TREATISE ONLINE

Number 54

Part E, Revised, Volume 4, Chapter 20A:

Radiocyaths and Potientially Allied Taxa

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2012

KU PALEONTOLOGICAL INSTITUTE
The University of Kansas

Lawrence, Kansas, USA
ISSN 2153-4012 (online)
paleo.ku.edu/treatiseonline

PART E, REVISED, VOLUME 4, CHAPTER 20A: RADIOCYATHS AND POTENTIALLY ALLIED TAXA

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Radiocyaths show superficial similarity to archaeocyaths in size, shape, and gross morphology, and typically co-occur with them. They were first described from the lower Cambrian of South Australia as *Heterocyathus* R. Bedford & W. R. Bedford, 1934, a preoccupied name later substituted with *Radiocyathus* Okulitch, 1937. This latter was to become the eponymous genus for the entire group (Debrenne, H. Termier, & G. Termier, 1970).

Radiocyath skeletons may range up to 20 cm in height and 12 cm in diameter, although the majority are around 2–5 cm diameter. Apart from some branching *Girphanovella* Zhuravleva and *Gonamispongia* Korshunov, they are solitary. The skeleton may be globular, conical, or pyriform, composed of one or two walls, the walls in the latter being linked by radial rods, thus superficially resembling certain species of the archaeocyath *Dokidocyathus* Taylor. Nevertheless, radiocyaths differ fundamentally from archaeocyaths in that their walls are constructed of more or less uniformly arranged nesasters (Debrenne, H. Termier, & G. Termier, 1971): solid starlike structures consisting of 6–20 coplanar rays radiating from a central boss. Walls range from those apparently composed of relatively isolated nesasters, as in the poorly preserved *Kuraya* Romanenko (treated herein as a probable synonym of *Uranosphaera* R. Bedford & W. R. Bedford), to those constructed of nesasters whose rays are intricately linked to form a continuous skeletal network, as in *Radiocyathus* Okulitch and *Girphanovella* Zhuravleva. Nesasters may be two layered, as, for example, in *Radiocyathus* Okulitch, in which nesasters have an internal layer of radial rays that fuse with rays of adjacent nesasters at angled junctions, and an external layer of anastomosing rays and tangential linking cross pieces that constitute a microporous sheath (Debrenne, H. Termier, & G. Termier, 1970; Kruse, 1991).

The lower end of the skeleton appears to have been closed. The upper end is not commonly preserved, and a distal opening is confirmed only in *Uranosphaera* R. Bedford & W. R. Bedford, which bears a circular opening about one third the equatorial skeleton diameter. Skeletal growth was from the lower end, with intermingling of differently sized nesasters in some taxa implying that additional nesasters may have been subsequently inserted interstitially (Zhuravlev, 1986). Alternatively, the organism may simply have exerted little control over nesaster size at the growing edge, with resultant size variation.

Historically, most studied specimens have been secondarily silicified, dolomitized, or phosphatized. The microstructure of unaltered specimens is typically a mosaic of equant calcite spar, suggestive of an original aragonitic skeletal mineralogy

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based on the comparative approach of JAMES and KLAPPA (1983). Exceptionally, ZHURAVLEV (1986) reported what may be an original microstructure: a fabric of interlocking isometric microgranules 3–6 µm in size, although this may represent contamination due to intergrowth with archaeocyaths.

Neither the rank of radiocyathan suprageneric taxa nor the placement of genera within family-rank taxa is universally agreed. ZHURAVLEV and SAYUTINA (1985), in their restudy of *Kuraya* ROMANENKO (a probable synonym of *Uranosphaera* R. BEDFORD & W. R. BEDFORD) and *Gonamispongia* KORSHUNOV, suggested that one-walled forms are merely incompletely mineralized or preserved two-walled forms. These authors placed *Gonamispongia* KORSHUNOV in their two-walled Radiocyathinae (Hetairacyathidae herein), as it has rods projecting radially inward from its wall nesasters; they further amalgamated Girphanovellidae with Radiocyathidae (as Radiocyathinae). ZHURAVLEVA and MYAGKOVA (1987) assigned *Gonamispongia* KORSHUNOV to a separate subfamily.

The class has been allied variously with spiculate (especially heteractinide) sponges or archaeocyaths (R. BEDFORD & W. R. BEDFORD, 1934; OKULITCH, 1935, 1955; R. BEDFORD & J. BEDFORD, 1937; ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964; ZHURAVLEVA in ZHURAVLEVA, ZADOROZHNAYA, & others, 1967; KORSHUNOV, 1968; ROMANENKO, 1968; ROZANOV & ZHURAVLEV, 1992; FINKS & RIGBY, 2004), or considered as a problematic class of uncertain affinity (HILL, 1965, 1972). RIGBY and NITECKI (1975), erroneously believing the nesasters to be sutured, claimed for *Uranosphaera* R. BEDFORD & W. R. BEDFORD a close relationship to chancelloriids. These latter are now recognized as a group of nonporiferan epithelium-bearing metazoans (MEHL, 1996; BENGTSON & HOU, 2001; JANUSSEN, STEINER, & ZHU, 2002).

