GENERAL FEATURES OF THE ARCHAEOCYATHA

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INTRODUCTION

The Archaeocyatha represent the first substantial diversification of the phylum Porifera, to which they are now generally assigned as a distinct class. They flourished in carbonate shelf and reef environments of the early Cambrian; a depauperate stock persisted into the late Cambrian. They were the first Paleozoic metazoans to engage in extensive bioconstruction, in some regions building reef complexes rivalling those of the present. Their exquisite, morphologically varied, calcareous skeletons provide the basis for a more or less precise biozonation, particularly well developed for the Siberian region. *In situ* archaeocyaths are known from all continents except South America, where archaeocyaths have recently been reported in allochthonous blocks.

HISTORICAL OVERVIEW

Archaeocyaths were first discovered along the shores of Forteau Bay in southern Labrador, Canada by the hydrographer Captain H. W. BAYFIELD, who later (BAYFIELD, 1845) reported them as the coral *Cyatho-phyllum*. Specimens were renamed by BILL-INGS (1861) as *Archeocyathus* (subsequently spelled *Archaeocyathus*), destined to become the eponymous genus for the entire group.

BORNEMANN (1884, 1886) was the first to undertake a regional monographic study of archaeocyaths—from Sardinia—and to establish them as a group of high taxonomic rank: the class Archaeocyatha. The taxonomic affinities of archaeocyaths have been debated since that time (Fig. 490). TAYLOR (1910, p. 177) was the first author to recognize and elaborate on their distinctiveness, considering them as intermediate between Porifera and Coelenterata.

Thereafter, archaeocyaths were seldom compared with sponges and were established as a separate phylum by VOLOGDIN and ZHURAV-LEVA (1947) and OKULITCH and DE LAUBENFELS (1953). These authors emphasized the differences between archaeocyaths and sponges, among which the total absence of spicules in archaeocyaths was thought particularly significant. Nevertheless, while paleontologists generally accepted the concept of an independent phylum (e.g., ZHURAVLEVA, 1960b, p. 79; DEBRENNE, 1964, p. 106–107; HILL, 1965, p. 49, 1972, p. 50), some prescient sponge specialists (VACELET, 1964, p. 109; ZIEGLER & RIETSCHEL, 1970) remained opposed. The rediscovery of living sponges capable of secreting massive calcareous skeletons has since confirmed the archaeocyaths as members of the phylum Porifera.

The first higher subdivisions of Archaeocyatha were established by TAYLOR (1910, p. 105), who distinguished five families based on intervallum structure. OKULITCH (1935b) and the BEDFORDS (R. BEDFORD & J. BEDFORD, 1936, 1937, 1939; R. BEDFORD & W. R. BEDFORD, 1934, 1936) subsequently united the families into orders according to their style of ontogenetic development. VOLOGDIN (1936, 1937a, 1937b) proposed two classes, Regularia and Irregularia, on the basis of morphological differences of the secondary calcareous skeleton, as now understood. Initially, VOLOGDIN was not supported by his contemporaries. OKULITCH (1943, 1955a, p. 8) established three classes: (1) one walled, with central cavity empty; (2) two walled; and (3) central cavity full. At that time, about 400 species of archaeocyaths had been described, of which over 230 were due to VOLOGDIN's studies on material from the former USSR (Siberian Platform, Altay-Sayan, Tuva, Urals, Kazakhstan) and
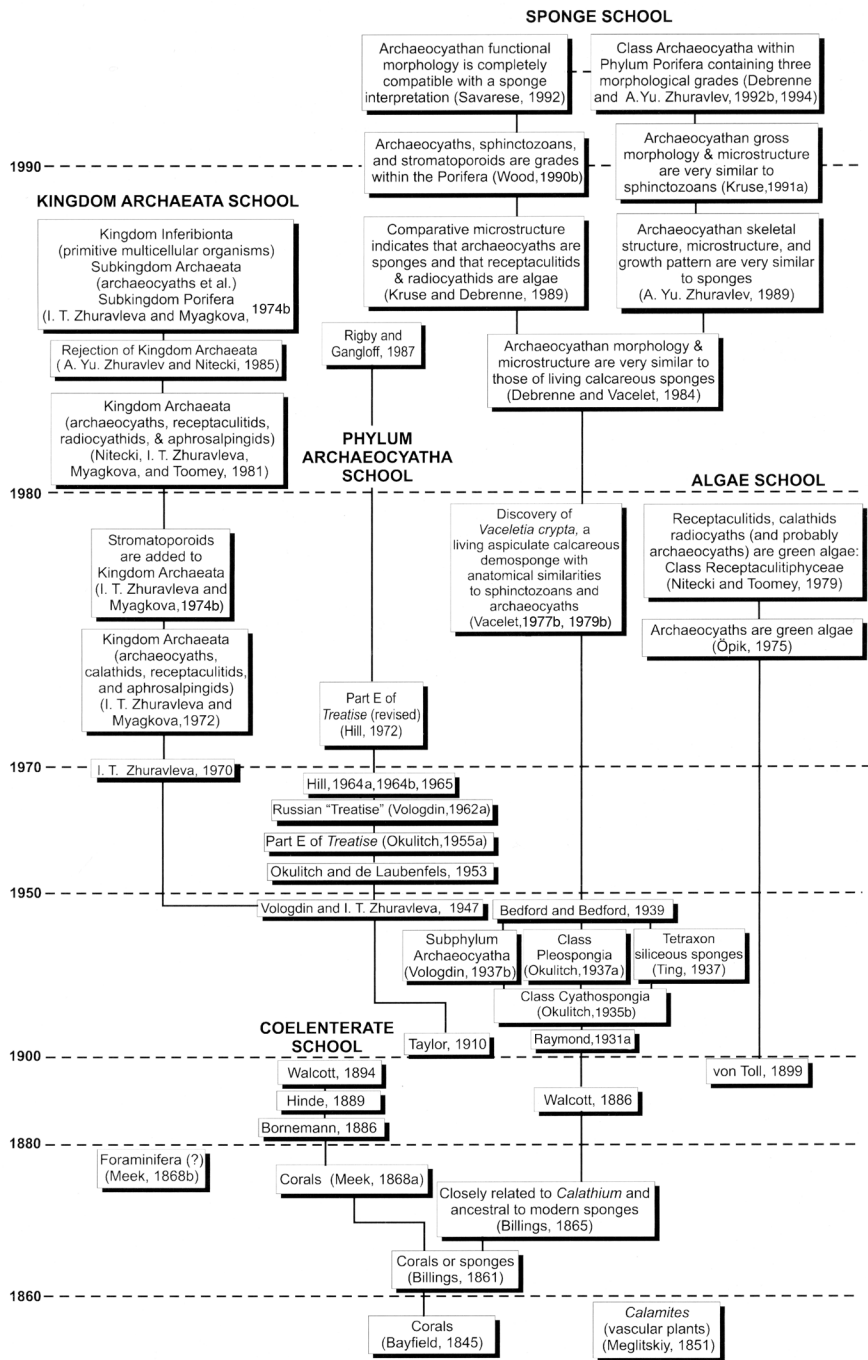
SPONGE SCHOOL

Archaeocyathan functional morphology is completely compatible with a sponge interpretation (Savarese, 1992)

Class Archaeocyatha within Phylum Porifera containing three morphological grades (Debrenne and A.Yu. Zhuravlev, 1992b, 1994)

1990

Archaeocyaths, sphinctozoans, and stromatoporoids are grades within the Porifera (Wood, 1990b)

Archaeocyathan gross morphology & microstructure are very similar to sphinctozoans (Kruse, 1991a)

KINGDOM ARCHAEATA SCHOOL

Kingdom Inferibionta (primitive multicellular organisms) Subkingdom Archaeata (archaeocyaths et al.) Subkingdom Porifera (I. T. Zhuravleva and Myagkova, 1974b)

Comparative microstructure indicates that archaeocyaths are sponges and that receptaculitids & radiocyathids are algae (Kruse and Debrenne, 1989)

Archaeocyathan skeletal structure, microstructure, and growth pattern are very similar to sponges (A. Yu. Zhuravlev, 1989)

Rejection of Kingdom Archaeata (A. Yu. Zhuravlev and Nitecki, 1985)

Rigby and Gangloff, 1987

Archaeocyathan morphology & microstructure are very similar to those of living calcareous sponges (Debrenne and Vacelet, 1984)

Kingdom Archaeata (archaeocyaths, receptaculitids, radiocyathids, & aphrosalpingids) (Nitecki, I. T. Zhuravleva, Myagkova, and Toomey, 1981)

PHYLUM ARCHAEOCYATHA SCHOOL

ALGAE SCHOOL

1980

Stromatoporoids are added to Kingdom Archaeata (I. T. Zhuravleva and Myagkova, 1974b)

Discovery of *Vaceletia crypta*, a living aspiculate calcareous demosponge with anatomical similarities to sphinctozoans and archaeocyaths (Vacelet, 1977b, 1979b)

Receptaculitids, calathids radiocyaths (and probably archaeocyaths) are green algae: Class Receptaculitiphyceae (Nitecki and Toomey, 1979)

Archaeocyaths are green algae (Öpik, 1975)

Kingdom Archaeata (archaeocyaths, calathids, receptaculitids, and aphrosalpingids) (I. T. Zhuravleva and Myagkova, 1972)

Part E of *Treatise* (revised) (Hill, 1972)

1970

I. T. Zhuravleva, 1970

Hill, 1964a, 1964b, 1965

Russian "Treatise" (Vologdin, 1962a)

Part E of *Treatise* (Okulitch, 1955a)

Okulitch and de Laubenfels, 1953

1950

Vologdin and I. T. Zhuravleva, 1947

Bedford and Bedford, 1939

Subphylum Archaeocyatha (Vologdin, 1937b)

Class Pleospongia (Okulitch, 1937a)

Tetraxon siliceous sponges (Ting, 1937)

Class Cyathospongia (Okulitch, 1935b)

COELENTERATE SCHOOL

Taylor, 1910

Raymond, 1931a

1900

Walcott, 1894

von Toll, 1899

Hinde, 1889

Walcott, 1886

Bornemann, 1886

1880

Foraminifera (?) (Meek, 1868b)

Corals (Meek, 1868a)

Closely related to *Calathium* and ancestral to modern sponges (Billings, 1865)

Corals or sponges (Billings, 1861)

1860

Corals (Bayfield, 1845)

Calamites (vascular plants) (Meglitskiy, 1851)

FIG. 490. History of phylogenetic interpretations of archaeocyaths (adapted from Rowland, 2001).

Mongolia. Rich collections from a diversity of localities provided him with much material for the study of morphology and the elaboration of a theoretical approach to classification. However, it was ZHURAVLEVA (1955b) who established a firmer basis for the distinction of the Regularia and Irregularia from her study of skeletal ontogeny. She also defined orders and families based on intervallar and wall structures respectively—criteria still broadly applied in the current classification. In 1960, she corrected the names Regularia and Irregularia to Regulares and Irregulares (as subclasses), to avoid confusion with the major subdivisions of the Echinoidea and Cystoidea (ZHURAVLEVA, 1960b, p. 80, 267).

Since the early 1960s, the archaeocyathan genus has become a taxonomic category whose definition has achieved general consensus among specialists. It is based upon variations of skeletal elements, particularly within designated categories of wall construction and the presence or absence of supplementary elements. An increase in the number of described genera from this time reflects both the publication of regional monographs and a tendency to oversplit taxa on criteria not now considered to be of generic significance.

By the mid-1970s, the Regulares had been intensively investigated. Their elegant porous skeleton proved to be an ideal model for the application of VAVILOV's (1922) principle of homologous series in hereditary variability, thus strengthening the basis for classification (ROZANOV in ROZANOV & MISSARZHEVSKIY, 1966, p. 73; ROZANOV, 1973, p. 50, 1974). VAVILOV's principle postulates that within a particular clade, such as a family, constituent species and genera display a common, but limited set of homologous character states that have parallels in closely related clades. Morphological attributes of as yet undiscovered clade members may thereby be predicted. Archaeocyathan evolution was used to establish four early Cambrian stages in Siberia (ROZANOV, 1973, p. 80). Comprehensive studies by ZHURAVLEVA, DEBRENNE,

ROZANOV, and others were the basis for the successful revision of the *Treatise on Invertebrate Paleontology*, Part E, by HILL (1972).

The 1970s and 1980s were a period of accumulation of comprehensive regional material. Monographic compilations treated archaeocyaths from throughout the former USSR, Western Europe, Morocco, China, Australia, Antarctica, South Africa, and western and eastern North America, including Greenland.

The rediscovery of sponges having massive calcareous skeletons, with or without spicules, transformed conceptions of the affinities of groups such as archaeocyaths, sphinctozoans, stromatoporoids, and others. One of the most striking finds was of *Vaceletia crypta* (VACELET), an extant chambered demosponge with a massive calcareous skeleton devoid of spicules (VACELET, 1977b). Such discoveries forced a reconsideration of the nature of archaeocyaths (DEBRENNE & VACELET, 1984; PICKETT, 1985b; ZHURAVLEV, 1985).

This accumulation of regional data, together with the new actualistic model of archaeocyathan functional morphology, culminated in a thorough revision of taxonomy, ontogeny, ecology, biostratigraphy, and biogeography by DEBRENNE, ZHURAVLEV, and ROZANOV (1989), DEBRENNE, ROZANOV, and ZHURAVLEV (1990), and DEBRENNE and ZHURAVLEV (1992b). This work resulted in a drastic decrease in the total number of genera in the group, from 587 before 1989 to 298. Aspects of the relationship between archaeocyaths and sponges were also extensively discussed, affirming the Archaeocyatha as a class within the phylum Porifera. These publications, together with the earlier compilation of HILL (1972) and the summary revision of DEBRENNE, ZHURAVLEV, and KRUSE (2002), form the basis for the present work.

SYSTEMATIC POSITION AMONG METAZOA

On the basis of superficial similarities, archaeocyaths have been attributed to a variety of groups, including corals, sponges,

protists, and algae, regarded as an independent phylum, or united with aphrosalpingoids (actually thalamid sponges) and receptaculitaleans (algae or lower invertebrates) as a separate kingdom (ZHURAVLEVA & MYAGKOVA, 1987, p. 174). A historical compendium of the systematic attributions of Archaeocyatha is provided by DEBRENNE and ZHURAVLEV (1992b, table I). Extant sponges with a nonspiculate skeleton (*Acanthochaetetes wellsi* HARTMAN & GOREAU, *Vaceletia crypta* [VACELET], and others) show similarities to archaeocyaths in architecture, skeletal structure (both primary and secondary), functional morphology, and evolutionary trends (DEBRENNE & VACELET, 1984; PICKETT, 1985b; ZHURAVLEV, 1985, 1989, 1993; DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 152; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 197; KRUSE, 1990a; SAVARESE, 1992, 1995; WOOD, ZHURAVLEV, & DEBRENNE, 1992). Such similarities favor a close taxonomic relationship between archaeocyaths and calcified sponges.

VACELET (1985) drew a comparison between Archaeocyatha and Hexactinellida in that both groups have a complicated skeleton, which in hexactinellides is probably due to their syncytial organization and relatively advanced conductive system (BERGQUIST, 1985). DEBRENNE and ZHURAVLEV (1994) proposed that shared similarities with regard to immune reactions and modes of asexual reproduction, particularly intracalicular budding and the interpreted presence of crypt cells, support a closer affinity of Archaeocyatha with demosponges than with other classes of Porifera. These hypotheses remain to be confirmed.

MORPHOLOGY

The archaeocyathan skeleton is typically a narrow conical cup with porous outer and inner walls, connected by longitudinal partitions (septa and others). This architecture is distinctive of the archaeocyaths, though structures mimicking septa are known, for example, in the Early Devonian thalamid sponge *Radiothalamos* PICKETT &

RIGBY (1983) and its allies. As well, archaeocyaths exhibit almost the entire range of growth forms found in calcified sponges: thalamid (sphinctozoan) (ZHURAVLEV, 1989; DEBRENNE & WOOD, 1990), stromatoporoid (ZHURAVLEV, 1990a), and chaetetid (DEBRENNE, KRUSE, & ZHANG, 1991) (Fig. 491). Organisms with these skeletal morphologies were previously considered as separate groups of cnidarians, sponges, or even algae. However, studies of living representatives have established their individual systematic positions and hence their polyphyletic origin (VACELET, 1979b, 1983; VAN SOEST, 1984; REITNER & ENGESER, 1985; WOOD, 1987; WOOD & REITNER, 1988; DEBRENNE, 1991). Each group had been described with its own nomenclature; to avoid confusion, a synonymized nomenclature was proposed by ZHURAVLEV, DEBRENNE, and WOOD (1990).

