing the distribution of microfossils within the Mbuji-Mayi Supergroup.

Kondopoga Formation, Karelia, Russia (Javaux et al., 2012). Only *T. aimika* may be a useful index fossil due to its relatively short stratigraphic extension (Moczydlowska, 2008; Sergeev, 2009). Indeed, *T. aimika* is reported from rocks ranging from the Late Mesoproterozoic: the Lakhanda Group, Siberia (Hermann, 1990; Semikhatov et al., 2000 and Yankauskas et al., 1989); the Lone Land Formation, Canada (Samuelsson and Butterfield, 2001) and the El

Mreiti Formation, Mauritania (Beghin et al., in review), to pre-Sturtian successions: the Liulaobei Formation, China (Tang et al., 2013); the Wynniatt Formation, Canada (Butterfield, 2005a,b; Butterfield and Rainbird, 1998); the Sirbu shale Formation, India (Srivastava, 2009); the Svanbergfjellet Formation, Spitsbergen (Butterfield et al., 1994); the Alinya Formation, Australia (Zang, 1995); the Chichkan Formation, Kazakhstan (Sergeev and Schopf,
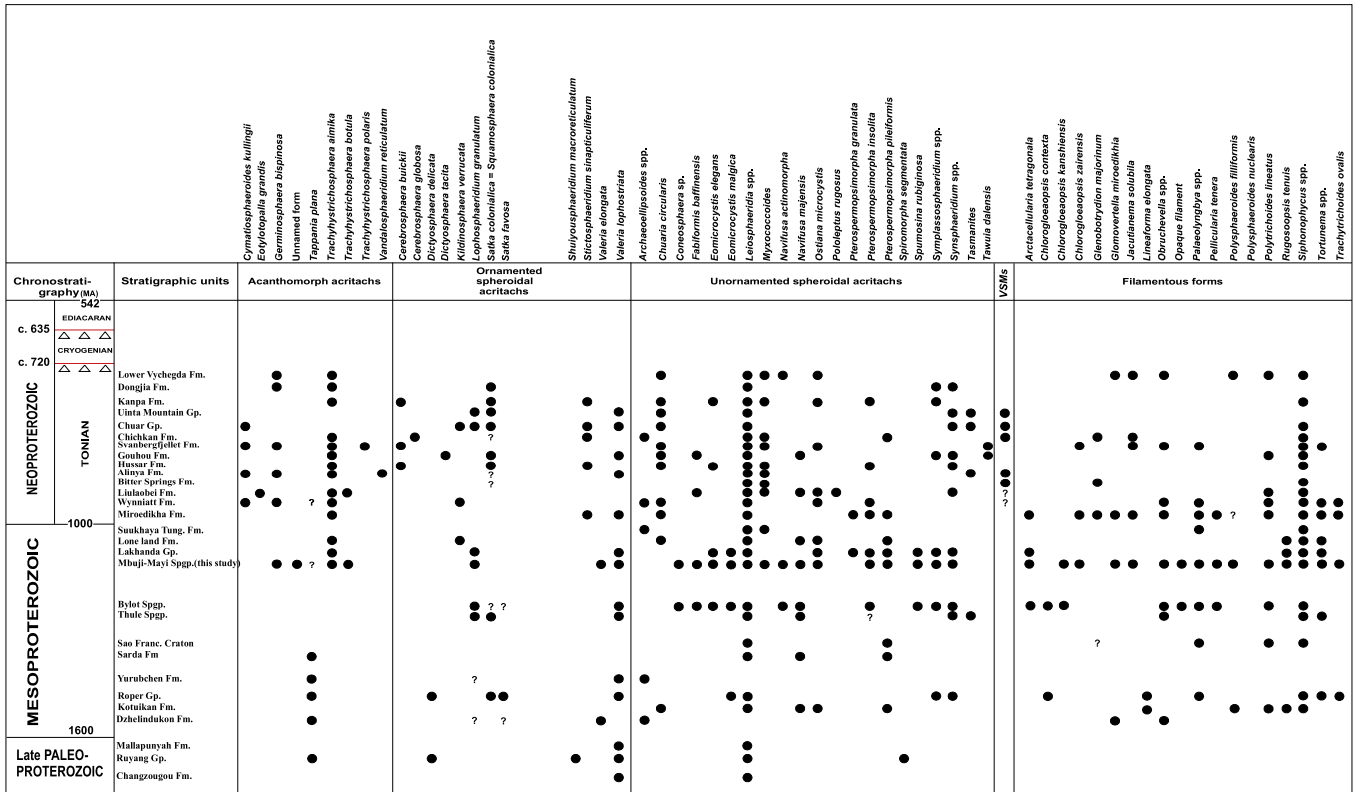
Fig. 14. Distribution of the main types of microfossils from the Late Paleoproterozoic through the Tonian, based on compilation data from some representative assemblages. The relative positions or orders are still uncertain and some of their possible ages may overlap. Therefore, species are listed alphabetically, and their order here has no indication on their relative position in each period (details on location, ages and various references, see in text), nor on biological affinities. Acanthomorph and ornamented spheroidal acritarchs are interpreted as eukaryotic (see text) while unornamented sphaeromorphs and filamentous forms include taxa that are eukaryotic (such as *Jacutienema*, *Lineaforma*, *Pterospermopsimorpha*, *Tasmanites*), others that could be prokaryotic or eukaryotic (*Arctacellularia*, *Leiosphaeridia*), and probable bacteria (*Siphonophycus...*). Cryogenian limits come from the new Precambrian chart (2015) of the International Commission on Stratigraphy (www.stratigraphy.org). The triangle symbol marks the chronostratigraphic level of the Sturtian and Marinoan glaciation intervals. Dark circles denote presence (unquantified abundance) of taxa. Question mark denotes form assumed similar to a putative species (e.g. *Tappania*? sp., in this study). Fm. – Formation; Gp. – Group; Spgp. – Supergroup; *VSMs*, vase-shaped microfossils.