More recent studies have related the class most closely to the Early Ordovician–Permian receptaculitaleans, a group popularly allied with calcareous algae (NITECKI, 1972; CAMPBELL, HOLLOWAY, & SMITH, 1974; RIETSCHEL, 1977; NITECKI & DEBRENNE, 1979; BEADLE, 1988), though most recently regarded as problematic (neither sponges, nor dasycladalean algae) by NITECKI and MUTVEI (1996) and M. H. NITECKI, MUTVEI, and D. V. NITECKI (1999). In the receptaculitalean model, homology is drawn between the receptaculitalean merom (consisting of shaft, inner platelike foot and outer quadribrachial structure with surmounting head plate) and the radiocyathan radial rod connecting corresponding inner and outer nesasters (NITECKI & DEBRENNE, 1979; NITECKI & TOOMEY, 1979; MYAGKOVA, 1985; ZHURAVLEV & SAYUTINA, 1985; ZHURAVLEV, 1986). This proposed affinity with receptaculitaleans is consistent with microstructural (KRUSE & DEBRENNE, 1989) and mineralogical comparisons (DZIK, 1994; NITECKI & MUTVEI, 1996). Nevertheless, because of continuing uncertainty regarding their affinities, the Radiocyatha are included in the present *Treatise* revision.

A dissenting view of phylogenetic relationships was advanced by ZHURAVLEVA AND MYAGKOVA (1987). These authors grouped radiocyaths together with heteractinide sponges, chancelloriids, and some receptaculitaleans in a phylum, Receptaculita, itself grouped with the phylum Archaeocyatha, as the subkingdom Archaeata in the kingdom Inferibionta. The Archaeata-Inferibionta concept has not found favor with other researchers.

Radiocyaths appeared on the Siberian Platform in the late Tommotian, spread into adjacent Altay Sayan, Tuva, Mongolia, and Transbaikalia in the early Atdabanian and had reached Morocco, Australia, Antarctica, and Laurentia by the Botoman. As with archaeocyaths, their range contracted thereafter; the latest radiocyaths are from the middle Toyonian of South Australia.

Limited paleoecological studies indicate that at least some radiocyaths were reef dwellers or constructors. They contributed to reefs in the Tommotian of the Siberian Platform, Atdabanian of Mongolia and central Australia, and Toyonian of South Australia (KENNARD, 1991; KRUSE, 1991; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; KRUSE, ZHURAVLEV, & JAMES, 1995; KRUSE & others, 1996).

?Class RADIOCYATHA Debrenne, H. Termier, & G. Termier, 1970

[Radiocyatha DEBRENNE, H. TERMIER, & G. TERMIER, 1970, p. 120] [=order Hetairacyathida R. BEDFORD & J. BEDFORD, 1937, p. 27, *nom. correct.* OKULITCH, 1955, p. 18, *pro* order Hetairacyathina R. BEDFORD & J. BEDFORD, 1937, p. 27, *nom. nov. pro* order Heterocyathina OKULITCH, 1935, p. 90, based on junior homonym; =order Uranosphaerina R. BEDFORD & J. BEDFORD, 1939, p. 82; =subclass Uranocyatha OKULITCH, 1943, p. 42; =order Radiocyatales DEBRENNE, H. TERMIER, & G. TERMIER, 1970, p. 120, *nom. transl.* NITECKI & TOOMEY, 1979, p. 728, *ex* class Radiocyatha DEBRENNE, H. TERMIER, & G. TERMIER, 1970, p. 120; =Radiocyathaceae OKULITCH, 1955, p. 18, *nom. transl.* ZHURAVLEV & SAYUTINA, 1985, p. 54, *ex* Radiocyathidae OKULITCH, 1955, p. 18; =order Radiocyathida ZHURAVLEVA & MYAGKOVA, 1987, p. 73]

One- or two-walled globular, conical, or pyriform skeletons constructed of nesasters; corresponding nesasters of inner and outer wall linked by radial rods, which may bifurcate toward outer wall, in two-walled forms; rods project radially inward from wall of some one-walled forms; original skeletal mineralogy aragonitic. [The rank of Radiocyatha is uncertain (DEBRENNE, H. TERMIER, & G. TERMIER, 1970).] *lower Cambrian (Tom.3–Toy.2).*