The remarkable similarity of thalamid archaeocyaths and extant thalamid demosponges (*Vaceletia* PICKETT) has been frequently noted (DEBRENNE & VACELET, 1984; ZHURAVLEV, 1985; KRUSE, 1990a). A great diversity of morphological elements (SENOWBARI-DARYAN & SCHÄFER, 1986; RIGBY, FAN, & ZHANG, 1989a; SENOWBARI-DARYAN, 1990; BOĬKO, BELYAEVA, & ZHURAVLEVA, 1991, pl. 42,*3*) has been observed in thin sections of thalamid sponges, which are referable mainly to the demosponges, although a minority are calcareans. These structures are similar to some archaeocyathan elements (e.g., syringes, taenialike structures). The presence of outer wall microporous sheaths in the two groups is especially significant for functional morphology. Some Carboniferous and Mesozoic chaetetid sponges have continuous tabulae (WEST & CLARK, 1984) and porous calicles. In *Chaetetes* FISCHER VON WALDHEIM, the fiber bundles forming the tabulae result from the progressive bending of fibers issuing from the longitudinal axis; they converge at the center of the functional cavity but do not coalesce, and a central pore may be present. On the contrary, chaetetid archaeocyathan tabulae
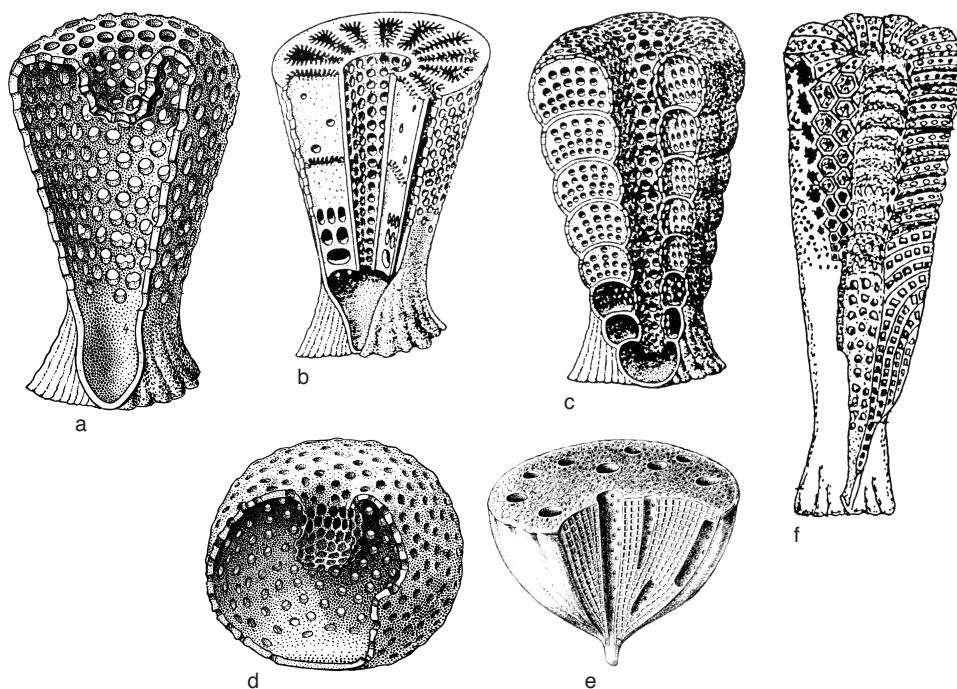
FIG. 491. Archaeocyathan architecture; *a,* one-walled conical; *b,* two-walled conical; *c,* multichambered conical (thalamid); *d,* single-chambered subspherical (Debrenne, Rozanov, & Zhuravlev, 1990); *e,* chaetetid; *f,* syringoid (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

are produced by the secondary skeleton and are continuous. Both might correspond to an externalization of the soft tissue in the skeleton, but are nevertheless convergent. The facultative presence of intracalicular (septal) spines and astrorhizae has been reported in some genera of chaetetid demosponges and chaetetid archaeocyaths (WEST & CLARK, 1983; DEBRENNE & ZHURAVLEV, 1994).

MORPHOLOGY OF PRIMARY SKELETON

Archaeocyathan taxonomy is derived from ontogenetic studies, which have established the order of appearance and complication of the various structural elements constituting the archaeocyathan cup (R. BEDFORD & J. BEDFORD, 1939; ZHURAVLEVA, 1960b). On the principle that ontogenetically earlier appearing features are accorded higher taxonomic rank, orders are delineated by architecture of the cup; suborders by the basic intervallar structures present, and

for modular forms, mode of increase (Fig. 492); superfamilies by the outer wall type; families by the inner wall type; genera by specified variants of wall and intervallar structures; and species by variation in shape, size, and number of skeletal constituents.

Six orders and 12 suborders are thus recognized within the class (DEBRENNE, ZHURAVLEV, & ROZANOV, 1989; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990; ZHURAVLEV, 1990a; DEBRENNE, 1991; DEBRENNE & ZHURAVLEV, 1992b) (Fig. 491):

Monocyathida (one-walled conical cup)
Ajacicyathida (archaeocyathan architecture: two-walled cup with septa as radial partitions)
　Dokidocyathina (intervallum with septa bearing one longitudinal pore row)
　Ajacicyathina (intervallum with septa bearing several longitudinal pore rows)
　Erismacoscinina (intervallum with septa and plate tabulae)

Putapacyathida (archaeocyathan architecture: two-walled cup with plate tabulae only)

Capsulocyathida (thalamid cup with inner wall of invaginal type)

Capsulocyathina (cup single-chambered and subspherical, or multichambered without septa)

Coscinocyathina (cup multichambered, intervallum with septa)

Archaeocyathida (archaeocyathan architecture: two-walled cup with radial partitions other than septa)

Loculicyathina (pseudocolonies by interparietal budding, intervallum with pseudosepta)

Anthomorphina (pseudocolonies by external budding, intervallum with pseudosepta and membrane tabulae)

Archaeocyathina (pseudocolonies by external budding and/or longitudinal subdivision, intervallum with taeniae, pseudosepta, or dictyonal network)

Dictyofavina (branching or massive pseudocolonies by intercalicular budding, intervallum with calicles)

Syringocnemina (pseudocolonies by longitudinal fission, intervallum with syringes)

Kazachstanicyathida (thalamid and stromatoporoid architecture)

Kazachstanicyathina (initial chambers hollow and elongate, pillars in subsequent chambers)

Altaicyathina (initial chambers subspherical, pillars in all chambers).

Architecture

The architecture of a two-walled cup is determined by the development of its component longitudinal platelike elements. No other sponge group is known that exhibits an archaeocyathan architecture. This architecture, characterized by (pseudo)septa, (pseudo)taeniae, tabulae, syringes, and/or dictyonal network, is typical of Ajacicyathida and Archaeocyathida.

The chaetetid architecture (intervallum with calicles), ontogenetically proceeds from a typical archaeocyathan development with taeniae, which, with growth, is transformed into calicles (Fig. 491e). The syringoid architecture (Fig. 491f) is developed from the chaetetid. Like the chaetetid, syringoid forms are not exclusive to the archaeocyaths, being known, for example, among Permian sphinctozoan sponges (e.g., *Tebagathalamia* in SENOWBARI-DARYAN & RIGBY, 1988).

The rare, thalamid architecture consists of a succession of chambers that are initially subspherical (Fig. 491c), but in some forms become more laterally elongate (see Fig. 513b). Chambers generally contain longitudinal elements (pillars). Growth proceeds by the distal addition of chambers. It is a typical architecture of sphinctozoan demosponges and calcareans.

Cup Size and Shape

Across the above categories, the typical solitary conical cup may expand slowly or rapidly to generate a spectrum of shapes from subcylindrical, through narrowly and widely conical, to discoid. Increase in the rate of expansion with growth produces a bowl-shaped cup. A typical ajacicyathide conical cup is of the order of 5–15 mm in diameter and several centimeters in height, but exceptionally may attain a height of 1.5 m. Discoid cups such as in the archaeocyathide *Okulitchicyathus* ZHURAVLEVA may attain a diameter of half a meter but are generally several centimeters in diameter.

Transverse or longitudinal folding may complicate the basic conical cup shape. Where this is regular and affects both walls, as in some Ajacicyathida, it is treated as a generic criterion (e.g., *Orbicyathus* VOLOGDIN with periodic, synchronous, transverse folds of both walls giving rise to undulose longitudinal section; *Orbiasterocyathus* ZHURAVLEVA with both walls longitudinally folded, resulting in stellate transverse section). The plicate wall, in which each intersept is individually folded to form a sharp mid-interseptal longitudinal ridge, is also a generic criterion,
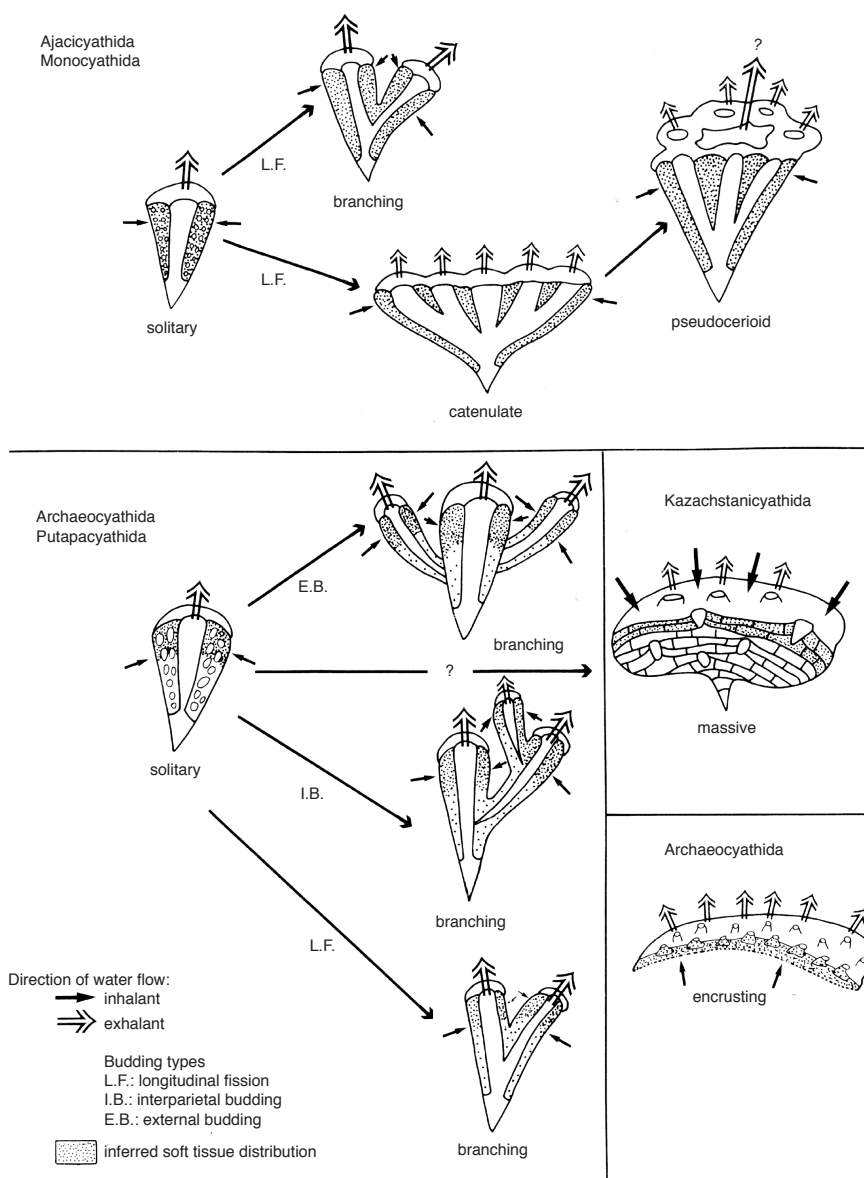
FIG. 492. Development of modular archaeocyath types based on module organization and mode of proliferation; possible evolutionary pathways from an ancestral solitary cup are indicated (Wood, Zhuravlev, & Debrenne, 1992).

e.g., *Rozanovicoscinus* DEBRENNE with plicate outer wall (Fig. 492, Fig. 493a).

In Archaeocyathida, only the outer wall may be folded, with transverse folds generating an undulose longitudinal section, e.g., *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD (Fig. 494c).

Subspherical cups may show a variety of regularly or irregularly arranged prominences and indentations, as in *Capsulocyathus* ZHURAVLEVA (Fig. 493b, Fig. 493d). In conical cups, such as those of *Batschykicyathus* ZHURAVLEV, prominences are evenly arranged in single planes, several
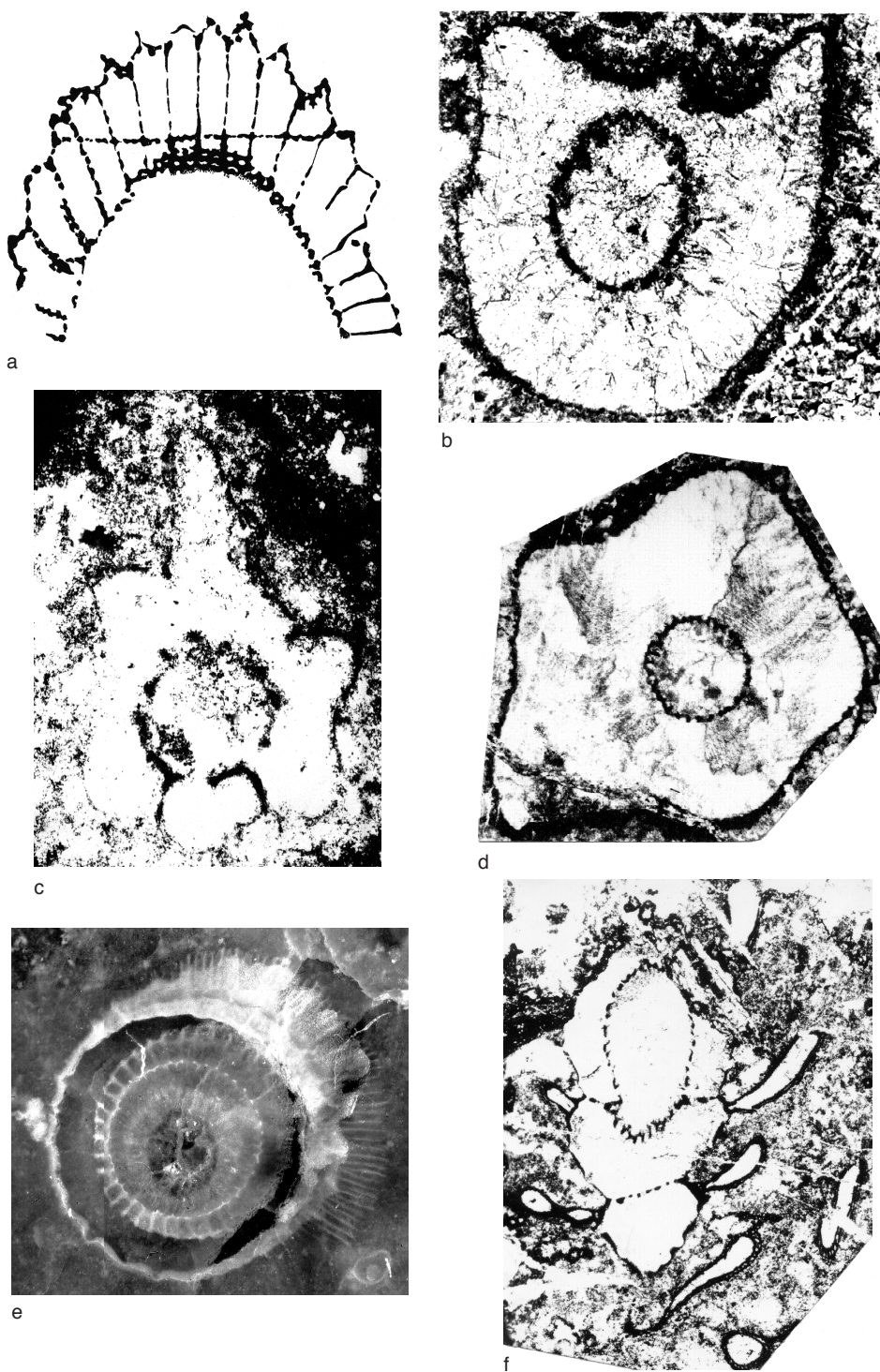
Fig. 493. *(For explanation, see facing page).*

to a cup (Fig. 493c). The distinctively shaped cup of *Yukonensis* ÖZDIKMEN (Fig. 493e–f) consists of a subcylindrical cup with periodic constrictions, each with an accompanying umbrella-like corolla of hollow shafts and connecting membranes.

Cup Modularity

As with sponges generally, archaeocyaths were probably not true colonial organisms. However, it is possible to apply the concept of sponge modularity to archaeocyaths and hence to treat a single central cavity with its surrounding elements as analogous to the osculum of a sponge (KOLTUN, 1988) or to an aquiferous unit space in stromatoporoid sponges (WOOD, 1987). Hence an archaeocyathan skeleton that is not a single cup is described as modular (Fig. 492) (previously, colonial).

Modularity is common in the Archaeocyathida, Putapacyathida, and Kazachstanicyathida and also occurs in some members of most other orders (e.g., branching *Archaeolynthus polaris* [VOLOGDIN] in Monocyathida).

Modularity in archaeocyaths is understood in terms of the individual aquiferous unit: that portion of an archaeocyathan cup with a number of inhalant openings converging on a single exhalant opening (osculum) (WOOD, ZHURAVLEV, & DEBRENNE, 1992). Most archaeocyaths are therefore solitary, their conical cups bearing a single osculum represented by the central cavity orifice. Some, however, are multioscular and thus modular, generating branching, catenulate, pseudocerioid, massive, and encrusting forms (Fig. 495).

Proliferation of modules is by several methods: longitudinal fission and external, interparietal, and intercalicular budding (DEBRENNE, ZHURAVLEV, & KRUSE, 2002; longitudinal subdivision, external and intervallar budding respectively of WOOD, ZHURAVLEV, & DEBRENNE, 1992). Longitudinal fission produces branching, catenulate and pseudocerioid morphology (Fig. 492, Fig. 495a–c; see Fig. 523b). In external budding, a bud arises on the outer wall of the cup, whereas in interparietal budding, the bud arises within the intervallum. Both produce branching modularity (Fig. 492, Fig. 519d). Intercalicular budding generates buds inside a single calicle to produce branching and massive morphology (see Fig. 523a). As well, some encrusting and massive morphologies could form by individualization of additional aquiferous units within a modular skeleton (Fig. 492, Fig. 495d–e).

Living organisms exhibit a wide spectrum of degrees of bodily integration, and archaeocyaths are no exception. In considering the archaeocyaths, WOOD, ZHURAVLEV, and DEBRENNE (1992) categorized branching and laminar modularity as having low integration, as constituent modules were either isolated or discrete yet connected. Catenulate and pseudocerioid forms, with adjacent confluent units having no separating wall, were considered to be of medium integration. Highly integrated forms were the massive and encrusting types, notably among the Kazachstanicyathida, that lack separating walls or septa between aquiferous units. Massive forms present thalamid-stromatoporoid and chaetetid architectures (see Fig. 513b).