2010) and the Lower Vychegda Formation, Russia (Vorob'eva et al., 2009a,b). Moreover, *T. aimika* co-occurs with *T. botula* previously reported in the Liulaobei Formation (Tang et al., 2013).

In summary, the Mbuji-Mayi assemblage has a transitional composition of Late Mesoproterozoic and Early Neoproterozoic (pre-Sturtian) assemblages known worldwide.

Comparison with worldwide marine assemblages (Figs. 14 and 15) permits to suggest assemblages useful for global pre-Sturtian Proterozoic biostratigraphy, although adjustments may be needed as new assemblages are discovered in the future:

- For the Late Paleoproterozoic – Early Mesoproterozoic: *Archaeoellipsoides spp.*, *Dictyosphaera delicata*, *L. granulatum*, *Satka favosa*, *Squamosphaera colonialica*, *T. plana*, *T. ovalis*, *V. lophostriata*, are common, and *Lineaforma elongata*, *Shuiyousphaeridium macroreticulatum*, as well as *V. elongata* have more local distributions.
- For the Middle Mesoproterozoic – Early Neoproterozoic (Tonian): *Archaeoellipsoides spp*, *A. tetragonala*, *G. bispinosa*, *J. solubila*, *L. granulatum*, *T. aimika*, *V. lophostriata* are widespread; *K. verrucata* and *Simia annulare* are common but not ubiquist; *S. colonialica*, and *V. elongata* has a more restricted distribution.
- Within the above time range, a few species have shorter stratigraphic range and are reported only in Tonian (pre-Sturtian) rocks so far: *Cerebrosphaera buickii*, *Cymatiosphaeroides kullingii*, *T. botula*, *Vandalosphaeridium reticulatum*, and *VSMs*.

6. Conclusions

The exceptionally diverse and well-preserved organic-walled microfossil assemblage from the Mbuji-Mayi Supergroup is dominated by sphaeromorph acritarchs and filamentous forms, and a moderate diversity of eukaryotes. A total of 49 taxa belonging to 27 genera were identified, including 11 species of unambiguous eukaryotes, 10 species of possible eukaryotes or prokaryotes and 28 species of probable bacteria. This is one of the first detailed microfossil studies in the Mesoproterozoic–Neoproterozoic interval in Central Africa, revealing the occurrence of several taxa, including acanthomorphs, for the first time in Africa, but known elsewhere except for one unnamed, possibly new, species. Comparison with other microfossil assemblages shows that the Mbuji-Mayi assemblage is likely Late Mesoproterozoic–Early Neoproterozoic in age. This biostratigraphic constraint is consistent with available geochronological data (Cahen et al., 1984; Delpomdor et al., 2013a; François et al., 2015, in prep.).