Family HETAIRACYATHIDAE R. Bedford & J. Bedford, 1937

[Hetairacyathidae R. BEDFORD & J. BEDFORD, 1937, p. 27, *nom. nov. pro* Heterocyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 6, based on junior homonym] [=Radiocyathidae OKULITCH, 1955, p. 18; =Girphanovellidae DEBRENNE, H. TERMIER, & G. TERMIER, 1971, p. 442; =Kazakovicyathidae KONYUSHKOV, 1972, p. 130; =family Radiocyataceae OKULITCH, 1955, p. 18, *nom. correct.* NITECKI & TOOMEY, 1979, p. 728, *pro* Radiocyathidae OKULITCH, 1955, p. 18; =family Girvanovellaceae DEBRENNE, H. TERMIER, & G. TERMIER, 1971, p. 442, *lapsus calami pro* Girphanovellaceae, *nom. correct.* NITECKI & TOOMEY, 1979, p. 728, *pro* Girphanovellidae DEBRENNE, H. TERMIER, & G. TERMIER, 1971, p. 442; =Radiocyathaceae ZHURAVLEV & SAYUTINA, 1985, p. 54, *nom. transl. et correct. ex* Radiocyathidae OKULITCH, 1955, p. 18; =Radiocyathinae OKULITCH, 1955, p. 18, *nom. transl.* ZHURAVLEV & SAYUTINA, 1985, p. 54, *ex* Radiocyathidae OKULITCH, 1955, p. 18; =Gonamispongiinae ZHURAVLEVA in ZHURAVLEVA & MYAGKOVA, 1987, p. 74]

Cup two-walled. *lower Cambrian (Tom.3–Toy.2).*

Radiocyathus OKULITCH, 1937 (April), p. 252, *nom. nov. pro Heterocyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 7 (type, *H. minor*, SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20), *non* MILNE-EDWARDS & HAIME, 1848, p. 323 (type, *H. aequicostatus*, SD MILNE-EDWARDS & HAIME, 1850, p. xv), cnidarian [**Heterocyathus minor* R. BEDFORD & W. R. BEDFORD, 1934, p. 7; SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20; holotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 32; HILL, 1965, pl. 12,*4;* DEBRENNE, H. TERMIER, & G. TERMIER, 1970, pl. 4,*1-3,* pl. 5,*1;* M, S4196, NHM, London and PU87211, USNM, Washington, D.C.] [=*Hetairacyathus* R. BEDFORD & J. BEDFORD, 1937 (September), p. 27, *nom. nov. pro Heterocyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 7 (type, *H. minor*, SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20), *non* MILNE-EDWARDS & HAIME, 1848, p. 323 (type, *H. aequicostatus,* SD MILNE-EDWARDS & HAIME, 1850, p. xv), cnidarian]. Cup conical to pyriform, nesasters linked, of constant size and number of rays; outer wall with microporous sheath. *lower Cambrian (Atd.4–Bot.3)*: Australia, Antarctica.——FIG. 1,*1a–d*. **R. minor* (R. BEDFORD & W. R. BEDFORD); *a–c,* Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; *a–b,* holotype, USNM PU87211; *a,* transverse view, ×3; *b,* tangential view of outer wall (at left) and inner wall (at right), ×3; *c,* holotype NHM S4196, tangential view of outer wall (at bottom) and inner wall (at top), ×3 (Debrenne, H. Termier, & G. Termier, 1970); *d,* Wilkawillina Limestone, Botoman, Wirrealpa Mine, South Australia, Australia, specimen SAM P47956, tangential section of outer wall, ×9 (Kruse, 1991).

Blastasteria DEBRENNE, H. TERMIER, & G. TERMIER, 1971, p. 442 [**B. bedfordorum*; OD; holotype, R. BEDFORD & W. R. BEDFORD, 1936, fig. 39; M; P922/3, SAM, Adelaide; =*Uranosphaera hexaster* R. BEDFORD & W. R. BEDFORD, 1936, p. 10, *non* R. BEDFORD & W. R. BEDFORD, 1934, p. 7]. Cup globular, nesasters independent. *lower Cambrian (Bot.3)*: Australia.——FIG. 1,*2a–b*. **B. bedfordorum*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, SAM P922/3; *a,* sketch of transverse view, ×3; *b,* sketch of outer wall in tangential view, ×6 (R. Bedford & W. R. Bedford, 1936).