FIG. 493. Archaeocyathan cup shapes; *a,* longitudinally plicate cup of *Rozanovicoscinus stellatus* GRAVESTOCK, Botoman, Ajax Limestone, Mount Aroona, South Australia, Australia, oblique section, NL82013, MNHN, ×7 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* subspherical cup of *Capsulocyathus irregularis* (ZHURAVLEVA), Botoman, Salaany Gol Formation, Salaany Gol, Tsagaan Oloom province, western Mongolia, oblique longitudinal section, 3302/3023, PIN, ×16 (Voronin & others, 1982); *c,* regularly bulging outer wall in *Batschykicyathus angulosus* ZHURAVLEV, Atdabanian, Pestrotsvet Formation, Bachyk Creek, Lena River, Sakha (Yakutia), Russia, transverse section, paratype, 3848/504, PIN, ×22 (Zhuravlev, Zhuravleva, & Fonin, 1983); *d,* same as view *b,* transverse section, 3302/3025, PIN, ×17 (Voronin & others, 1982); *e,* multichambered cup and corolla (at top and right) of *Yukonensis yukonensis* (HANDFIELD), Botoman, Adams Argillite, Tatonduk River, Alaska, United States, transverse section, locality USGS 5156C, collection not located, ×24 (Debrenne, Zhuravlev, & Kruse, 2012b); *f, Yukonensis yukonensis* (HANDFIELD), cup with shafts of successive corollas (at right), Botoman, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90149, GSC, ×7 (Voronova & others, 1987).
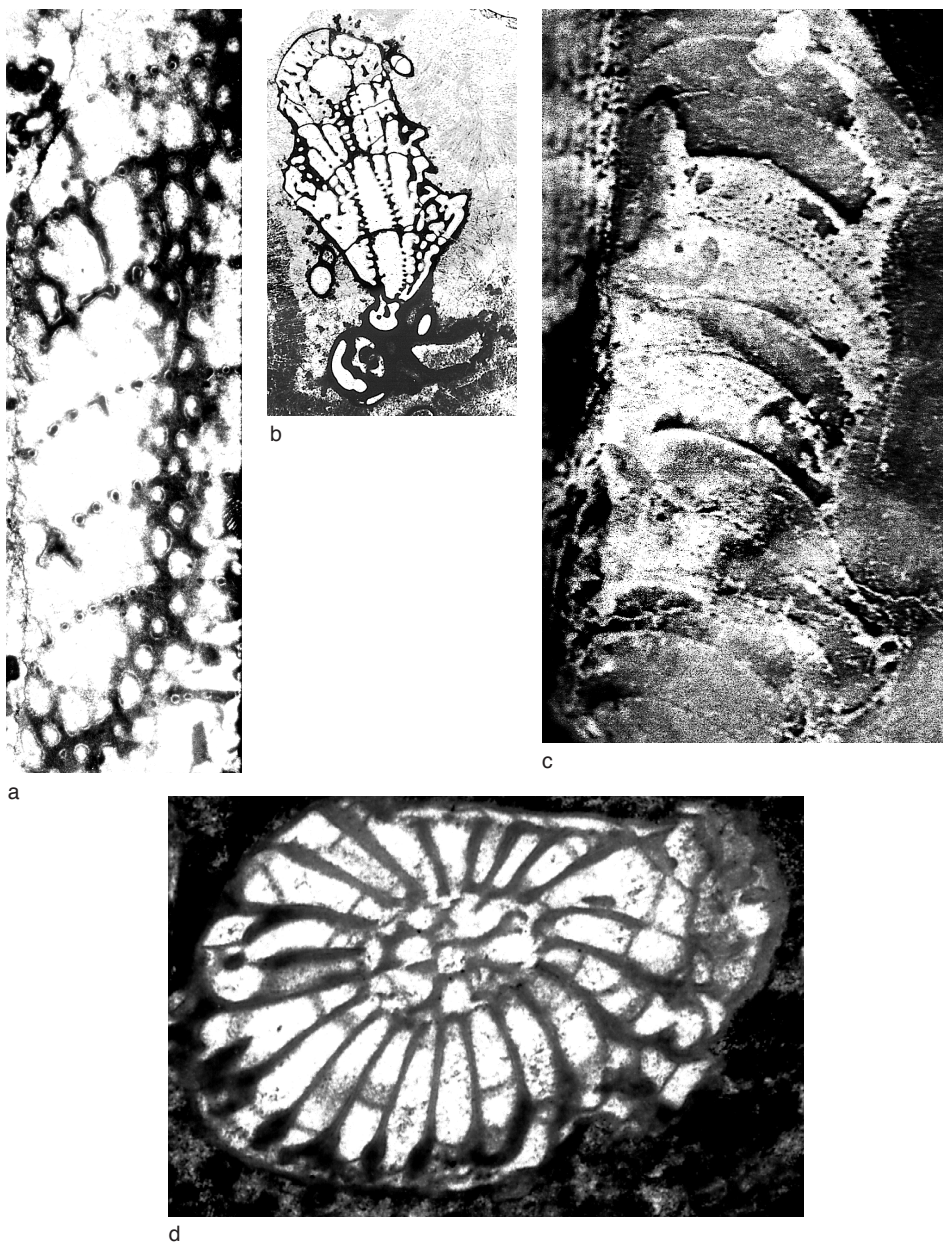
FIG. 494. Transverse folds and pseudoseptal porosity; *a,* irregular pseudoseptal porosity in *Cellicyathus* sp., Botoman, Chara Formation, Peleduy River, Sakha (Yakutia), Russia, longitudinal section (outer wall to left), 4451/18, PIN, ×20 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* coarsely porous pseudosepta in *Cambrocyathellus proximus* (FONIN), Tommotian, Pestrotsvet Formation, Lena River, Sakha (Yakutia), Russia, longitudinal section, 4451/8, PIN, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* transverse outer wall folds and finely porous pseudosepta in *Pycnoidocoscinus pycnoideum* R. BEDFORD & W. R. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paratype, P991, SAM, ×5 (Debrenne, 1974a); *d,* aporose pseudosepta in *Anthomorpha margarita* BORNEMANN, Botoman, Matoppa Formation, Cuccuru Contu, Sardinia, Italy, transverse section, paratype, M84138, MNHN, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
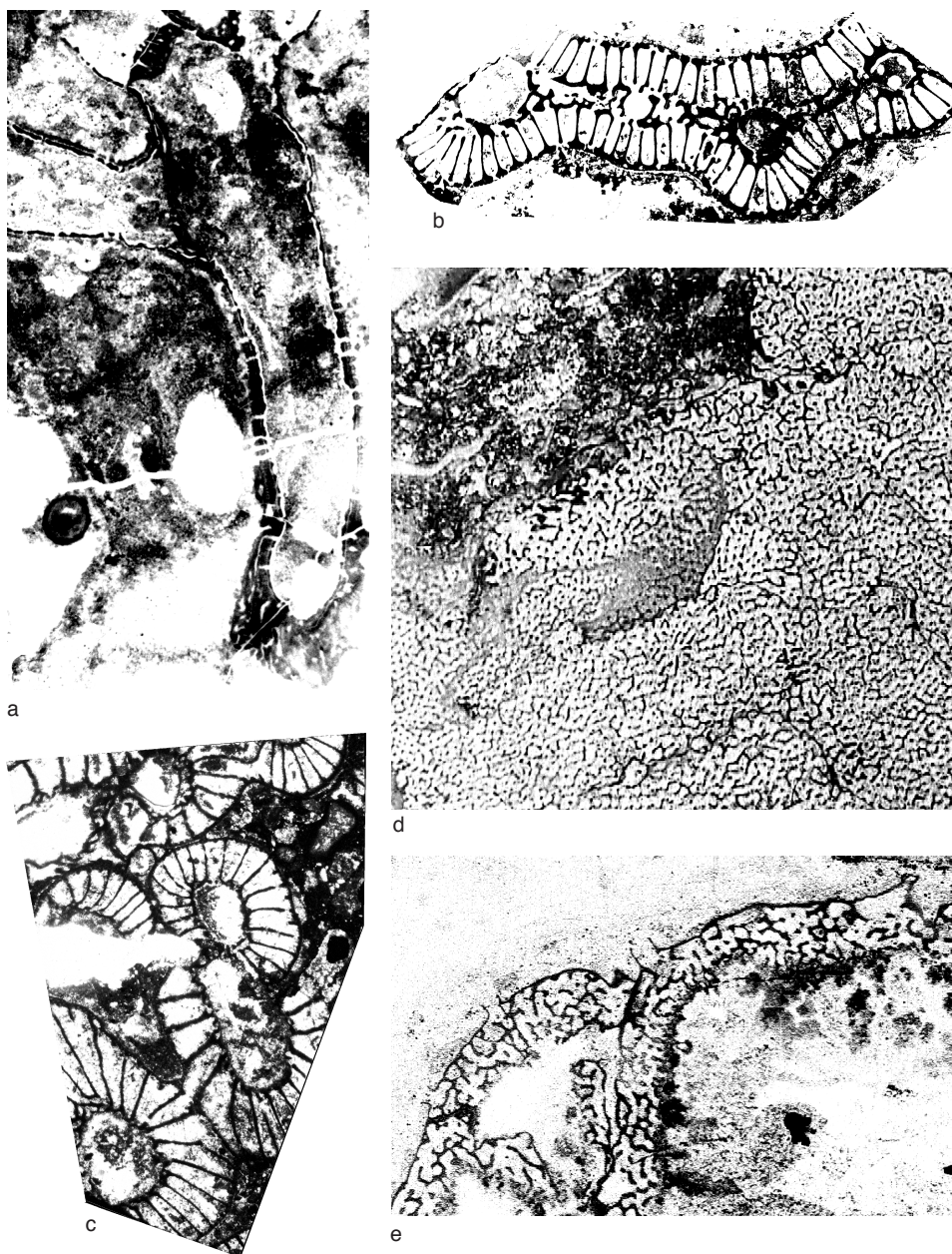
FIG. 495. Modularity in archaeocyaths; *a,* longitudinal subdivision in branching *Archaeolynthus polaris* (VOLOGDIN), Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, longitudinal section, 3848/564, PIN, ×7.5 (Wood, Zhuravlev, & Debrenne, 1992); *b,* catenulate *Pluralicyathus heterovallum* (VOLOGDIN), Toyonian, Torgashino Formation, Uymen' River, East Sayan, Altay Sayan, Russia, transverse section, institution and collection number not known, ×2 (Wood, Zhuravlev, & Debrenne, 1992); *c,* pseudocerioid *Densocyathus sanashticolensis* VOLOGDIN, Botoman, Verkhnemonok Formation, Sanashtykgol Spring, West Sayan, Altay Sayan, Russia, transverse section, 4327/7, PIN, ×5 (Wood, Zhuravlev, & Debrenne, 1992); *d,* massive *Zunyicyathus grandis* (YUAN & ZHANG), Botoman, Jindingshan Formation, Jindingshan, Guizhou, China, transverse section, 85103, MNHN, ×5 (Debrenne, Kruse, & Zhang, 1991); *e,* encrusting *Retilamina amourensis* DEBRENNE & JAMES, Botoman, Forteau Formation, Mount St Margaret, Newfoundland, Canada, longitudinal section, paratype, 62127, GSC, ×5 (Debrenne & James, 1981).
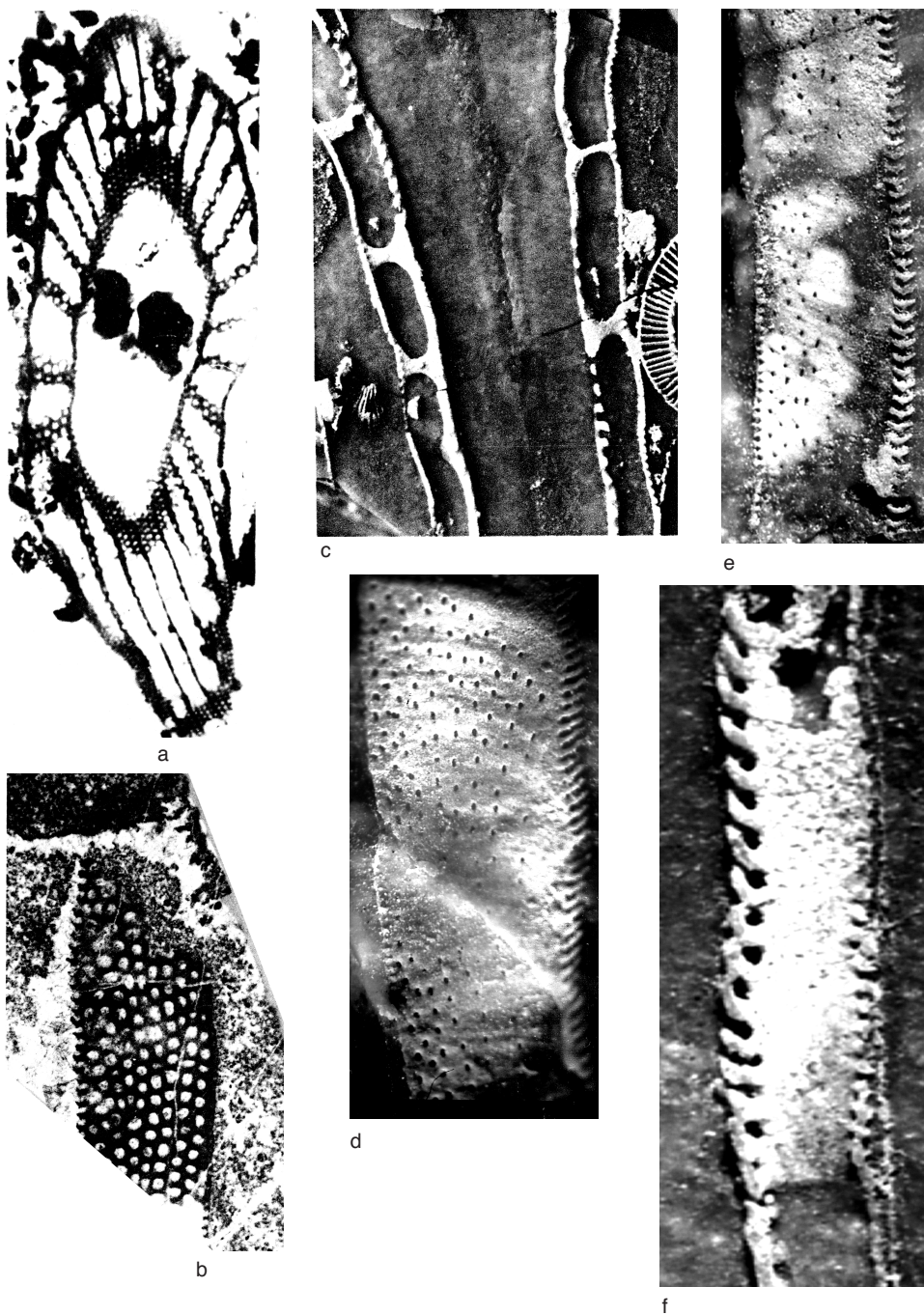
FIG. 496. Septal porosity in Ajacicyathida; *a,* completely porous septa in *Nochoroicyathus sunnaginicus* (ZHURAV-LEVA), Tommotian, Pestrotsvet Formation, Aldan River, Sakha (Yakutia), Russia, oblique section, 2411-35/4, PIN, ×6.5 (Debrenne & Voronin, 1971); *b,* completely porous septa in *Gordonicyathus xandarus* (KRUSE), Boto-man, Mount Wright Volcanics, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to right), FT.8475, holotype, F.83827, AM, ×12 (Kruse, 1982); *c,* septa bearing a single longitudinal pore row in *(Continued on facing page.)*

MORPHOLOGY OF MONOCYATHIDA, AJACICYATHIDA, PUTAPACYATHIDA, AND CAPSULOCYATHIDA

Wall and intervallum structures are sufficiently different between the above orders and the Archaeocyathida and Kazachstanicyathida to warrant separate treatments. Discussions by DEBRENNE, ROZANOV, and ZHURAVLEV (1990) and DEBRENNE and ZHURAVLEV (1992b) provide the basis for the following outline.

INTERVALLUM STRUCTURES

One or a combination of a variety of radial, transverse, and longitudinal skeletal structures may be present within the intervallum of two-walled cups. Those directly connecting both walls are first-order intervallar structures, whose presence or absence represents ordinal or subordinal taxonomic criteria. Those developed upon or between these are second-order intervallar structures, generally of genus- and species-level taxonomic value.

Septa

Septa are radial-longitudinal partitions linking inner and outer walls in conical cups; in nonconical cases, such as catenulate cups, they are not strictly radial, but nevertheless retain a perpendicular orientation to the walls. Most septa are planar, but a minority are wavy, as, for example, in *Leptosocyathus curviseptum* VOLOGDIN. In some taxa, septa may bifurcate toward the outer wall.

With cup growth, new septa are inserted at the outer wall as a rudimentary plate when the number of interseptal wall pores reaches a maximum for the species. This plate then grows more or less rapidly toward the inner wall (ZHURAVLEVA, 1960b).

Septal porosity has been widely accepted as a generic criterion ever since it was first espoused by DEBRENNE and VORONIN (1971). Two broad styles of septal porosity are thus recognized: completely porous and aporose to sparsely porous, based on the work of ROZANOV (1973), who documented two corresponding pathways of ontogenetic porosity development. In the first, an initial netlike (large-pored) porosity results in completely porous septa with generally ordered longitudinal rows of pores covering the entire septal area; in the second, initial porosity rapidly reduces or disappears with growth, producing mature septa in which pores are restricted in their distribution or even virtually absent. Netlike (pore diameter much greater than lintel width) and finely porous (pore diameter subequal to lintel width) variants are noted by DEBRENNE, ROZANOV, and ZHURAVLEV (1990) among completely porous septa, and sparsely porous (with consistent presence of rare pores), scattered porous (with porosity of only part of a septum), and perforate (with stirrup pores, together with scattered solitary pores, in median area of a septum) variants among aporose to sparsely porous septa, but these have only species-level significance (Fig. 496).