Although the Mbuji-Mayi eukaryotes do not display unique morphological characters permitting to relate them to modern protists and other eukaryotes, they could, based on molecular phylogenies (e.g. Eme et al., 2014), include stem group eukaryotes (before LECA, the last eukaryotic common ancestor), and stem and crown group members within crown groups (after LECA). Future micro-analyzes investigating the ultrastructure and chemistry of these microfossils may help refine their taxonomy (e.g. Javaux and Marshall, 2006). Regardless of taxonomy, these Meso
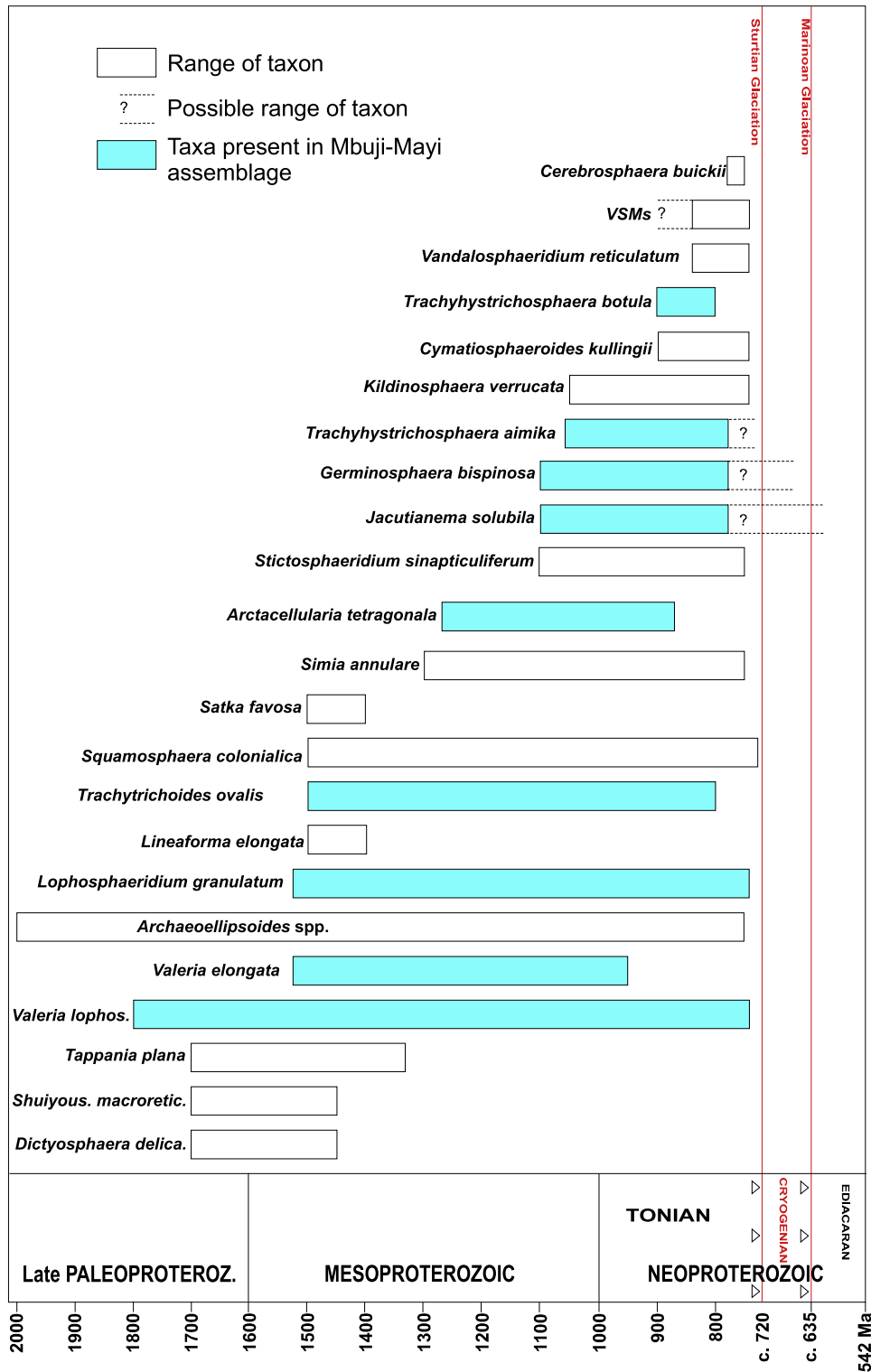
Fig. 15. Summary of microfossil assemblages useful for Proterozoic biostratigraphy (various references, see in text). Cryogenian limits come from the new Precambrian chart (2015) by International Commission on Stratigraphy (www.stratigraphy.org).

proterozoic–Neoproterozoic eukaryotes evidence the evolution of biological innovations such as a cytoskeleton and endomembrane system to control the plastic and complex morphology of process-bearing and ornamented acritarchs, life cycles with cyst and vegetative stages, and simple multicellularity. The diversity of eukaryotes observed here is broadly similar to worldwide contemporaneous marine successions. This confirms a general trend

of moderate eukaryotic diversification, despite the early development of the eukaryotic cell toolkit in the late Paleoproterozoic, until about 1100–800 Ma when diversification of crown group eukaryotes occurs (Knoll et al., 2006; Javaux, 2011; Javaux and Knoll, in press). This eukaryotic diversification is possibly linked to changing redox conditions (Planavsky et al., 2011) and associated nutrient availability, and to increased ecological interactions

including protist or animal predation (Butterfield, 2015; Knoll, 2014; Porter, 2011).

Acknowledgments

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.precamres.2016.05.017.

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