Girphanovella ZHURAVLEVA in ZHURAVLEVA, ZADOROZHNAYA, & others, 1967, p. 107 [**G. girphanovae*; OD; holotype, ZHURAVLEVA, ZADOROZHNAYA, & others, 1967, pl. 59,*1–2*, 325, TsSGM, Novosibirsk; =*Archaeocyathus neoproskurjakovi* VOLOGDIN, 1940, p. 56, holotype not designated, collection not located; =Dokidocyathina? *georgensis* ROZANOV in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 100, holotype, ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, pl. 16,*8*, GIN3461, PIN, Moscow] [=*Kazakovicyathus* KONYUSHKOV, 1972, p. 130 (type, *K. sajanicus,* OD)]. Cup conical to pyriform, nesasters linked, of variable size and number of rays; outer wall with possible

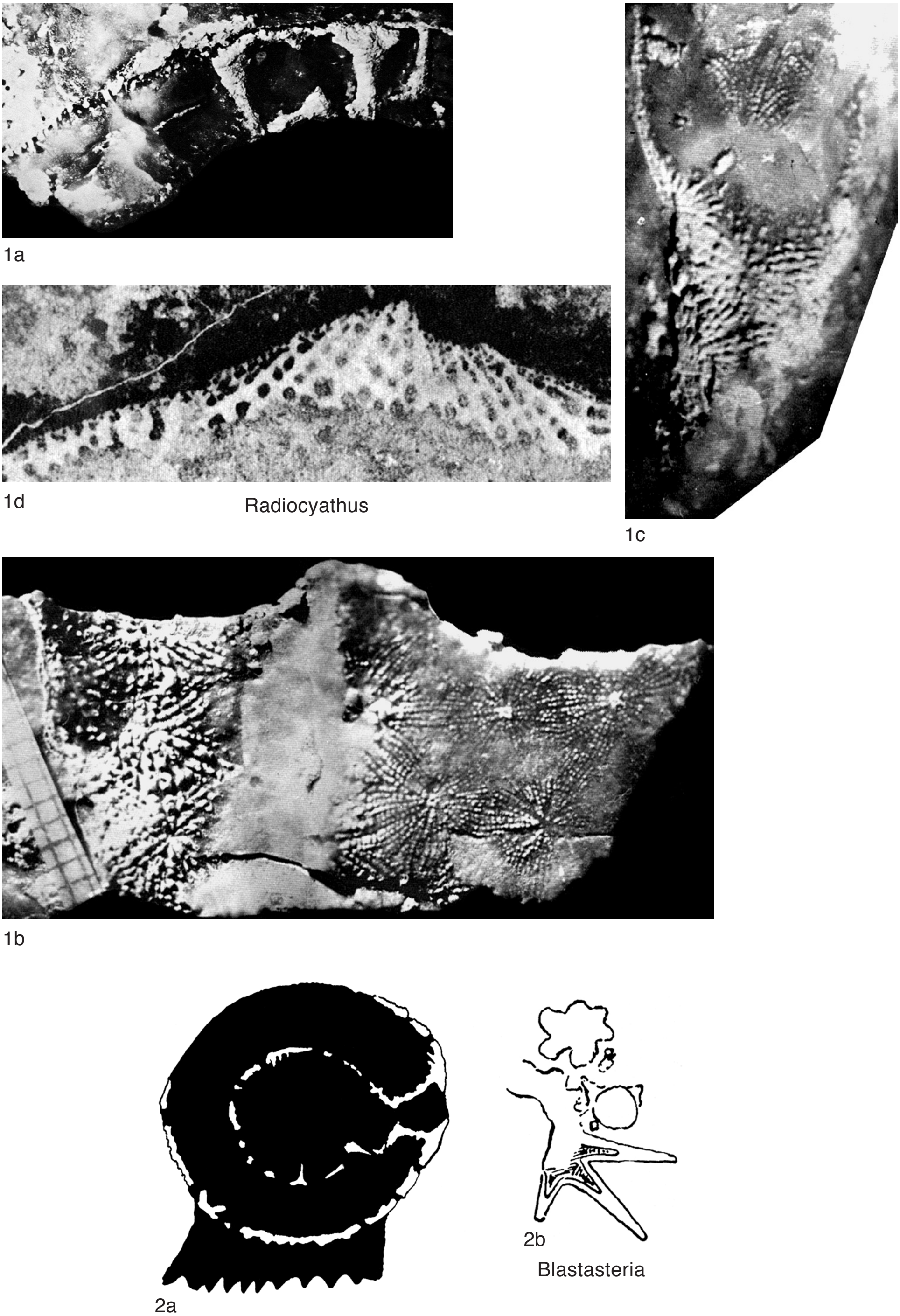

FIG. 1. Hetairacyathidae (p. 3).