In the case of septa with stirrup pores only (among the most aporose septal porosities known), early ontogenetic stages show septa with an initial single row of pores adjacent to either or both walls. With cup growth, this pore row gradually migrates into the wall to form a row of stirrup pores (arrested initial stage of septal development

FIG. 496. *(Continued from facing page).*
Dokidocyathus simplicissimus TAYLOR, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, lectotype, T1589A-B, SAM, ×3.5 (Taylor, 1910); *d,* sparsely porous septa in *Thalamocyathus tectus* DEBRENNE, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to left), 165, PU, ×10 (Debrenne, 1973); *e,* sparsely porous septa in *Thalamocyathus trachealis* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to left), paralectotype, T1585, SAM, ×10 (Debrenne, 1973); *f,* stirrup pores at junction of septa and inner wall in *Stapicyathus stapipora* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paratype, 86782, PU, ×12 (Debrenne, 1974b).
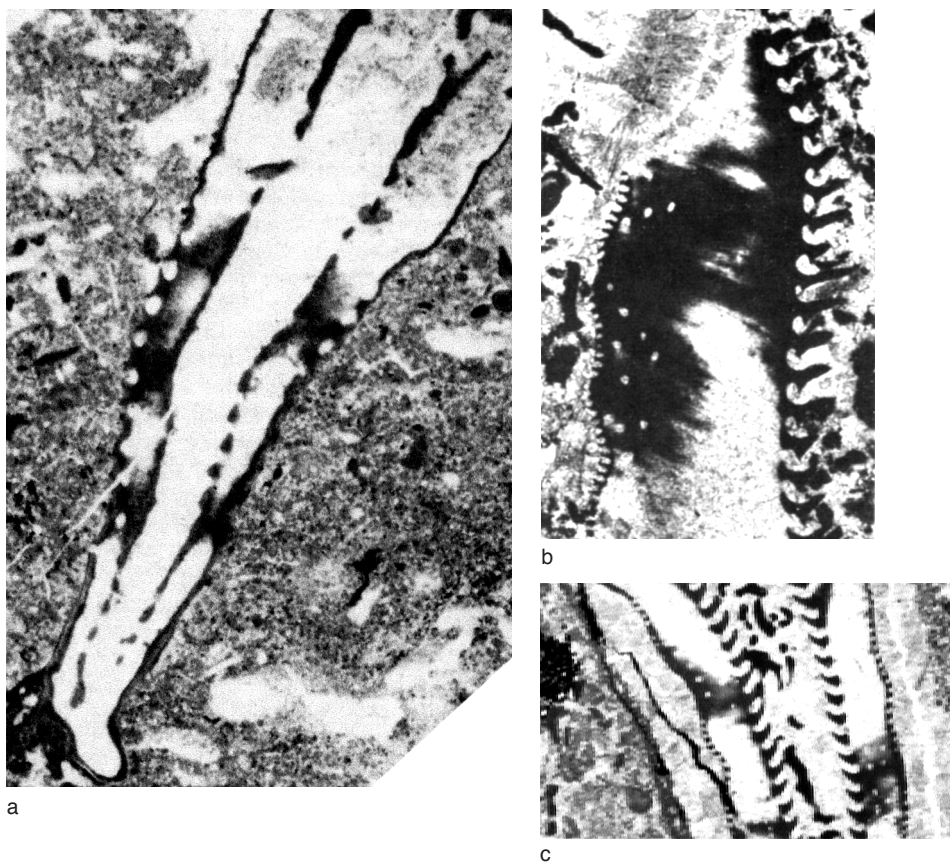
Fig. 497. Ontogenetic development of aporose to sparsely porous septa; *a,* arrested initial stage of pore development, in which a single pore row initially wholly within the septum migrates centrifugally during ontogeny to become a stirrup pore row along the outer wall, *Kisasacyathus caecum* (Gravestock), Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, longitudinal section of apex, paratype, P21481, SAM, ×15 (Gravestock, 1984); *b,* adult septal porosity concentrated adjacent to outer wall in *Sagacyathus stonyx* Kruse, Botoman, Mount Wright Volcanics, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left) FT.8492, paratype, F.83568, AM, ×10 (Kruse, 1982); *c,* same, juvenile septal porosity across entire septum, longitudinal section, FT.8491, holotype, F.83576, AM, ×10 (Kruse, 1982).

of Gravestock [1984]) (Fig. 497a). In fact, this same ontogenetic lateral migration of pores also operates in septa with scattered porosity of several pores adjacent to one wall (Fig. 497b–c).

Kruse (1982), supported in part by Gravestock (1984), considered that the distinction between these two styles of septal porosity was independent of pore size and that septal coefficient (pore diameter:lintel width) is arbitrary and without biological significance. He proposed that pore distribution, rather than pore size, was diagnostic.

Rozanov (1973) related the observed ontogenetic reduction of septal porosity to the stratigraphic succession of archaeocyath taxa. Species with aporose to sparsely porous septa are descended from completely porous ancestors by heterochronic acceleration. Thus, Tommotian and Atdabanian forms with completely porous septa were gradually supplanted by less porous Botoman and Toyonian forms.

Alternatively, Zhuravlev (1986a) reported an influence of facies upon septal porosity: genera with aporose to sparsely porous septa

(*Leptosocyathus* Vologdin, *Plicocyathus* Vologdin, *Robustocyathellus* Konyushkov) were predominant in reef facies, while their completely porous analogues (*Tennericyathus* Rozanov, *Tumulocyathus* Vologdin, *Rotundocyathus* Vologdin) occupied back-reef facies. Septal porosity may therefore be an ecological adaptation. This proposal draws some support from the flume tank testing of skeletal models, by which Savarese (1992) concluded that porous septa are advantageous at low free-stream velocities, whereas aporose septa are better adapted to higher-energy environments. A compilation of field data from Mexico, South Australia, and Mongolia by Debrenne and Zhuravlev (1996) provides some further support.

Synapticulae

Synapticulae are second-order, rodlike structures that link adjacent septa, perpendicularly to obliquely, to provide structural support. They are typically of circular cross section, thickening slightly toward each septum. Associated septa tend to be bifurcating, with netlike porosity; synapticulae are rarely associated with aporose to sparsely porous septa, and never with pectinate tabulae. Where septa are wavy, synapticulae tend to link opposing septal crests. Synapticulae are generally randomly arranged. In some cases, synapticulae are concentrated at discrete transverse planes to form synapticular tabulae, which may include additional linking lintels (Fig. 498f).

With the sole known exception of the erismacoscinine *Muchattocyathus* Rozanov, all synapticulate genera within the orders here considered belong to the Ajacicyathina. They are restricted to the Atdabanian and Botoman stages and equivalent strata. The presence or absence of synapticulae is a genus-level criterion.

Interseptal Plates

These porous plates link adjacent septa. They are known from the beginning of the Tommotian stage, in *Nochoroicyathus sunnaginicus* (Zhuravleva). Their taxonomic value is low.

Plate Tabulae

Plate tabulae are porous, flat to slightly arched transverse plates connecting the walls of two-walled cups. Unlike tabular walls (see below), walls in forms with plate tabulae are independent, with tabula and wall connecting at a high angle. Plate tabulae are characteristic of the Erismacoscinina, Putapacyathida, and some Loculicyathina. They may be densely or sparsely distributed, but in either case tend to be evenly spaced. In Erismacoscinina, they are usually located at the same level in all or several interseptal loculi.

Tabular porosity in erismacoscinines may consist of normal pores (pore diameter not greater than interpore distance), retiform (large, subpolygonal) pores, heterogeneous pores, or slitlike pores (Debrenne, Rozanov, & Zhuravlev, 1990) (Fig. 498a–b). Only the last has generic significance.

In the more common case of plate tabulae with normal porosity, pores are arranged in septa-parallel rows where septa are completely porous, or irregularly where septa are aporose to sparsely porous. In the former, the largest pores are near the septa, since tabular pores are often associated with septa or walls by means of stirrup pores. Within any loculus, pore diameter is almost constant, and because a loculus is necessarily trapezoidal in transverse section, the number of septa-parallel pore rows increases toward the outer wall.

Slitlike tabulae have two septa-parallel rows in each loculus, with component pores being elongate, parallel to the cup walls (Fig. 498e).

Plate tabulae in Putapacyathida are typically planar and generally bear pores of irregular size and shape. These tabulae are often associated with redimiculi.

Tabular walls are characteristic of the Coscinocyathina: each tabula is downturned so that it is smoothly continuous with the outer and/or inner wall—except that [other than *Yukonensis yukonensis* (Handfield)] no genus with only an inner tabular wall is known (Fig. 498c).
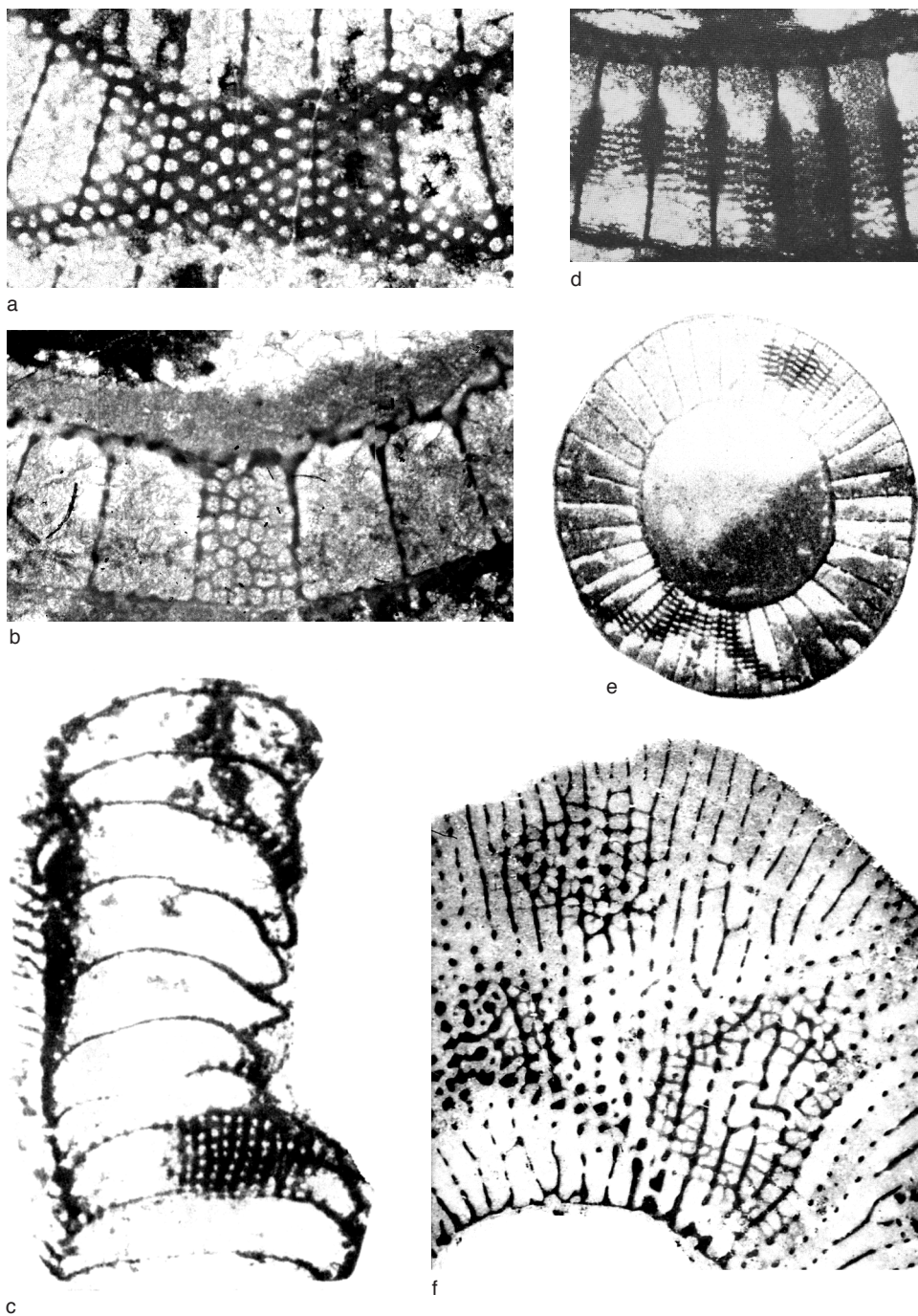
FIG. 498. Tabulae and tabula-like structures; *a,* regularly porous tabulae in *Erismacoscinus oymuranensis* ZHURAVLEV, Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, transverse section, 4220/13, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* retiform tabulae in *Erismacoscinus* sp., Botoman, Uba Formation, Tyrga River, Altay Mountains, Altay Sayan, Russia, transverse section, 4327/32, PIN, ×17 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications *(Continued on facing page.)*

No tabular-walled form is known that is also plicate. Contrastingly, pseudoclathrate wall structure is known only in forms with tabular walls.

The distinctive tabulae of *Yukonensis yukonensis* (HANDFIELD) (Capsulocyathina) comprise coplanar radial rods linked by lintels; rods are directed upward at a low angle from the inner to the outer wall and actually constitute a continuation of the inner wall (Fig. 493e–f).

Pectinate Tabulae

Each interseptal loculus of a pectinate tabula comprises girdling bolsters from which coplanar spines project, giving the appearance of opposed combs (Fig. 498d). Spines may bear secondary spinules along their length (plumose) or on the tip only (bushy), but spinules are generally absent. In some cases, the tips of these secondary spinules coalesce. Archaeocyaths with pectinate tabulae were at one time considered to be a separate suborder, Nochoroicyathina ZHURAVLEVA in VOLOGDIN, 1956 (ZHURAVLEVA, 1960b), but observation of the irregular, sporadic occurrence of pectinate tabulae (spacing of which may range from 0.1 mm to 30 mm in a single cup), their anomalously late appearance in ontogeny, and the co-occurrence of otherwise identical forms with and without pectinate tabulae eventually led to their rejection as a high-level taxonomic criterion. Pectinate archaeocyaths are now placed in the Ajacicyathina (DEBRENNE, ZHURAVLEVA, & ROZANOV, 1973).

Synapticular Tabulae

F. DEBRENNE, M. DEBRENNE, and ROZANOV (1976) documented synapticular tabulae in some species of *Afiacyathus* VORONIN (their *Axiculifungia* F. DEBRENNE & M. DEBRENNE). Such tabulae are constructed of coplanar synapticulae, in several adjacent intersepts or around the entire circumference of the cup (Fig. 498f). Additional linking lintels may be present, as in *A. tabulatus* DEBRENNE, or absent, as in *A. compositus* (DEBRENNE). Initially accorded genus-level significance, synapticular tabulae are now regarded as a species-level criterion only.

WALL TYPES

Wall with Simple Porosity

Wall with simple porosity describes a simple perforate plate, generally 0.05–0.15 mm thick, in which the pores are typically arranged in alternating longitudinal rows. In any one species, pore size and the number of pore rows per intersept tend to vary within narrow limits (see Fig. 514a); in septate, two-walled forms, the number of rows increases immediately before the insertion of a new septum. In most two-walled species, there are more pore rows per intersept in the outer wall than in the inner, and the latter tend to be larger. Those with only a single inner wall pore row are distinguished on this basis from otherwise similar forms at the generic level, e.g., *Rotundocyathus* VOLOGDIN (one pore row) versus *Nochoroicyathus* ZHURAVLEVA (several pore rows) in Ajacicyathidae. Stirrup pores, in which a pore row coincides with a septum, may be present in inner walls, either alone or together with additional interseptal pore rows (Fig. 496f). In the former case, they constitute a generic criterion. Inner wall pores formed by flexure of the inner edges of the septa are also distinguished at the genus level, e.g., *Kisasacyathus* KONYUSHKOV. Exceptionally, pores may be irregularly arranged.

FIG. 498. *(Continued on facing page).*
Scientifiques du Muséum national d'Histoire naturelle, Paris); *c*, tabular outer wall in *Clathricoscinus vassilievi* (VOLOGDIN), Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, longitudinal section (outer wall to right), 20-7 NR-62, institution not known, ×12 (Zhuravleva & others, 1967); *d*, pectinate tabula in *Nochoroicyathus mirabilis* ZHURAVLEVA, Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, transverse section, 4327/34, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e*, slitlike tabulae in *Retecoscinus sakhaensis* ZHURAVLEV, Tommotian, Medvezh'ya Formation, Moyero River, Krasnoyarsk region, Russia, transverse section, 1181 334b/1-b, PIN, ×8 (Zhuravleva, 1960b); *f*, tabula-like structure in *Afiacyathus tabulatus* DEBRENNE, Atdabanian, Amouslek Formation, Amouslek, Morocco, transverse section, M80254, MNHN, ×6 (F. Debrenne, M. Debrenne, & Rozanov, 1976).
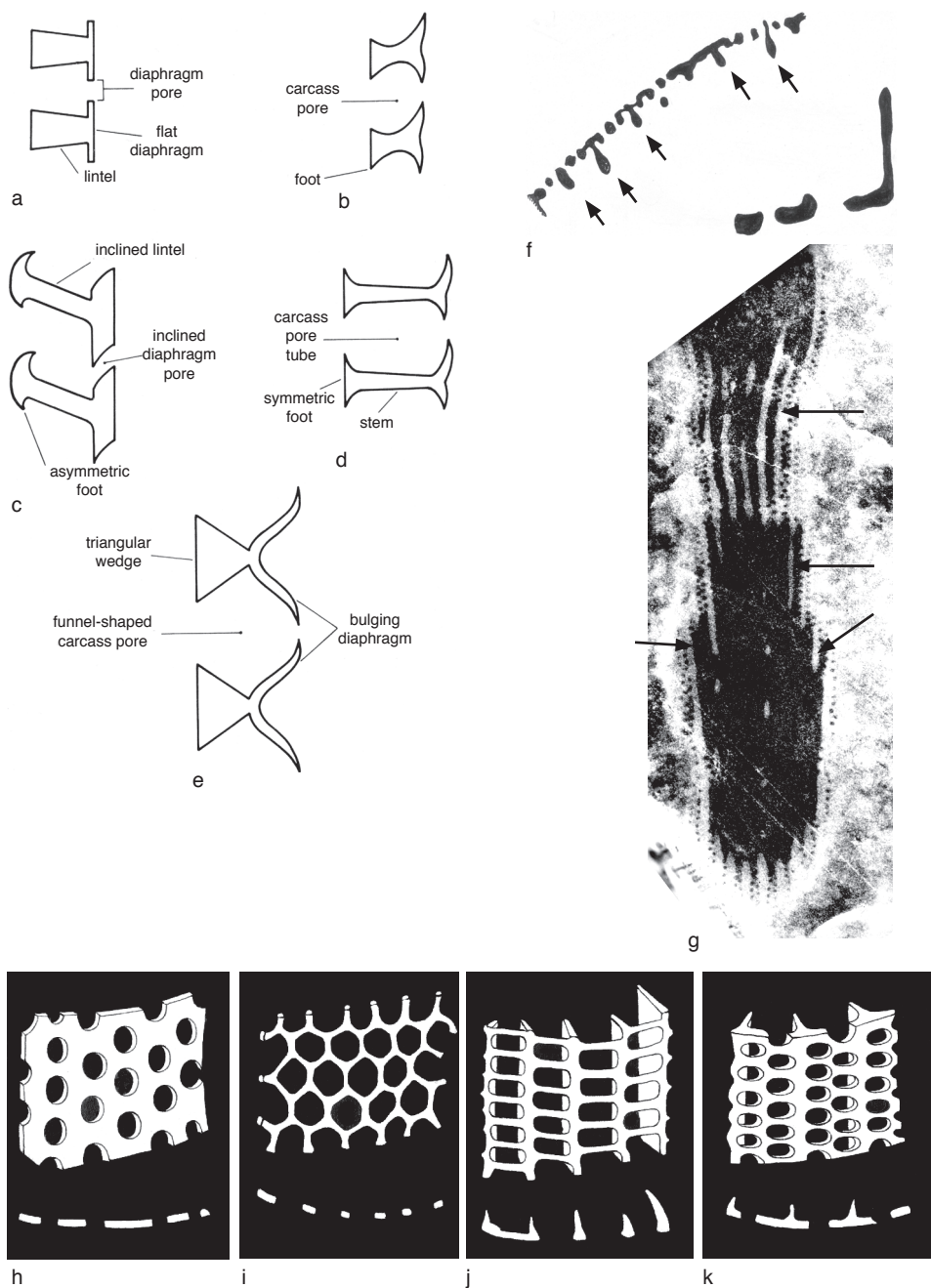
FIG. 499. Outer wall simple pores and redimiculi; *a–e,* schematic sections of varieties of flat (*a–d*) and convex (*e*) diaphragm pores in longitudinal section, intervallum to left (Gravestock, 1984); *f,* outer wall redimiculi (*arrows*) of *Dokidocyathus lenaicus* ROZANOV, Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, transverse section (outer wall at top), GIN3461/15, PIN, ×10; *g,* same, outer wall redimiculi (*arrows*) and intervallar flattened rods, tangential longitudinal section, 3848/585, PIN, ×6.5; *h–k,* schematic reconstructions of varieties of outer wall simple pores: *h,* normal pores, *i,* netlike pores, *j,* slitlike pores, *k,* elliptical pores (*f–k,* Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

While pore size tends to increase slightly with cup growth, the ratio of pore diameter to the width of the intervening lintels remains more or less constant. This can be a useful measurement for distinguishing species. By definition, pore diameter equals or exceeds wall thickness (see discussion of walls with canals below). Pores may be cylindrical, funnel shaped or, in outer walls, bear thin skeletal diaphragms constricting the external orifice to a central hole (Fig. 499a–e). Funnel-shaped and diaphragm pores were promoted as family-group characters by ZHURAVLEVA and ELKINA (1974), but due to their inconsistent development within species, and even within individual cups, they are now regarded as a variant of simple porosity, without value above the species level.

