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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 Zhuravlev and Gonomispongia 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 Dokido-cyathus 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.
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 supra-generic 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, Konushkov, & 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 quadribracial 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 Ardabanian 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 paleocological studies indicate that at least some radiocyaths were reef dwellers or constructors. They contributed to reefs in the Tommotian of the Siberian Platform, Atabanian of Mongolia and central Australia, and Toyonian of South Australia (Kennard, 1991; Kruse, 1991; Wood, Zhuravlev, & Chimed Tseden, 1993; Kruse, Zhuravlev, & James, 1995; Kruse & others, 1996).

**Class RADIocyatha**

Debrenne, H. Termier, & G. Termier, 1970


One- or two-walled globular, conical, or pyriform skeletons constructed of nasasters; corresponding nasasters 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–Tóy.2).

**Family HETAIracYATHIDAE**

R. Bedford & J. Bedford, 1937


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

**Radiocyathed 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, NMNH, London and PUBL211, USNM, Washington, D.C.] =Heterocyathus 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, nasasters 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. *H. minor* (R. Bedford & W. R. Bedford); a–c, Ajax Limestone, Botoman, Ajax Mine, South Australia, Australia; a–b, holotype, USNM PUBL211; a, transverse view; *X*; *b*, tangential view of outer wall (at left) and inner wall (at right); *X*; c, holotype NMNH S4196, tangential view of outer wall (at bottom) and inner wall (at top); *X* (Debrenne, H. Termier, & G. Termier, 1970); d, Wilkawillina Limestone, Botoman, Wirreala Mine, South Australia, Australia, specimen SAM P47956, tangential section of outer wall, *X* (Kruse, 1991).


**Girphanovella** Zhuravleva in Zhuravleva, Zadorozhnaya, & others, 1967, p. 107 [*G. girphanovae*; OD; holotype, Zhuravleva, Zadorozhnaya, & others, 1967, pl. 59, 1–2, 325, TsSgM, Novosibirsk; =Archaeocythus neosparsjurakovi Volodgin, 1940, p. 56, holotype not designated, collection not located; =Dokidocyathina? georgensis Rozanov in Zhuravleva, Konyschkov, & Rozanov, 1964, p. 100, holotype, Zhuravleva, Konyschkov, & Rozanov, 1964, pl. 16,8, GIN3461, PIN, Moscow] =Kazakocyathus Konyschkov, 1972, p. 130 (type, *K. sajaniicus*, OD). Cup conical to pyriform, nasasters 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–Bot.2)**; Siberian Platform, Altay Sayan, Tuva, Mongolia, Transbaikalia, Australia, ?Morocco, Canada. ——Fig. 2a–f. G. neoproskursjakovii (Vologdin): a–b, =G. girphonova 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. geor R. Bedford & J. Bedford, 1936, pl. 29, R.: ?Altay Sayan, Australia. ——among 3–6; ?R. Bedford & J. Bedford, 1936, p. 22; =U. polyaster R. Bedford & J. Bedford, 1936, p. 127 [*Fig. 1a–v, 84/3, YaFAN, Yakutsk]. Cup one-walled. **lower Cambrian (Bot.1–Bot.3).**

**Class UNCERTAIN**
** MORPHOLOGICALLY SIMILAR BUT PROBABLY NOT ALLIED TO ARCHAEOCYATHA OR RADIOCYATHA**

*Acanthinocyathus* R. Bedford & W. R. Bedford and *Osadchites* ZHURAVLEVA share a morphology of radial rods linking more or less identical units of the inner and outer wall, a character reminiscent of Radiocycathyta (NITECKI & DEBRENNE, 1979, p. 14; DEBRENNE, ZHURAVLEV, & ROZANOVA, 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 and W. R. Bedford (1934) and OKULITCHE (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 ROZANOVA (1989).

**Order ACANTHINOCYATHIDIDA**

R. Bedford & W. R. Bedford, 1936


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. Hetairacythidae and Uranosphaeridae (p. 6).
Fig. 4. Acanthocystidae (p. 9).
Family ACANTHINOCYATHIDAE
R. Bedford & W. R. Bedford, 1936


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

Acanthocyathus R. Bedford & W. R. Bedford, 1936, p. 11, nom. nov. pro Acanthocyathus R. Bedford & W. R. Bedford, 1936, 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, pl. 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 Lime- stone, Botoman, Ajax Mine, South Australia, Australia, lectotype, NHM S4166; a, longitudinal view, x2.5; b, longitudinal view, x2.5 (Hill, 1965); c–d, Cymbre Vale Formation, Botoman, Mount Wright, New South Wales, Australia, AM F.83608; c, transverse section, AM FT.14180, x3; d, longitudinal section, AM FT.14179, x3 (Kruse, 1982).

Osachithes Zhuravleva in Zhuravleva & others, 1997, p. 167 [*O. danaeae; OD; holotype, Zhuravleva & others, 1997, pl. 13, 3, 917175, 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; interradial rods linked by subsidiary lintels. lower Cambrian (Atd.1–Atd.2): Al tay Sayan, Mongolia.——Fig. 4, 2, *O. danaeae, USA Formation, Atdabanian, Kiya River, Kuznetsk Altau, Altay Sayan, Russia, holotype, TsSGM 917175, transverse section, x8 (Zhuravleva & others, 1997).

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Romanenko, E. V. 1968. Kembriyskie gubki otryada Receptaculitida [Cambrian sponges of the order Heteractinellida Altya] [Cambrian sponges of the order Heteractinellida from the Altya]. Paleontologicheskiy Zhurnal 2:134–137, 3 fig.
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