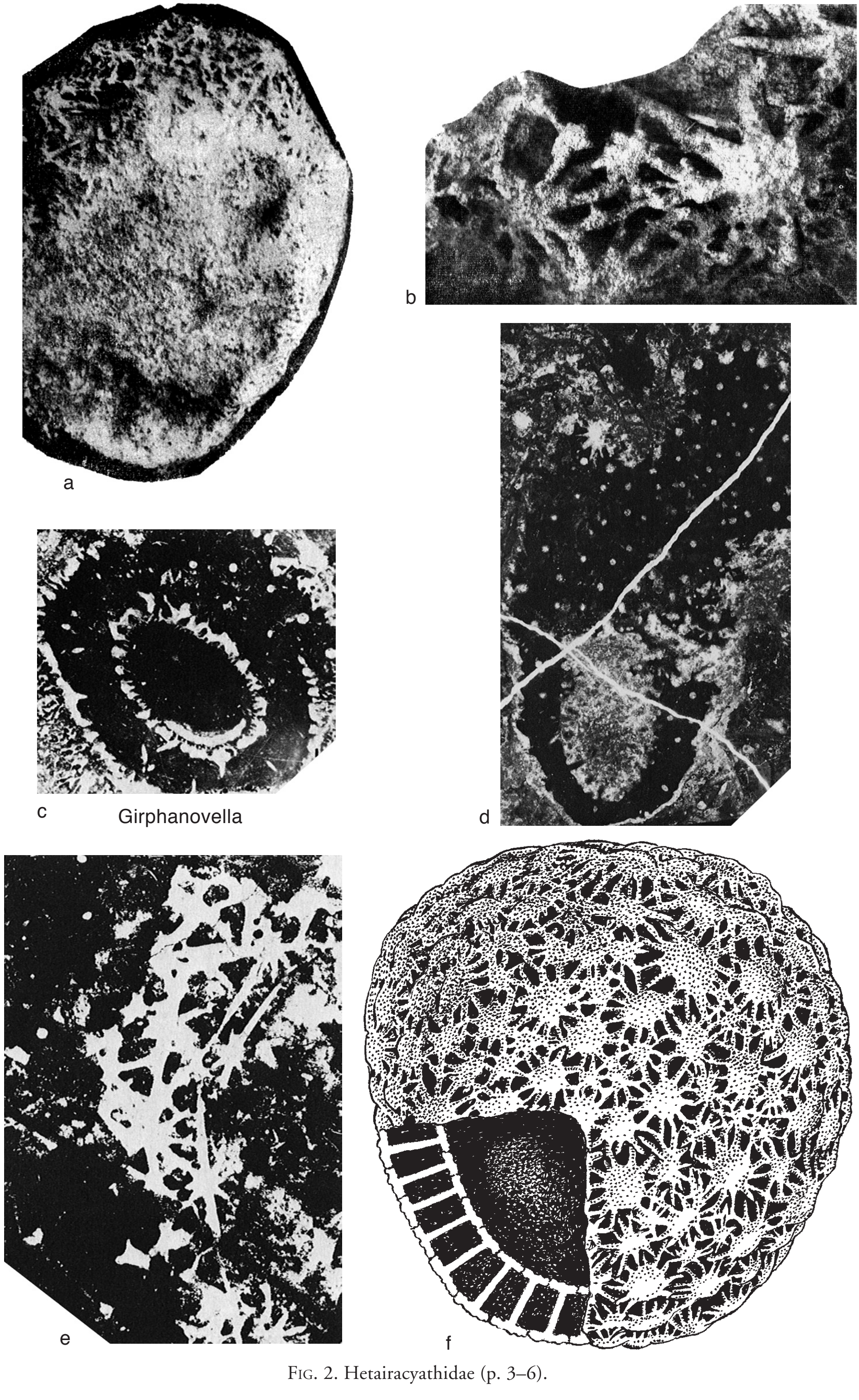

FIG. 2. Hetairacyathidae (p. 3–6).

microporous sheath. *lower Cambrian (Atd.1–Toy.2)*: Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Australia, ?Morocco, Canada.——FIG. 2*a–f*. *G. neoproskurjakovi* (VOLOGDIN); *a–b*, =*G. girphanovae* ZHURAVLEVA, Shangan Formation, Botoman, Shivelig-Khem River, Eastern Tannu-Ola Range, Tuva, Russia, holotype TsSGM 325; *a,* external view, ×1.8; *b,* tangential view of outer wall, ×10 (Zhuravleva, Zadorozhnaya & others, 1967); *c–e*, =*G. georgensis* (ROZANOV); *c,* Bystraya Formation, Atdabanian, Georgievka, Argun' River, Transbaikalia, Russia, specimen PIN 3900/35, oblique transverse section, ×3; *d–e,* Salaany Gol Formation, Atdabanian, Mount Zuune Arts, Tsagaan Oloom province, Mongolia; *d,* specimen PIN 3482/51, oblique longitudinal section, ×3; *e,* specimen PIN 3482/53, tangential section of inner wall, ×6 (Zhuravlev, 1986); *f,* Shangan Formation, Shivelig-Khem River, Eastern Tannu-Ola Range, Tuva, Russia, reconstruction based on etched specimens, external longitudinal view, ×1.5 (T. Gerasimova, new).