Pore orifices are generally rounded to subquadrate or subhexagonal in shape, but in rare instances may be slitlike (Fig. 499h–k). The slitlike condition is distinguished from all other pore shapes as a generic criterion, as in *Svetlanocyathus* MISSARZHEVSKIY and ROZANOV (Fig. 499j). In a few cases, outer walls are penetrated by pores of two distinct size ranges (*Cryptoporocyathus* ZHURAVLEVA, *Kyarocyathus* KRUSE).

Simple walls may bear spines, protruding externally from an outer wall, into the central cavity from an inner wall, or within the plane of the pore orifice in either wall. Spines have a narrow base relative to bracts (see following section) and taper to a point at the free end. Redimiculi adorn the intervallum side of one or both walls in some forms (Fig. 499f–g).

Intersepts of either wall may be consistently crenulate [smoothly convex, as in *Nochoroicyathus kokoulini* KORSHUNOV and *Rotundocyathus floris* (VORONIN)] or plicate (folded to form a sharp mid-interseptal ridge, separating planar to subplanar lateral flanks, as in *Rozanovicoscinus* DEBRENNE) (Fig. 493a).

Wall with Bracts or Scales

Pores of an otherwise simple wall may be partially constricted by bracts or scales (Fig. 500). Bracts cover a single pore; scales cover two or more laterally adjacent pores. Scales are planar or curved (S-shaped or V-shaped). Laterally adjacent bracts may mutually fuse across several pores of a horizontal file. Such fused bracts are reminiscent of annuli, but remain incomplete; forms with fused bracts are categorized together with those bearing bracts or scales. Fused bracts are planar or S-shaped. Bracts and scales may also bear spines.

The present taxonomy is based on a conception of bracts that is more restrictive than previously employed: namely, it is based primarily on bracts that exhibit a cupped shape. The bract is thereby taken here to have an area of attachment to the wall that is sufficiently broad as to almost span the width of the associated pore, and this attachment area possesses a discernible curvature around the pore rim. Conversely, structures with narrower attachment areas, which typically taper to a point, are regarded as spines and, hence, are non-diagnostic at the genus level.

Bracts or scales may also be supplementary additions to canals (see discussion of walls with canals below) or other wall types. The presence of such supplementary bracts is accorded genus-level status in the present taxonomy, but may prove in future to be a species-level character only (see discussion of innovations in archaeocyathan taxonomy, p. 907–908).

Distinctive arcuate bracts on the inner wall canals of *Kordecyathus* MISSARZHEVSKIY are likewise treated as modified cupped bracts; they arch to link the lower and upper canal rims and may narrow toward upper rims. As these bracts are attached to the central cavity side of a wall with canals, they are regarded as supplementary.

The distinction between spines (see previous discussion of walls with simple porosity) and bracts may nevertheless be difficult to determine in some instances. It is acknowledged that some genera assigned here to families with simple inner walls have spines that may yet prove upon reassessment to be cupped bracts. Examples of potentially relevant genera are in the suborder Ajacicyathina: (i) in the simple outer-walled Ajacicyathidae, *Orbicyathellus* OSADCHAYA, *Robustocyathellus* KONYUSHKOV, and *Nochoroicyathellus* OSADCHAYA, which may each be better assigned to the bractose Densocyathidae; and (ii) in the tumulose outer-walled Tumulocyathidae, *Isiticyathus* KORSHUNOV and *Kotuyicyathellus* OSADCHAYA, which might
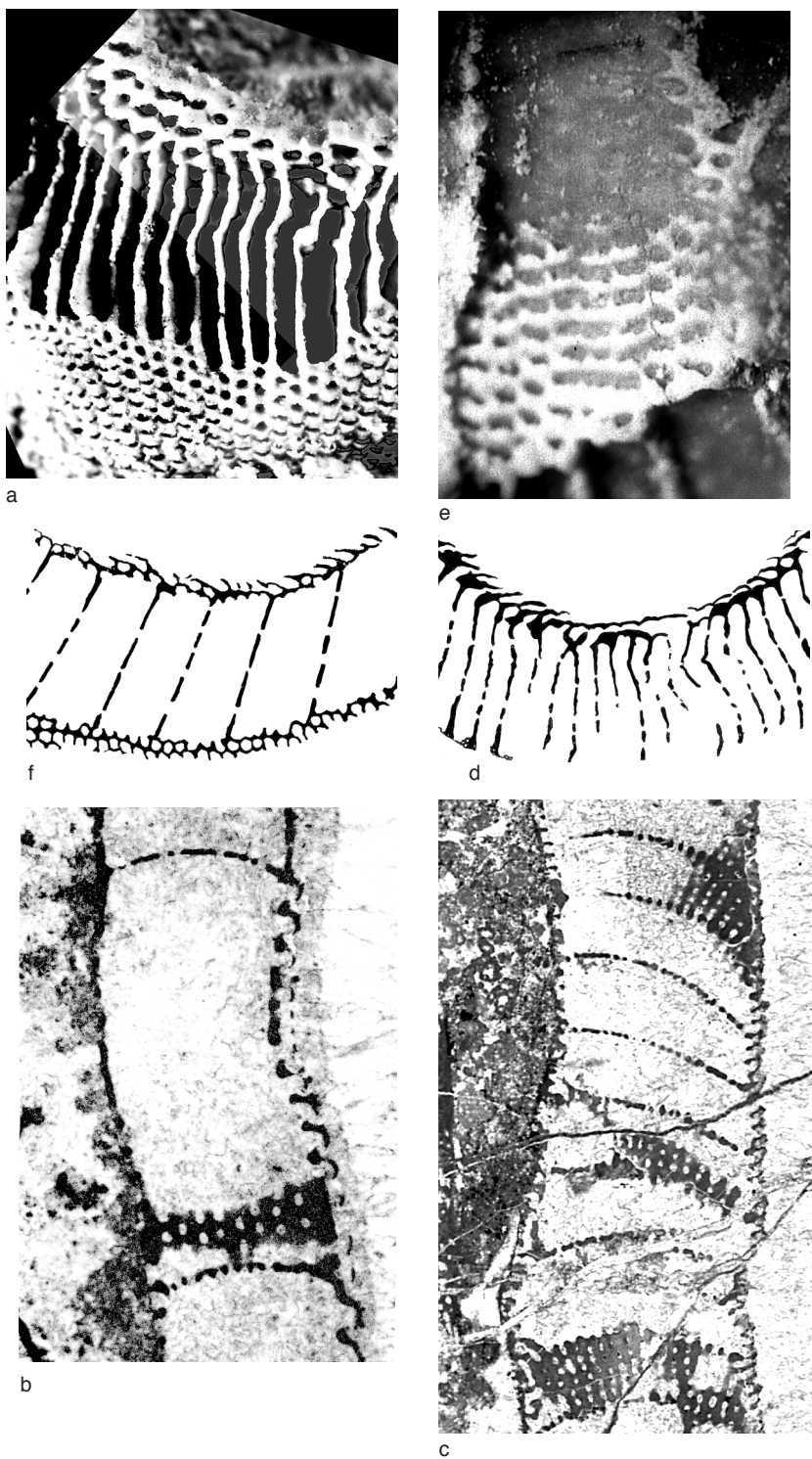
FIG. 500. *(For explanation, see facing page).*

belong in the Sanarkocyathidae. Similarly, in the suborder Erismacoscinina there are: (i) the simple-walled Asterocyathidae, with *Antoniocoscinus* ZHURAVLEV, that might belong in the bractose Rudanulidae; and (ii) in the Rozanovicyathidae, the genus *Rozanovicyathus* KORSHUNOV, that might require redefinition within a revised, bractose inner-walled family.

An alternative proposal, not employed in the present taxonomy, is to treat bracts together with spines as simple-walled forms and to retain separate families only for those genera with inner wall scales. The consequence of this would be to transfer all such bractose genera to their corresponding simple inner-walled family. Thus, for example, in the ajacicyathine family Densocyathidae, genera such as *Dailycyathus* DEBRENNE, *Deceptioncyathus* GRAVESTOCK, and *Khirgisocyathus* VORONIN would be transferred to the Ajacicyathidae.

These issues will continue to be a matter of debate among specialists. Indeed, there is no consensus among the present authors concerning the delimitation of bracts and spines. The definition of bracts given above and applied in the present taxonomy is the majority view (DEBRENNE and KRUSE). However, unpublished observations by ZHURAVLEV highlight variation among late Atdabanian–early Botoman *Coscinocyathus* BORNEMANN on the Siberian Platform. Within this region, southern populations of *Coscinocyathus isointervallumus* ZHURAVLEVA (1960b) display well-developed bracts, each supporting a spine, on their inner wall pores, whereas in otherwise morphologically similar northern populations (identified by ZHURAVLEV [1990b] as *C. marocanoides* ZHURAVLEVA [in DATSENKO & others, 1968]), the inner wall pores bear a spine supporting a second-order spinule. This variation may be treated as either intra- or interspecific. Such examples illustrate the necessity for comprehensive revisions based on large, sufficiently representative population samples in order to more completely understand the taxonomic value of the various elements termed bracts and spines.

For the present, in the absence of additional relevant published data, we follow with few modifications the systematic principles outlined by DEBRENNE, ZHURAVLEV, and KRUSE (2002, p. 1544–1546).

Wall with Annuli

Either wall may bear regularly spaced planar, S-shaped, or V-shaped annuli. Commonly, each inner wall intersept of an annulate form has only a single, longitudinal pore row; less commonly, there are several. Annuli are much more common on the inner wall than the outer: outer wall annuli are known only in the atabulate family Sigmocyathoidea, in which all three known constituent genera bear S-shaped annuli. V-shaped annuli may be upright or inverted (a genus-level distinction), or may bear a short, arête-like carina, extending from the apex of each V, and coplanar with one limb of the V (Fig. 501).

FIG. 500. Bracts and scales; *a,* probable upwardly projecting cupped bracts on outer wall of *Russocyathus rodionovae* ZHURAVLEVA, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, external view of cup in longitudinal section (outer wall at bottom), 4137/14-4, PIN, ×14 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* downwardly projecting cupped bracts on inner wall of *Polycoscinus cymbricensis* (KRUSE), Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.12784, holotype, FT.8270, 8271, 8581, 8582, 12784, AM, ×16 (Kruse, 1982); *c,* upwardly projecting S-shaped scales on inner wall of *Xestecyathus zigzag* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.12793, holotype, F.83405, AM, ×10 (Kruse, 1982); *d,* horizontal to upwardly projecting curved scales, fused into pseudoannuli on inner wall of *Rectannulus* sp., Botoman, Usa Formation, Kuznetsk Alatau, Russia, transverse section, 4327/76, PIN, ×7 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* upwardly projecting planar fused bracts on inner wall of *Cadniacyathus asperatus* R. BEDFORD & J. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, internal view of cup in longitudinal section, lectotype, 86616(1), USNM, ×14 (Debrenne, 1974b); *f,* upwardly projecting S-shaped scales on inner wall of *Tennericyathus malycanicus* ROZANOV, Atdabanian, Pestrotsvet Formation, Malykan, Lena River, Sakha (Yakutia), Russia, transverse section, GIN2034/14, PIN, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

Most annuli have smooth inner rims; in a minority of genera these are denticulate, e.g., *Sagacyathus* KRUSE (Fig. 501e).

Wall with Canals

By definition, canal length is greater than diameter. Inner wall canals may be noncommunicating (Fig. 502), or communicating with their neighbors via porelike openings along their length (Fig. 503). These two conditions are considered sufficiently distinct in their hydrodynamic properties to warrant placement in separate family-level taxa. Only noncommunicating canals are known for the outer wall.

Like simple pores, canals are typically arranged in alternating longitudinal rows, and forms with a single canal row per inner wall intersept are distinguished at the genus level from those with several canal rows per inner wall intersept. In yet other genera, each inner wall canal row coincides with a septum to form stirrup canals. Some genera have spongiose inner walls constructed of waved, anastomosing, communicating canals, e.g., *Kiwicyathus* DEBRENNE & KRUSE (Fig. 503b). Genera such as *Ethmophyllum* MEEK have complex, doubly zoned inner walls, with anastomosing, waved canals arising from the fluted inner edges of the septa, so that the wall has an overall upright V-shaped appearance (Fig. 503c–e).

Exceptionally, canals may span several intersepts, e.g., *Gnaltacyathus* KRUSE (Fig. 502b). Some genera (e.g., *Ethmocyathus* R. BEDFORD & W. R. BEDFORD) bear inner wall canals formed by flexure of the inner edges of the septa. Canals may be straight, S-shaped, or V-shaped, branching or nonbranching, discrete or anastomosing, and may project horizontally, obliquely upward, or obliquely downward with respect to the wall.

Some canal-bearing genera also bear supplementary structures, generally bracts, attached to the free ends of their canals; if canals and supplementary structures are obliquely, but oppositely, oriented, an overall upright or inverted V-shaped appearance is imparted to the wall. In practice, care is needed to distinguish this condition from true V-shaped canals. A spine or small plate may arise from the apex of each constituent canal-bract couplet in some such forms, e.g., the outer wall of *Ethmophyllum* MEEK (Fig. 503c).

Wall with Microporous Sheaths

Microporous sheaths are much more common on the outer wall than on the inner; examples of the latter are *Membranacyathus* ROZANOV and *Bipallicyathus* ZHURAVLEV. They are typically supported on an otherwise simple porous wall with constituent framework (or carcass) pores with a diameter of 0.15–0.25 mm, but exceptionally they are supported on S-shaped canals in *Hupecyathellus* ROZANOV.

ROZANOV (1973) first elaborated the important distinction between the two major variants of the microporous sheath: attached and independent (his erbocyathoid and pretiosocyathoid types respectively) (Fig. 504). These two variants represent a suprafamilial criterion.

Attached sheaths are generally a feature of walls in which the framework pores are funnel shaped, widening toward the exterior so that the lintels are externally narrow and arête-like (see Fig. 514b). Finer rodlike or

FIG. 501. Annuli; *a,* upwardly projecting S-shaped annuli on inner wall of *Stillicidocyathus sigmoideus* (R. BEDFORD & J. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, internal view of cup in longitudinal section, holotype, 86750, PU, ×4.5 (Debrenne, 1970a); *b,* upright V-shaped annuli on inner wall of *Thalamocyathus trachealis* (TAYLOR), Botoman, allochthonous, Whichaway Nunataks, Antarctica, oblique section, S8413-5, NHM, ×5 (Hill, 1965); *c,* upright V-shaped annuli on inner wall of *Aporosocyathus gnaltaensis* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.14168, paratype, F.83604, AM, ×10 (Kruse, 1982); *d,* schematic section of inverted V-shaped annuli on inner wall of *Svetlanocyathus primus* MISSARZHEVSKIY & ROZANOV, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, longitudinal section (outer wall to right), ×9 (Missarzhevskiy & Rozanov, 1962); *e,* upright V-shaped annuli bearing denticulate rims on inner wall of *Sagacyathus stonyx* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, oblique section, FT.8499, paratype, FT.8498–8500, AM, ×3.5 (Kruse, 1982); *f,* ?horizontally projecting planar annuli bearing short beams that support microporous sheath on inner wall of *Compositocyathus muchattensis* (ZHURAVLEVA), Atdabanian, Pestrotsvet Formation, Mukhatta Creek, Lena River, Sakha (Yakutia), Russia, transverse section, holotype, 205/47a, TsSGM, ×10 (Zhuravleva & Zelenov, 1955).
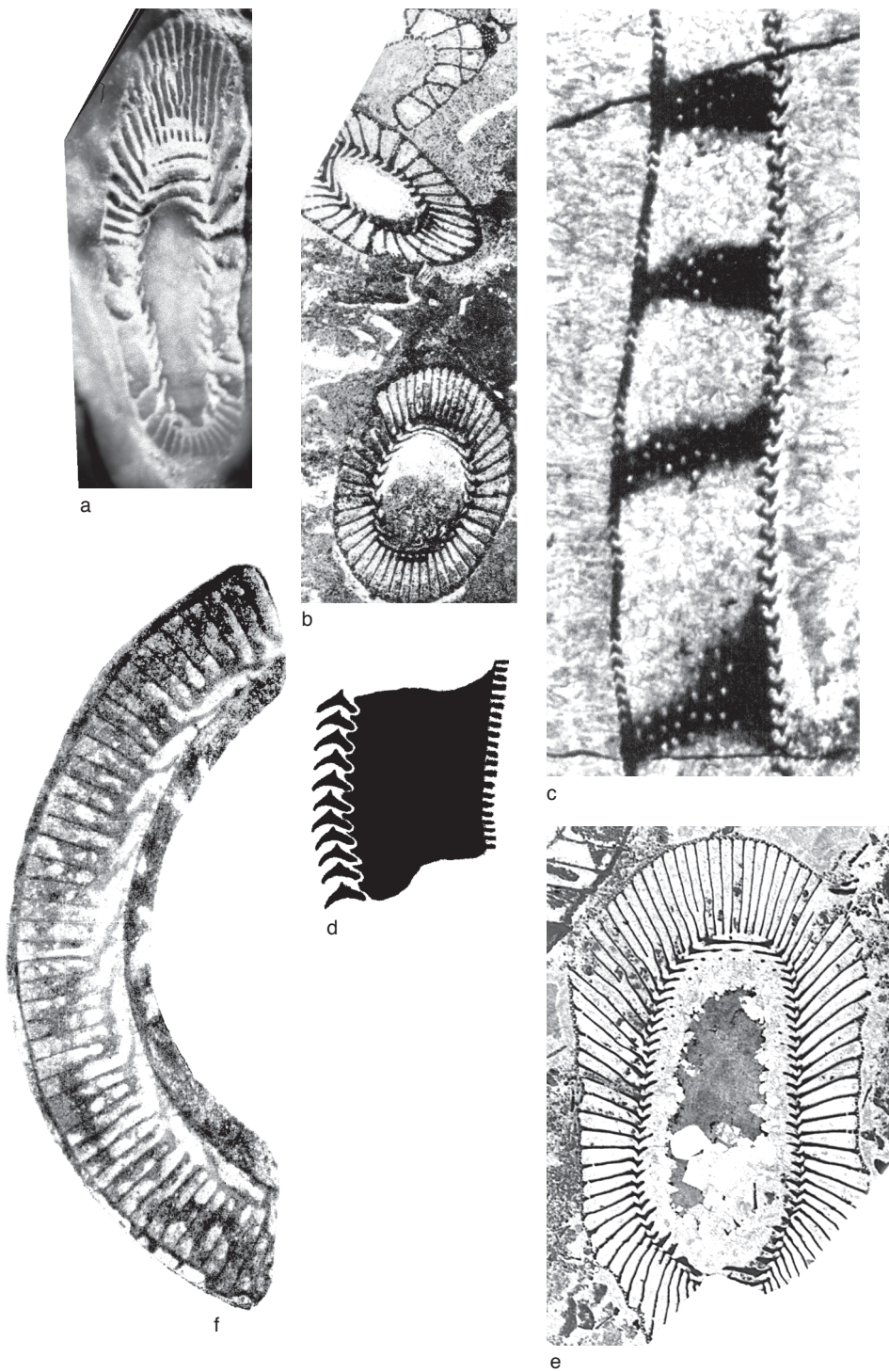
FIG. 501. *(For explanation, see facing page).*