Gonamispongia KORSHUNOV, 1968, p. 127 [**G. ignorabilis*; OD; holotype, KORSHUNOV, 1968, fig. 1a–v, 84/3, YaFAN, Yakutsk]. Cup conical to pyriform, nesasters linked, of constant size and number of rays; rods extend radially inward from nesaster centers. *lower Cambrian (Tom.3–Atd.1)*: Siberian Platform.——FIG. 3,*1a–b*. **G. ignorabilis*, Pestrotsvet Formation, Tommotian, Knyaz'-Yurakh Creek, Algoma and Gonam rivers, Sakha (Yakutia), Russia, holotype, YaFAN 84/3; *a,* longitudinal section, ×1.5; *b,* detail of wall in tangential section, ×10 (Korshunov, 1968).

Family URANOSPHAERIDAE R. Bedford & J. Bedford, 1936

[Uranosphaeridae R. BEDFORD & J. BEDFORD, 1936, p. 22] [=family Uranosphaeraceae R. BEDFORD & J. BEDFORD, 1936, p. 22, *nom. correct.* NITECKI & TOOMEY, 1979, p. 728, *pro* Uranosphaeridae R. BEDFORD & J. BEDFORD, 1936, p. 22; =Uranosphaerinae R. BEDFORD & J. BEDFORD, 1936, p. 22, *nom. transl.* ZHURAVLEV & SAYUTINA, 1985, p. 60, *ex* Uranosphaeridae R. BEDFORD & J. BEDFORD, 1936, p. 22]

Cup one-walled. *lower Cambrian (Bot.1–Bot.3).*

Uranosphaera R. BEDFORD & W. R. BEDFORD, 1934, p. 7 [**U. polyaster*; SD R. BEDFORD & W. R. BEDFORD, 1936, p. 20; holotype, R. BEDFORD & W. R. BEDFORD, 1934, fig. 35; DEBRENNE, H. TERMIER, & G. TERMIER, 1971, pl. 29,*3–6;* M, S4199, NHM, London] [?=*Kuraya* ROMANENKO, 1968, p. 135 (type, *K. sphaerica,* OD)]. Cup globular, nesasters linked. *lower Cambrian (?Bot.1, Bot.3)*: ?Altay Sayan, Australia.——FIG. 3,*2a–c*. **U. polyaster*, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, holotype, NHM S4199; *a,* distal view, ×2.5; *b,* lower view, ×2.5; *c,* external tangential view of wall, ×6 (Debrenne, H. Termier, & G. Termier, 1971).

Class UNCERTAIN

MORPHOLOGICALLY SIMILAR BUT PROBABLY NOT ALLIED TO ARCHAEOCYATHA OR RADIOCYATHA

Acanthinocyathus R. BEDFORD & W. R. BEDFORD and *Osadchiites* ZHURAVLEVA share a morphology of radial rods linking more or less identical units of the inner and outer wall, a character reminiscent of Radiocyatha (NITECKI & DEBRENNE, 1979, p. 14; DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 77). In their original description of *Acanthinocyathus*, R. BEDFORD and W. R. BEDFORD (1934) drew attention to a similarity with the archaeocyath *Dokidocyathus* TAYLOR, which also bears radial intervallar rods in some species. R. BEDFORD & W. R. BEDFORD (1934) and OKULITCH (1935) viewed the walls as consisting of fused spicular elements, implying affinity with spiculate sponges. Most authors have nevertheless included *Acanthinocyathus* among the Archaeocyatha.

Acanthinocyathus R. BEDFORD & W. R. BEDFORD was known only from silicified specimens until well-preserved calcitic specimens with archaeocyath-like microgranular microstructure were described by KRUSE (1982). Despite this microstructural similarity, the genus has been excluded from the Archaeocyatha by DEBRENNE, ZHURAVLEV, and ROZANOV (1989).

Order ACANTHINOCYATHIDA R. Bedford & W. R. Bedford, 1936

[Acanthinocyathida R. BEDFORD & W. R. BEDFORD, 1936, p. 11, *nom. correct.* VOLOGDIN, 1962, p. 131, *pro* order Acanthinocyathina R. BEDFORD & W. R. BEDFORD, 1936, p. 11; *nom. nov. pro* Acanthocyathina OKULITCH, 1935, p. 90, invalid name based on junior homonym]

Cup conical to subcylindrical, two-walled; intervallum with radial rods arranged in longitudinal radial planes, rods linking corresponding intersections of inner and outer wall structures. *lower Cambrian (Atd.1–Bot.3).*