tapering lintels delineating the sheath micropores thereby radiate centripetally inward from the outer margins of the framework pores to form a more or less continuous sheet of micropores. Continuous sheaths cover the entire surface of the wall (Fig. 504b, Fig. 505a–d); discontinuous sheaths cover each framework pore separately (Fig. 504c, Fig. 505e–g). A common pattern of attached sheaths for any one framework pore is of a central micropore surrounded by a circlet of six similarly sized micropores (i.e., about seven micropores), but a greater or lesser number of micropores may be developed in different taxa (ROZANOV, 1973; KASHINA, 1979). A unique tylocyathoid-type of attached sheath is shown by *Tylocyathus* VOLOGDIN, in which the sheath is supported on longitudinally subrectangular framework pores, with two rows of micropores per framework pore; each micropore bears an S-shaped bract (Fig. 505j).

Independent sheaths are invariably continuous, supported by short perpendicular rods arising from the lintels of the framework pores (Fig. 504a, Fig. 505h–i). There is no direct participation of the pore lintels in this sheath variant, and pores need not be funnel shaped. The common micropore pattern is one of more or less regular, alternating rows. Micropores may be rounded or subpolygonal.

Wall with Tumuli

Tumuli are hollow, porous, hemispherical to prolately ellipsoidal domes covering the pores of outer walls; they are not known on inner walls. Tumulose walls exist in two variants: with simple or multiperforate tumuli (Fig.

506). Simple tumuli have a single small pore, usually located toward the lower side of the tumulus (Fig. 506b–c). In some cases, bracts have been incorrectly identified as tumuli, e.g., *Tumulifungia* ZHURAVLEVA, which actually bears cupped bracts on the outer wall. True tumuli will have similar morphology in either transverse or longitudinal section, and only rarely will the single pore be intersected.

Multiperforate tumuli, in contrast, possess many small pores, typically covering the entire surface of the tumulus (Fig. 506d–e).

Other Types of Wall

Other distinctive wall types are the clathrate type, with closely spaced longitudinal ribs (Fig. 506f); and the pseudoclathrate type, with longitudinal ribs and transverse linking lintels, together supported by short rods (Fig. 506a).

UPPER SURFACE STRUCTURES

Certain skeletal elements were evidently developed only once in the ontogeny of some cups, since they are always observed crowning the tops of cups but are never found within cups.

Peltae

Peltae are unique to the Monocyathida. They are horizontal, slightly convex plates developed as a continuation of the wall. Two broad types, nonporous and porous, can be recognized, but the distinction is accorded little taxonomic importance, even at species level. Earlier authors (e.g., ZHURAVLEVA, 1963b; OKUNEVA & REPINA, 1973; VOLOGDIN, 1977) recognized many more

FIG. 502. Noncommunicating canals; *a,* horizontal to upwardly projecting straight canals on inner wall of *Inessocyathus spatiosus* (BORNEMANN), Botoman, Matoppa Formation, San Pietro, Sardinia, Italy, transverse section, topotype, M84074, MNHN, ×2.3 (Debrenne, 1964); *b,* horizontal to upwardly projecting straight canals, each canal spanning several intersepts on inner wall of *Gnaltacyathus nodus* KRUSE, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, transverse section, FT.8495b, holotype, FT.8453, 8454, 8495b, AM, ×8 (Kruse, 1982); *c,* horizontal to upwardly projecting S-shaped canals on inner wall of *Rasetticyathus acutus* (BORNEMANN), Botoman, Matoppa Formation, Monte Cuccurinu, Sardinia, Italy, longitudinal section, M84036, MNHN, ×10 (Debrenne, 1972); *d,* horizontal to upwardly projecting S-shaped canals, bearing supplementary bracts externally on outer wall and inverted V-shaped canals on inner wall of *Porocoscinus rudens* (KRUSE), Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to left), FT.8295, holotype, F.83933, AM, ×8.5 (Kruse, 1982).
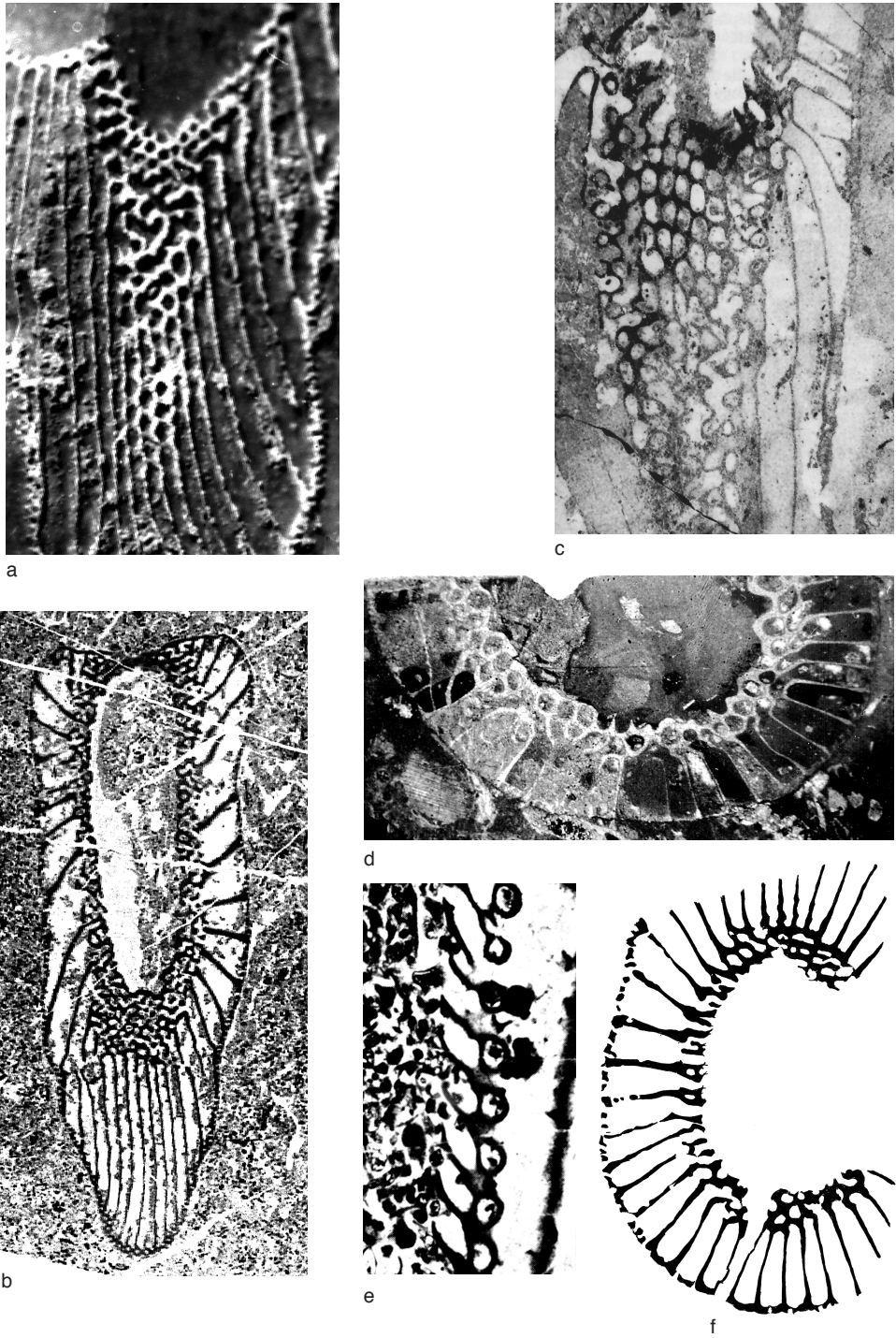
FIG. 503. *(For explanation, see facing page).*

variants, but these were based on differing orientations of section through the cup.

Nonporous peltae possess a central sag, bearing an orifice. The orifice may support a concave, finely perforated, saclike membrane directed into the inner cavity (Fig. 507.1). Nonporous peltae are known in some *Archaeolynthus* TAYLOR, *Palaeoconularia* CHUDINOVA, *Tumuliolynthus* ZHURAVLEVA, and *Propriolynthus* OKUNEVA.

Porous peltae are present in some other species of *Archaeolynthus* TAYLOR, *Palaeoconularia,* and *Propriolynthus*, and in some *Sajanolynthus* VOLOGDIN & KASHINA and *Melkanicyathus* BELYAEVA. Their porosity invariably matches that of the cup wall. Thus, in *Propriolynthus vologdini* (YAKOVLEV) and *Melkanicyathus operculatus* (MASLOV), the marginal area of the pelta bears bracts oriented in a reverse sense to those of the wall (Fig. 507.2b). *Archaeolynthus cipis* (VOLOGDIN) has spines on the wall and pelta (Fig. 507.2a).

Rims

Rims are restricted to two-walled cups. They include types in which the outer wall curves toward the inner wall; for example, in *Cordilleracyathus blussoni* HANDFIELD (Fig. 507.3) and species of *Irinaecyathus* ZHURAVLEVA, *Tegerocyathus* KRASNOPEEVA, *Plicocyathus* VOLOGDIN, and *Sekwicyathus* HANDFIELD. This type of rim is favored in genera with aporose to sparsely porous septa. Alternatively, the rim is the result of growth of the inner wall, complicated by fringelike skeletal processes (e.g., in *Nochoroicyathus sunnaginicus* [ZHURAVLEVA] and *Formosocyathus bulynnikovi* VOLOGDIN). In a third type, the rim is a horizontal plate covering the intervallum, as observed, for example, in *Nochoroicyathus* ZHURAVLEVA, *Baikalocyathus* YAZMIR, *Dokidocyathus* TAYLOR (Fig. 507.4), and *Siderocyathus* DEBRENNE & GANGLOFF.

MORPHOLOGY OF ARCHAEOCYATHIDA AND KAZACHSTANICYATHIDA

INTERVALLUM STRUCTURES

Intervallar structures in these two orders are more diverse than in those orders previously discussed.

Taeniae

Taeniae are homologous to septa in the other orders but are not limited to a single plane. Rather, component lintels diverge in orientation so that taeniae appear wavy. Most Archaeocyathida have taeniae, at least in early ontogeny. Some genera exhibiting taeniae throughout cup development were formerly described as bearing buttresses or struts adjacent to one or both walls, as in *Aruntacyathus* KRUSE (=*Spirocyathella* VOLOGDIN) by KRUSE and WEST (1980) (Fig. 508a) and *Spirillicyathus* R. BEDFORD & J. BEDFORD by GRAVESTOCK (1984) (Fig. 508b), or as wavy and dichotomous taeniae in *Pycnoidocyathus* TAYLOR by FONIN (1985) (Fig. 508c).

FIG. 503. Communicating canals; *a,* horizontal to upwardly projecting straight stirrup canals, branching toward central cavity, on inner wall of *Zonacyathus retezona* (TAYLOR), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, paralectotype, T1591, SAM, ×7 (Taylor, 1910); *b,* horizontal to upwardly projecting straight stirrup canals on inner wall of *Kiwicyathus nix* DEBRENNE & KRUSE, Botoman, Mt. Egerton, Byrd Glacier, Antarctica, longitudinal section, holotype VC19, VU, ×4.5 (Debrenne & Kruse, 1986); *c,* subspherical chambered canals each with base commencing in intervallum, canals subdivided by stipules on outer wall, and anastomosing, horizontal to upwardly and laterally projecting waved canals, arising from fluted inner edges of septa, on inner wall of *Ethmophyllum whitneyi* MEEK, Botoman, Rosella Formation, Kechika Mountains, British Columbia, Canada, longitudinal section (outer wall to right), 69269, GSC, ×7; *d,* same specimen, transverse section, ×7 (Mansy, Debrenne, & Zhuravlev, 1993); *e,* detail of anastomosing, horizontal to upwardly and laterally projecting waved canals, arising from fluted inner edges of septa, on inner wall of *Ethmophyllum whitneyi* MEEK, Botoman, Atan Group, Good Hope Lake, British Columbia, Canada, longitudinal section (intervallum to right), 25333, GSC, ×9 (Handfield, 1971); *f,* downwardly projecting straight canals, bearing supplementary bracts or annuli on central cavity side, on inner wall of *Irinaecyathus schabanovi* ROZANOV, Toyonian, Elanskoe Formation, Elanskoe, Lena River, Sakha (Yakutia), Russia, oblique transverse section, GIN4434/9, PIN, ×3 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
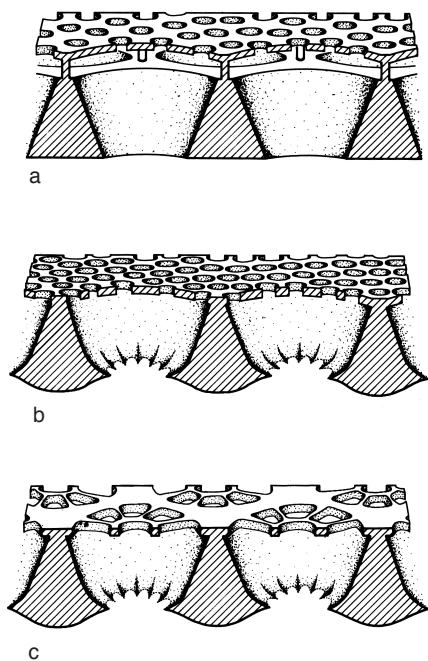
FIG. 504. Schematic sections of types of microporous sheath; *a,* independent sheath supported on short pillars; *b,* attached sheath, continuous over external surface; *c,* attached sheath, discontinuous, restricted to framework pore openings (Gravestock, 1984).

True taeniae are present only in adult cups of Archaeocyathina. Two taenial porosity types—coarsely porous and finely porous—are recognized, but porosity may vary between the two types in a single cup. In such cases, larger pores tend to be nearer the outer wall. Synapticulae are typically associated with taenial cups, but are not regularly arranged.

Pseudosepta

All other radial-longitudinal, platelike elements are ontogenetic derivatives of taeniae. Pseudosepta develop ontogenetically from taeniae as ordered, planar, porous partitions. They comprise regularly arranged lintels yet differ from true septa in their developmental pathway. Pseudosepta differ from septa in having no regularity in size or shape of their pores (Fig. 494a).

Pseudosepta may be coarsely or finely porous in Loculicyathina and Archaeocyathina, or aporose in Loculicyathina and Anthomorphina (Fig. 494b–d).

Synapticulae are not typically associated with pseudosepta.

Pseudotaenial and Dictyonal Network

Pseudotaenial structure comprises taeniae with regularly distributed synapticulae linking taeniae at each interpore lintel (Fig. 509a). Pseudotaeniae are invariably coarsely porous. They characterize the Archaeocyathina.

Pseudotaenial structure is morphologically transitional between true taeniae and dictyonal network. This latter comprises equidimensional synapticulae and radial and longitudinal taenial lintels, together forming an orthogonal network of rods, which may arch between the inner and outer wall in some taxa (Fig. 509c) and remain planar in others (Fig. 509b).

FIG. 505. Microporous sheaths; *a,* continuous attached sheath on outer wall of *Erugatocyathus krusei* GRAVESTOCK, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, tangential section, holotype, P21599, SAM, ×38 (Gravestock, 1984); *b–d,* continuous attached sheath on outer wall of *Erugatocyathus howchini* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia; *b,* tangential section, paratype, P21630, SAM, ×38; *c–d,* holotype, P21590-1, SAM, ×38; *c,* oblique section through outer wall; *d,* longitudinal section (intervallum to left) (Gravestock, 1984); *e–g,* partially discontinuous attached sheath on outer wall of *Erugatocyathus mawsoni* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia; *e,* tangential section, paratype, P21473-2, SAM, ×38; *f,* transverse section, intervallum to left, paratype, P21474-2, SAM, ×38; *g,* tangential section, paratype, P21466-2, SAM, ×38 (Gravestock, 1984); *h–i,* independent sheath on outer wall of *Agyrekocyathus dissitus* (KRUSE), Botoman, Mount Wright Volcanics and Cymbric Vale Formation, Mount Wright, New South Wales, Australia; *h,* transverse section, FT.8176, paratype, F.83942, AM, ×15; *i,* oblique section through outer wall, FT.8179, paratype, F.87962, AM, ×15 (Kruse, 1982); *j,* attached microporous sheath, each micropore bearing a cupped bract, on outer wall of *Tylocyathus bullatus* (ZHURAVLEVA), Botoman, Lenyaka Formation, Schamanikha River, Kolyma River basin, Russia, tangential section, specimen 3900/53, PIN, ×24 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
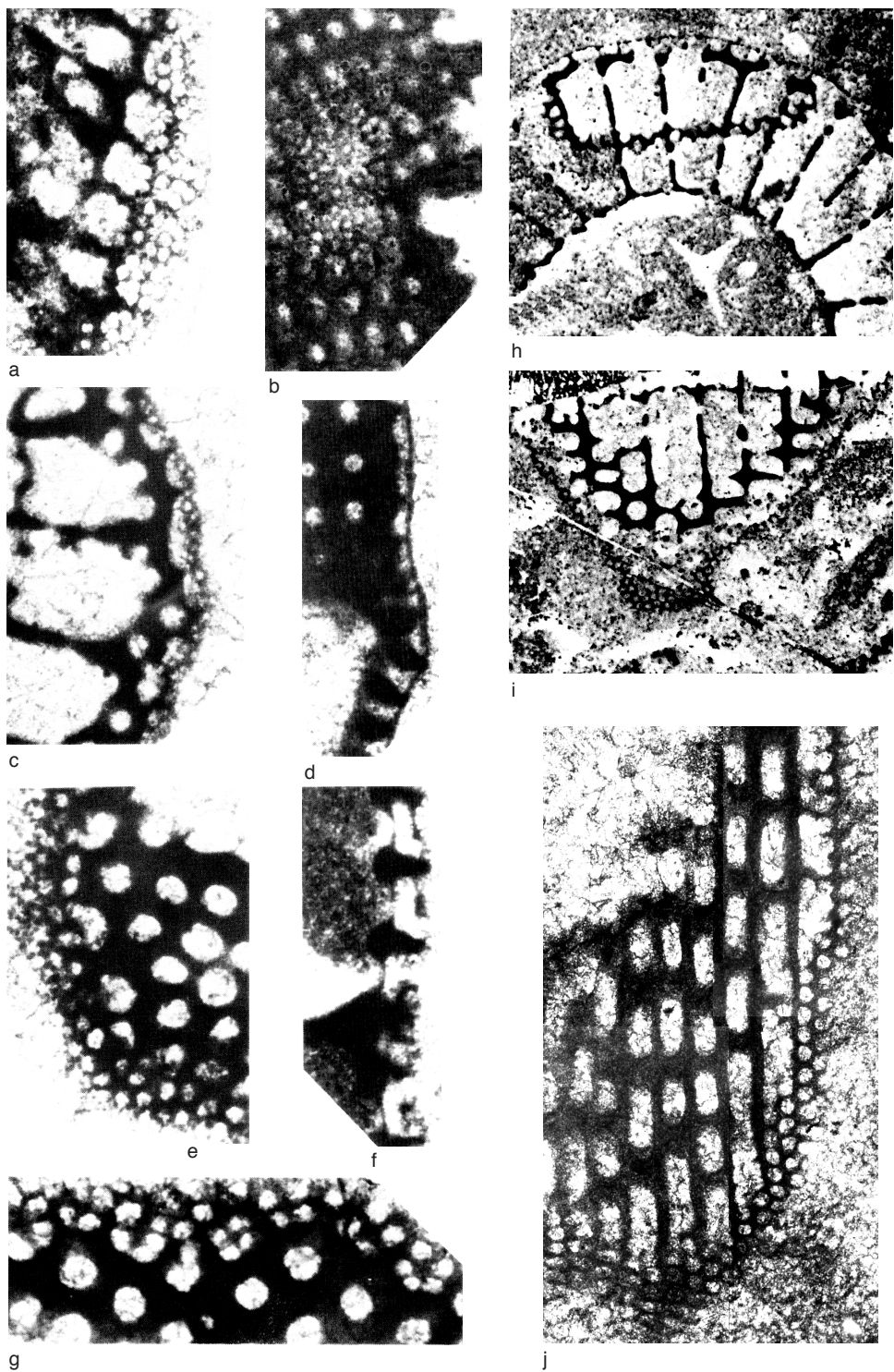
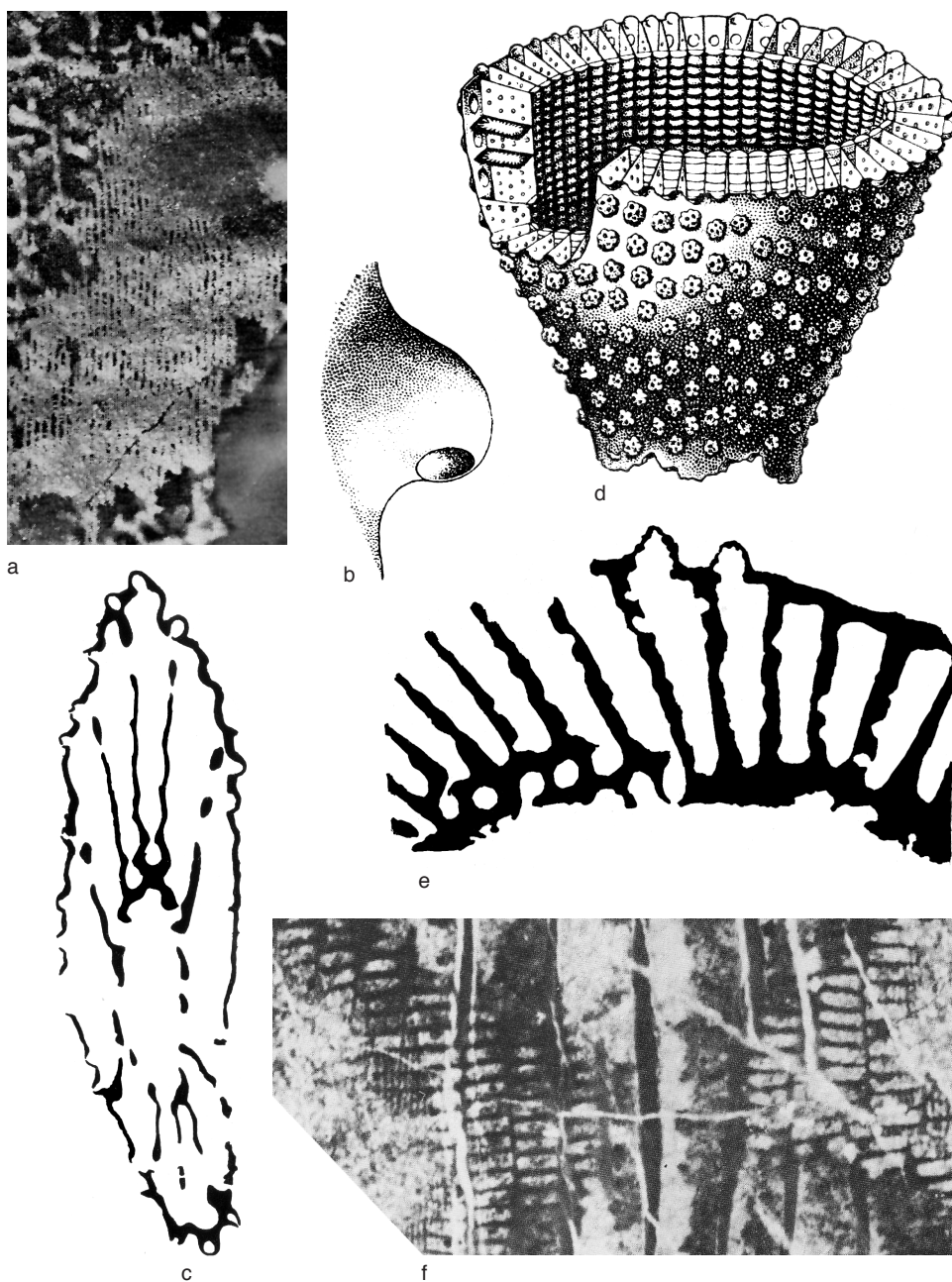FIG. 505. *(For explanation, see facing page).*

FIG. 506. Tumuli, clathri, and pseudoclathri; *a,* pseudoclathrate outer wall of *Clathricoscinus* sp., Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, external view, 4327/5, PIN, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* detail of simple tumulus on outer wall of *Tumulocyathus kotuyikensis* (ZHURAVLEVA), ×100 (Zhuravleva, 1960b); *c,* simple tumuli on plicate outer wall of *Plicocyathus rozanovi* (HANDFIELD), Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90125, GSC, ×12 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *d,* multiperforate tumuli on outer wall *(Continued on facing page.)*

Calicles

By analogy with other sponges of chaetetid architecture, longitudinal tubelike elements in archaeocyaths are termed calicles (WEST & CLARK, 1983). Calicles develop ontogenetically from taeniae and are diagnostic of the Dictyofavina (Fig. 510.1). They are tetragonal or hexagonal in cross section. Hexagonal calicles bear one or several longitudinal pore rows per facet, whereas tetragonal calicles invariably bear only one.

Syringes

Syringes (ZHURAVLEVA & MYAGKOVA, 1981) are diagnostic of the Syringocnemina. These are stacked radial tubes of hexagonal cross section, transverse across much of the intervallum, but typically curving downward near the inner wall (Fig. 510.3).

Like taeniae, syringes can be coarsely or finely porous, corresponding to one or several radial pore rows per component facet, respectively. The number of pore rows per facet (one versus several) is a generic criterion in this suborder. In most genera, this number is invariant for all facets. However, in *Pseudosyringocnema* HANDFIELD and *Williamicyathus* ZHURAVLEV, porosity of the two transverse facets differs from that of the four lateral facets comprising each syrinx, with one pore row per transverse facet and several pore rows per lateral facet (Fig. 510.2).

The syringes of *Syringothalamus* DEBRENNE, GANGLOFF, & ZHURAVLEV bear a single radial row of coarse pores per facet. In oblique section, these could potentially be confused with pseudotaenial or dictyonal network.

Tabulae

Pectinate tabulae are not known in these two orders. Most Archaeocyathina possess segmented tabulae, generally formed by the outer wall, and a few Loculicyathina (*Mikhnocyathus* MASLOV) have plate tabulae. Only *Anthomorpha* BORNEMANN and its allies (Anthomorphina) bear independent (membrane) tabulae. Membrane tabulae show some similarity to pectinate tabulae in Ajacicyathida, in that they are developed separately in each intersept. They are pierced by two poorly delineated radial rows of irregular pores per loculus, which are identical in morphology to that of the outer wall (Fig. 511).

The more common segmented tabulae tend to be irregularly spaced along the length of the cup, and between different cups, even from the same locality. A few genera, such as *Claruscoscinus* HANDFIELD, *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD, and *Gabrielsocyathus* DEBRENNE, show regular spacing of segmented tabulae. However, although these genera mimic Coscinocyathina and Kazachstanicyathida in this regard, their segmented tabulae develop late in ontogeny; this is not the case in these two ordinal taxa.

Segmented tabulae are extensions of the outer and/or inner wall, and so reflect the porosity of the parent wall. Thus, segmented tabulae of simple porosity accompany simple outer walls. Such tabulae are finely porous (Fig. 512a) or coarsely porous (Fig. 512b), according to wall porosity. In some *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD (outer wall basic simple), the tabular pores are slitlike (Fig. 512c).

Likewise, in Archaeocyathoidea (outer wall concentrically porous), tabular porosity is concentric (Fig. 512d), and in Metacyathoidea (outer wall compound), it is compound (Fig. 512f).

However, in the case of concentrically porous and compound walls, the tabular porosity is inconsistently conserved in some

FIG. 506. *(Continued from facing page).* of *Lenocyathus lenaicus* ZHURAVLEVA, schematic external view of cup, ×2.5 (Zhuravleva, 1960b); *e,* multiperforate tumuli on outer wall of *Torosocyathus provisus* KASHINA, Botoman, Usa Formation, Kuznetsk Alatau, Russia, transverse section (outer wall at top), GIN3878-4, PIN, ×45 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *f,* clathrate outer wall of *Clathrithalamus mawsoni* DEBRENNE & KRUSE, Botoman, Skackleton Limestone, Holyoake Range, Nimrod Glacier, Antarctica, tangential section, holotype, MG511, GNS, ×20 (Debrenne & Kruse, 1986).
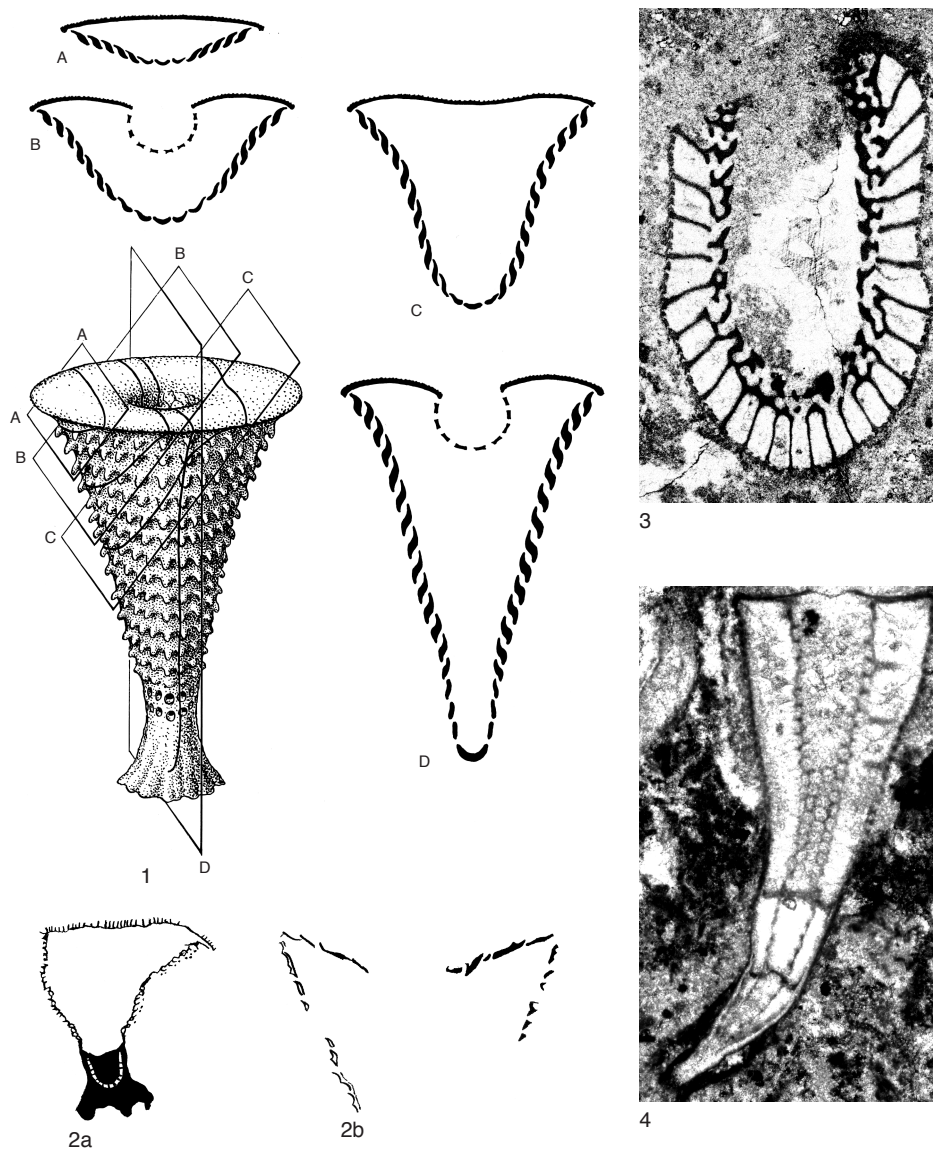
FIG. 507. Upper surface structures of cup; *1,* schematic reconstruction of nonporous pelta on cup of *Propriolynthus vologdini* (YAKOVLEV) with various possible sections, section B corresponding to *Globosocyathus bellus* OKUNEVA; *2a–b,* porous peltae; *2a,* porous pelta with spines on cup of *Archaeolynthus cipis* (VOLOGDIN), Botoman, Usa Formation, Sukhie Solontsy, Batenev Range, Kuznetsk Alatau, Russia, longitudinal section, holotype, 1924-43, PIN, ×16; *2b,* porous pelta with bracts on cup of *Melkanicyathus operculatus* (MASLOV), Atdabanian, Usa Formation, Bol'shaya Erba, East Sayan, Altay Sayan, Russia, longitudinal section, 1923-41-2, PIN, ×16; *3,* rim in which outer wall curves toward inner wall, *Cordilleracyathus blussoni* HANDFIELD, Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, oblique longitudinal section, 90140, GSC, ×8; *4,* rim as horizontal plate covering intervallum in *Dokidocyathus* sp., Botoman, Terekla Formation, Kurogan-Sakmara zone, western flank of Southern Urals, Russia, longitudinal section, 4327/38, PIN, ×20 (Debrenne, Rozanov, & Zhuravlev, 1990; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
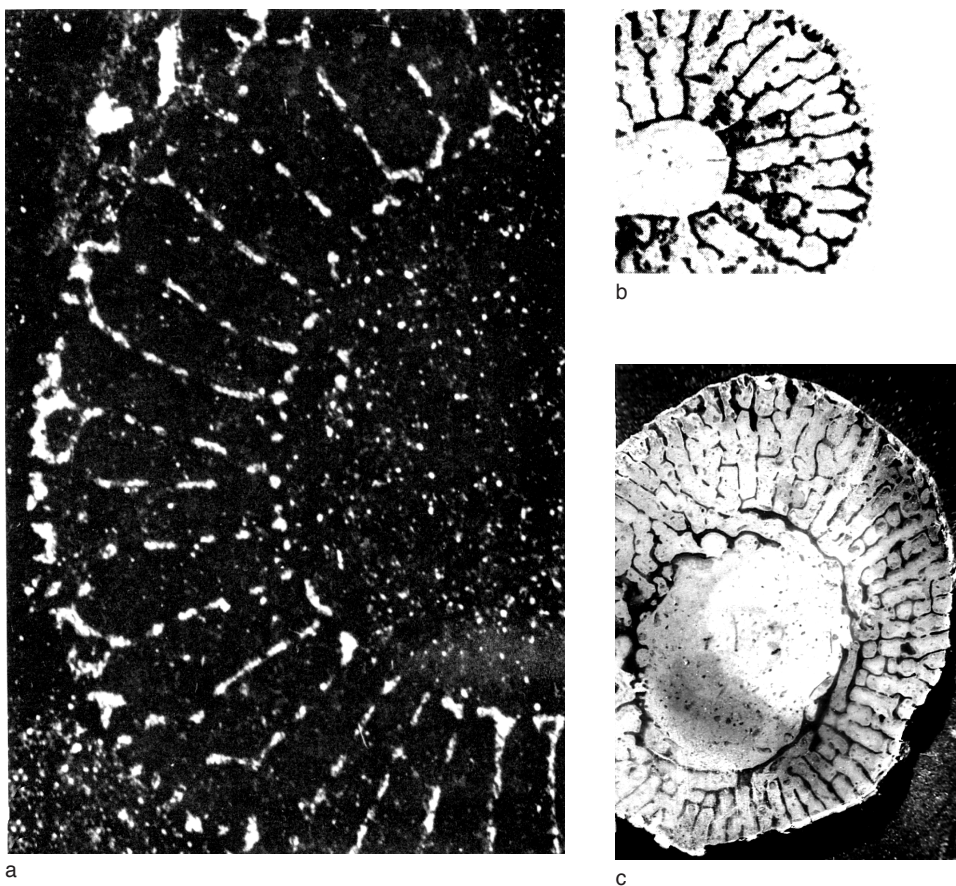
FIG. 508. Taeniae; *a,* taeniae with strutlike bifurcation adjacent to both walls in *Spirocyathella toddi* (KRUSE), Atdabanian, Todd River Dolostone, Ross River, Northern Territory, Australia, transverse section, FT.9947, specimen F.132942, AM, ×12 (Kruse & West, 1980); *b,* taenial bifurcation in intervallum and adjacent to outer wall (strutlike) in *Spirillicyathus tenuis* R. BEDFORD & J. BEDFORD, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, transverse section, P21411-2, SAM, ×5 (Gravestock, 1984); *c,* taenial bifurcation in intervallum of *Pycnoidocyathus sekwiensis* HANDFIELD, Botoman, Sekwi Formation, Caribou Pass, Northwest Territories, Canada, transverse section, 12362, GSC, ×2 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

taxa. In *Archaeopharetra* R. BEDFORD & W. R. BEDFORD, for example, concentric porosity can cover only the outer portion of a tabula, or can be completely absent. In some *Dictyosycon* ZHURAVLEVA, also with concentrically porous outer wall, segmented tabulae are nevertheless constructed only of coplanar, rodlike, intervallar elements (Fig. 512e).