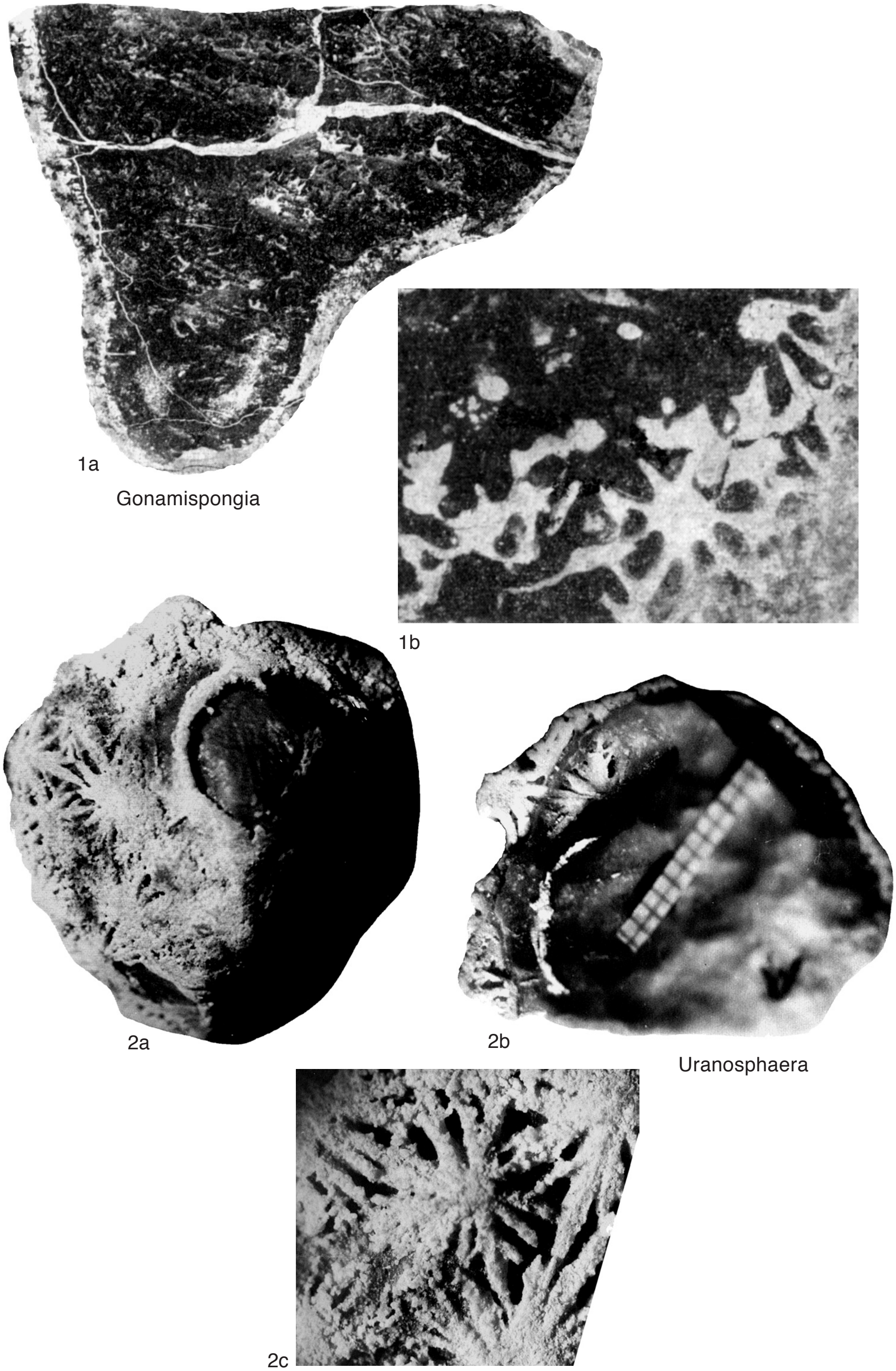

FIG. 3. Hetairacyathidae and Uranosphaeridae (p. 6).

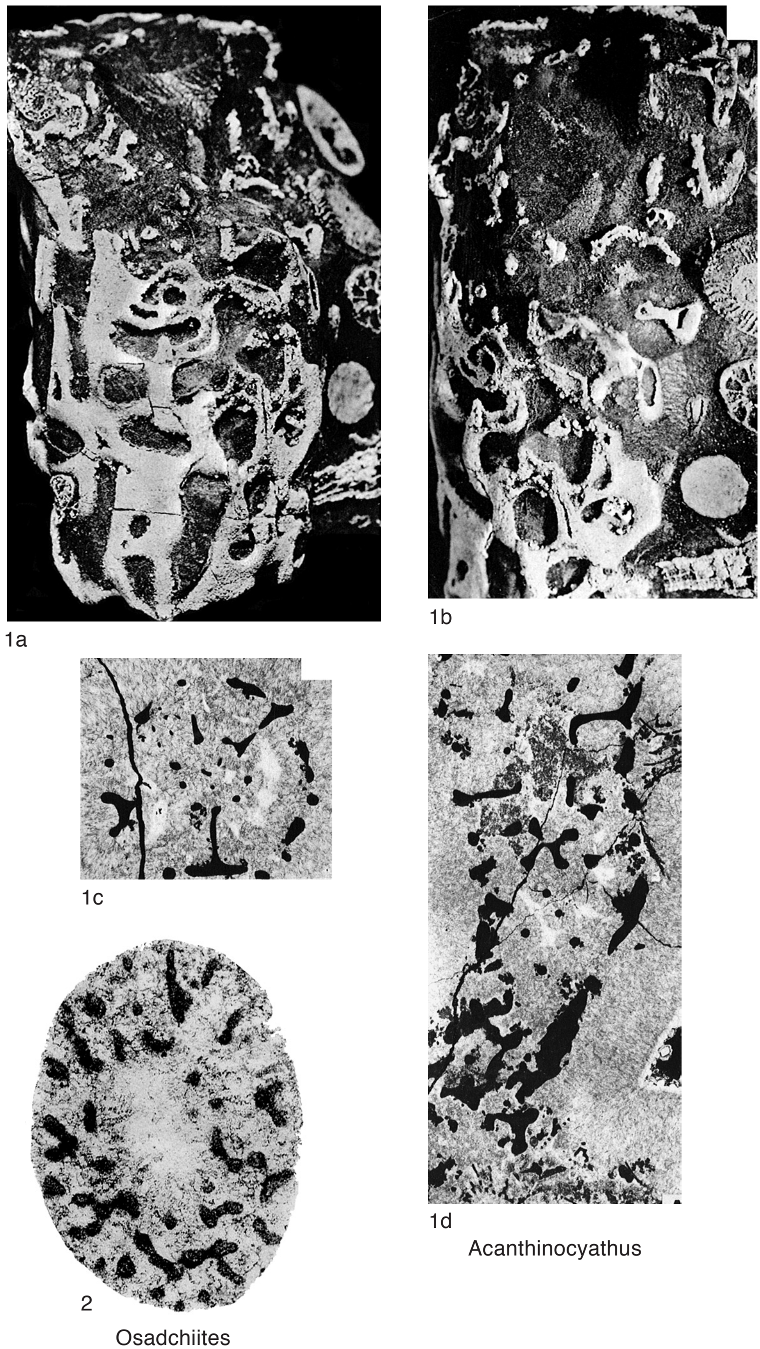

FIG. 4. Acanthinocyathidae (p. 9).

Family ACANTHINOCYATHIDAE R. Bedford & W. R. Bedford, 1936

[Acanthinocyathidae R. BEDFORD & W. R. BEDFORD, 1936, p. 11, *nom. nov. pro* Acanthocyathidae R. BEDFORD & W. R. BEDFORD, 1934, p. 4, invalid name based on junior homonym] [=Acantinocyathidae ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 99, *nom. null.*]

Outer and inner walls simple, each constructed of two sets of intersecting tangential diagonal rods. *lower Cambrian (Atd.1–Bot.3).*

Acanthinocyathus R. BEDFORD & W. R. BEDFORD, 1936, p. 11, *nom. nov. pro Acanthocyathus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4 (type, *A. apertus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4, M), *non* MILNE-EDWARDS & HAIME, 1848, p. 292, cnidarian [**Acanthocyathus apertus* R. BEDFORD & W. R. BEDFORD, 1934, p. 4; M; lectotype, HILL, 1965, pl. 2,*3;* DEBRENNE, 1969, pl. 2,*3;* SD DEBRENNE, 1969, p. 307, S4166, NHM, London] [=*Acantinocyathus* ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 100, *nom. null.*]. Outer and inner walls with subrounded to diamond-shaped pores in one longitudinal row per intersept, each outer wall pore bearing an upwardly projecting cornute spine. *lower Cambrian (Bot.3)*: Australia, Antarctica.——FIG. 4,*1a–d*. **A. apertus* (R. BEDFORD & W. R. BEDFORD); *a–b,* Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4166; *a,* longitudinal view, ×2.5; *b,* longitudinal view, ×2.5 (Hill, 1965); *c–d,* Cymbric Vale Formation, Botoman, Mount Wright, New South Wales, Australia, AM F.83608; *c,* transverse section, AM FT.14180, ×3; *d,* longitudinal section, AM FT.14179, ×3 (Kruse, 1982).

Osadchiites ZHURAVLEVA in ZHURAVLEVA & others, 1997, p. 167 [**O. denaevadae*; OD; holotype, ZHURAVLEVA & others, 1997, pl. 13,*3*, 917/5, TsSGM, Novosibirsk]. Outer and inner walls with subrounded to diamond-shaped pores in one longitudinal row per intersept, each outer wall pore bearing an upwardly projecting cornute spine; intervallar rods linked by subsidiary lintels. *lower Cambrian (Atd.1–Atd.2)*: Altay Sayan, Mongolia.——FIG. 4,*2*. **O. denaevadae*, Usa Formation, Atdabanian, Kiya River, Kuznetsk Alatau, Altay Sayan, Russia, holotype, TsSGM 917/5, transverse section, ×8 (Zhuravleva & others, 1997).

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