Tabulae with canals are known in *Maiandrocyathus* DEBRENNE & *Beltanacyathus* R. BEDFORD & J. BEDFORD (GRAVESTOCK, 1984), both Beltanacyathoidea (outer wall with subdivided canals).

Astrorhizae and Tubuli

Astrorhizae are recognized as a diagnostic feature of choanocyte-bearing organisms (HARTMAN, 1983; BOYAJIAN & LABARBERA, 1987). It is quite possible that many archaeocyaths had astrorhizal canals embedded in the soft tissue, as in some extant demosponges with nonspiculate
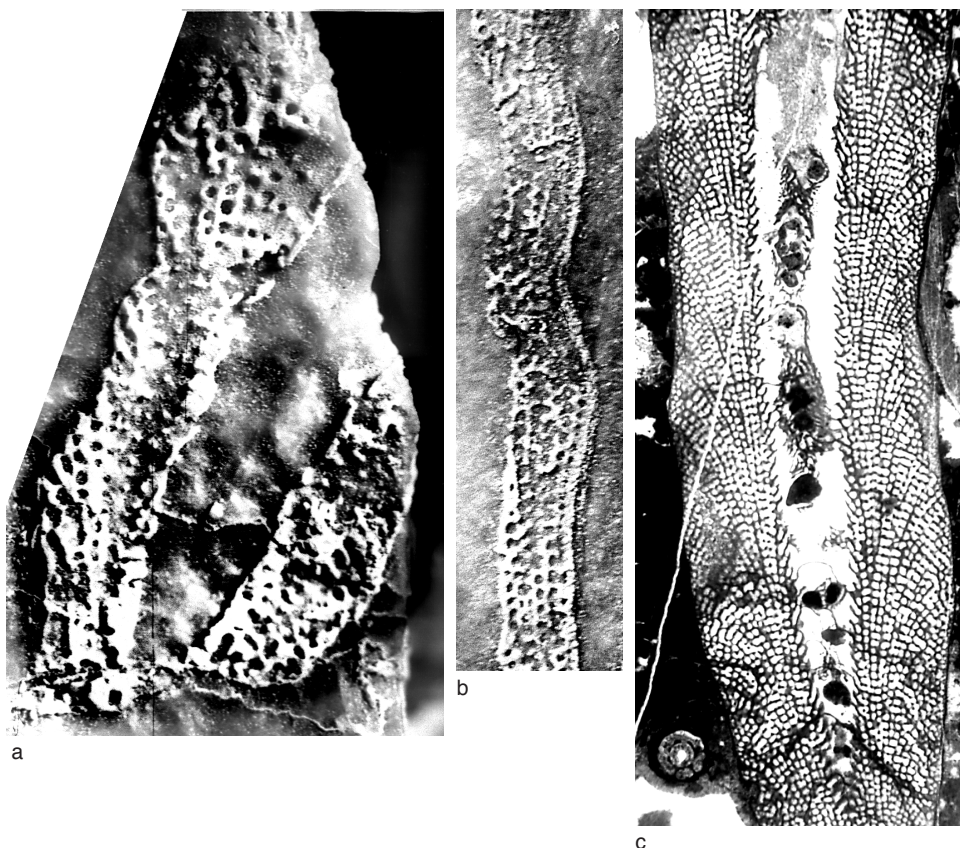
FIG. 509. Pseudosepta, pseudotaeniae, and dictyonal network; *a,* coarsely porous pseudotaeniae in *Archaeocyathus decipiens* R. BEDFORD & J. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section, holotype, 86670-247, PU, ×5.3 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *b,* pseudosepta in *Graphoscyphia graphica* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, longitudinal section (outer wall to right), paralectotype, P947-68, SAM, ×6 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* dictyonal network in *Fenestrocyathus complexus* HANDFIELD, Botoman, Sekwi Formation, Mackenzie Mountains, Northwest Territories, Canada, longitudinal section, paratype, 25390, GSC, ×4.5 (Handfield, 1971).

FIG. 510. Calicles and syringes; *1,* calicles of hexagonal cross section in *Usloncyathus araneosus* (GRAVESTOCK), Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, transverse section, paratype, P21663-3, SAM, ×10 (Gravestock, 1984); *2a–d,* schematic reconstructions of varieties of syrinx; *2a,* several pore rows per facet, as in *Syringocnema, Kruseicnema, Fragilicyathus, Tuvacnema*; *2b,* one pore row per transverse facet and several pore rows per lateral facet, as in *Pseudosyringocnema*; *2c,* one pore row per facet, as in *Syringothalamus*; *2d,* complex syrinx with one pore row per transverse facet and several pore rows per lateral facet, as in *Williamicyathus* (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *3,* syringes of hexagonal cross section with several pore rows per facet, *Syringocnema favus* TAYLOR, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, longitudinal section (outer wall to right), FT.9486, specimen F.83936, AM, ×10 (Kruse, 1982).
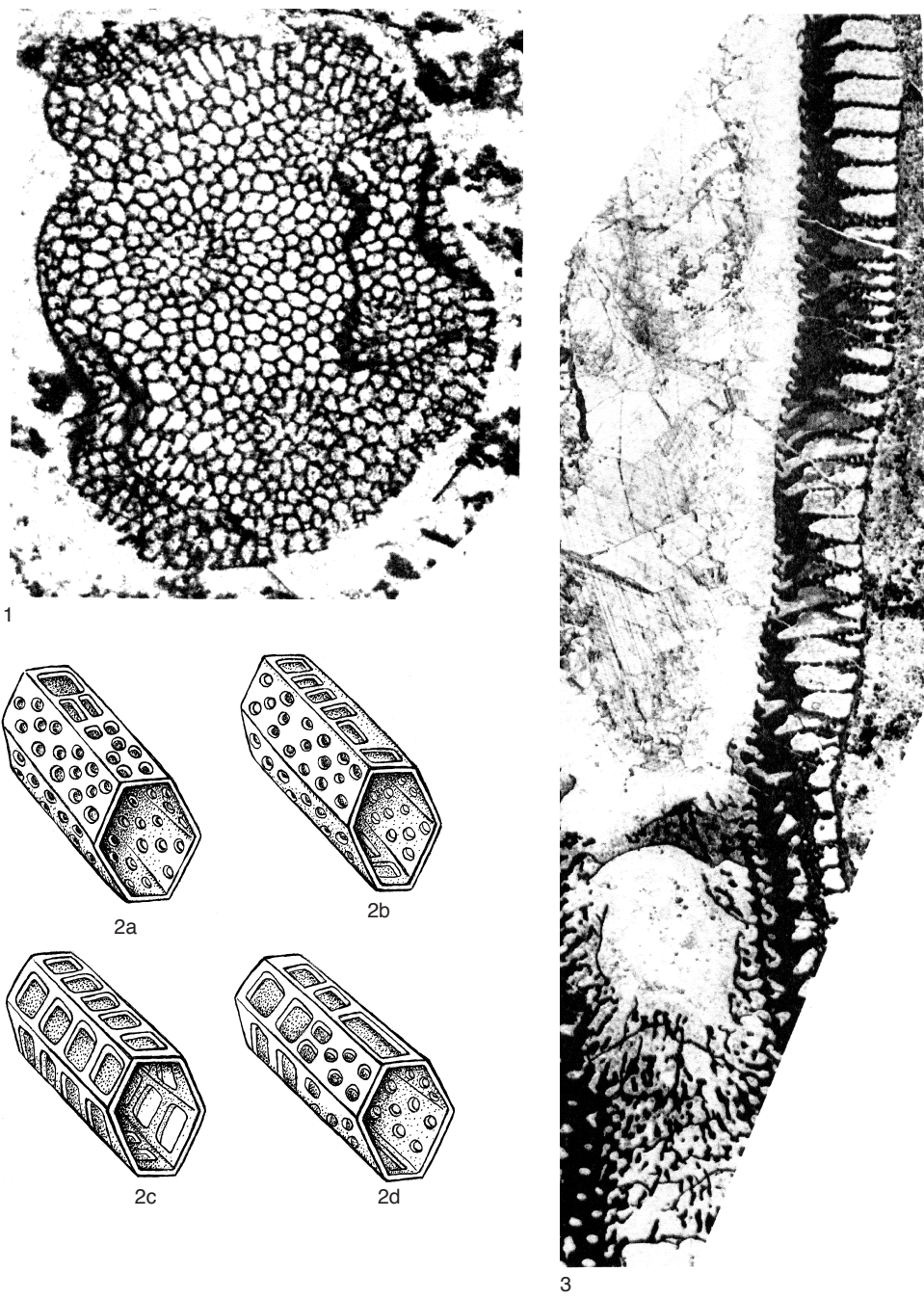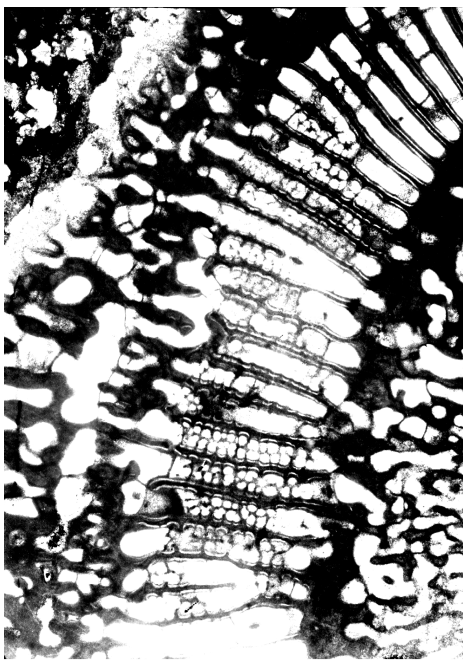
FIG. 510. *(For explanation, see facing page).*

FIG. 511. Membrane tabulae with two radial rows of irregular pores per loculus in *Shiveligocyayhus plenus* FONIN, Botoman, Shangan Formation, Shivelig-Khem River, Tuva, Russia, transverse section (outer wall to left), 1915/814, PIN, ×9.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

skeletons. Traces of this system were perhaps replicated in the secondary calcareous skeleton of some *Archaeocyathus yichangensis* YUAN & ZHANG (Fig. 513a). However, in only three species, *Palaeoconularia triangulata* (YAZMIR), *Altaicyathus vologdini* (YAVORSKY) (Fig. 513b), and *Landercyathus lewandowskii* DEBRENNE

& GANGLOFF (Fig. 513d), have traces of the astrorhizal canals been retained in the primary calcareous skeleton. Other species of *Altaicyathus* VOLOGDIN (Fig. 513c) and *Retilamina* DEBRENNE & JAMES (Fig. 495e) lack astrorhizae but possess chimneylike outpockets on the outer wall. Such a chimney might become a new central cavity during ontogeny. It is thus possible to consider these as homologous to astrorhizae.

Juvenile *Archaeocyathus* BILLINGS cups may also have tubelike structures on the outer wall, but, unlike chimneys, these are incurrent rather than excurrent adaptations. They are homologous to the exaulos of thalamid sponges *sensu* FINKS (1983).

Some cups contain porous, longitudinal, tubular structures in the central cavity (Fig. 494d). These structures were called tubuli by FONIN (1963) and are part of the secondary skeleton. Tubuli can be located anywhere within the central cavity; when located at its upper part, they act as excurrent adaptations. Tubuli could thus be related to excurrent canals of the cup, like similar structures in inozoan calcareans or in lithistide demosponges. All the above mentioned features (astrorhiza, chimney, exaulos, tubulus) can be well developed, or completely missing, in individuals of the same species.

Pillars

Pillars are longitudinal, rodlike elements directly linking adjacent tabulae. They characterize sponges with a stromatoporoid

FIG. 512. Segmented tabulae; *a,* finely porous segmented tabula in *Claruscoscinus mactus* (FONIN), Toyonian, Usa Formation, Matur River, Kuznetsk Alatau, Altay Sayan, Russia, oblique transverse section (outer wall at top), 2851/28, PIN, ×12; *b,* coarsely porous segmented tabula in *Cellicyathus* sp., Botoman, Chara Formation, Olekma River, Russia, oblique transverse section (outer wall at top), 4451/30, PIN, ×16 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* slitlike pores in segmented tabula of *Pycnoidocoscinus pycnoideum* R. BEDFORD & W. R. BEDFORD, Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, oblique transverse section (outer wall at top), paratype, P991, SAM, ×9 (Debrenne, 1974a); *d,* concentric porosity in segmented tabula of *Markocyathus clementensis* DEBRENNE, Botoman, Puerto Blanco Formation, Caborca, Sonora, Mexico, oblique transverse section, 90178, GSC, ×18; *e,* coplanar rodlike intervallar elements in segmented tabulae of *Dictyosycon* sp., Atdabanian, Altay Sayan, Russia, oblique transverse section, 4451/21, PIN, ×11; *f,* compound porosity in segmented tabulae of *Tabulacyathellus bidzhaensis* MISSARZHEVSKIY, Atdabanian, Salaany Gol Formation, Khasagt-Khayrkhan Range, Tsagaan Oloom province, western Mongolia, oblique longitudinal section, 4451/39, PIN, ×18 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
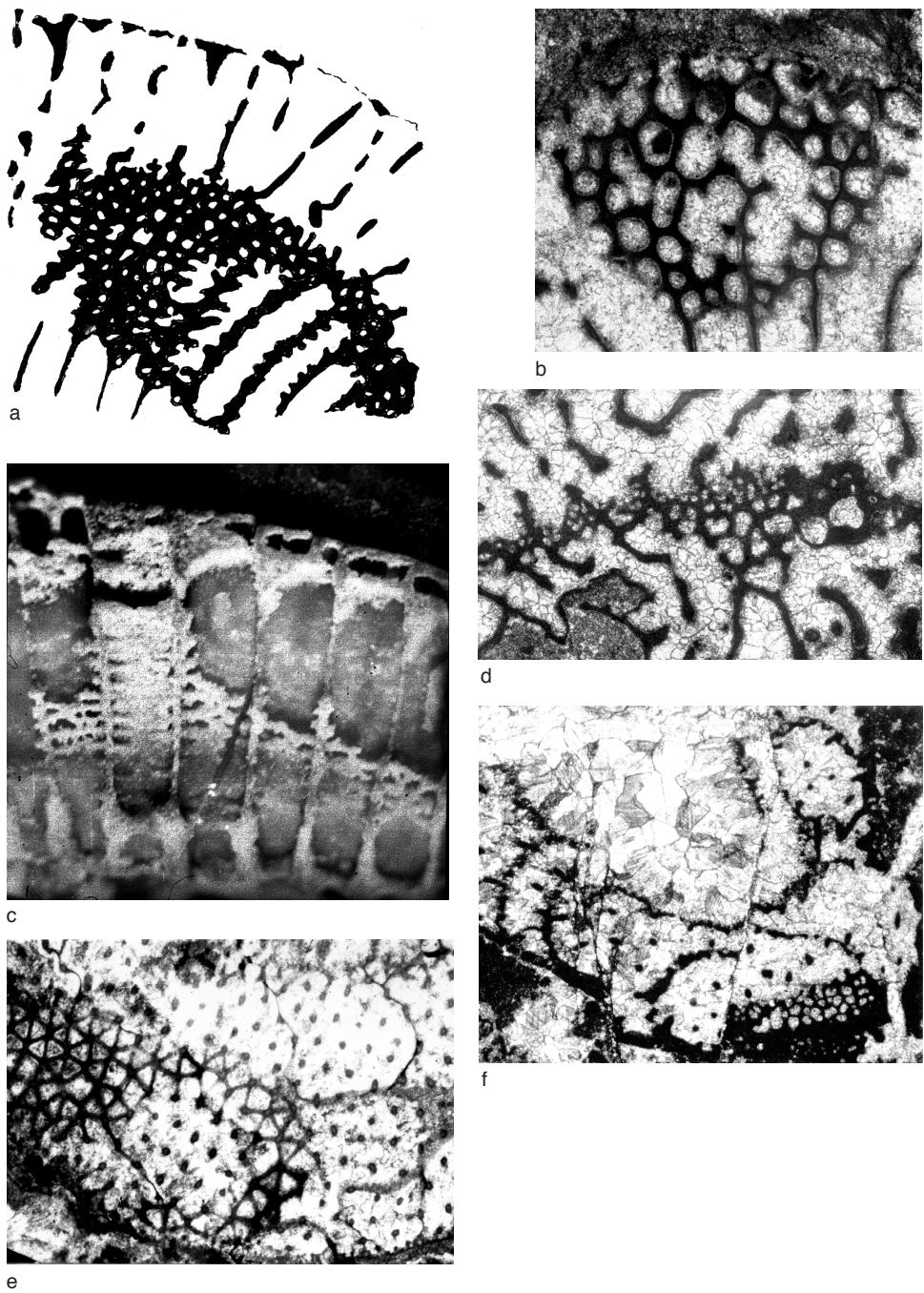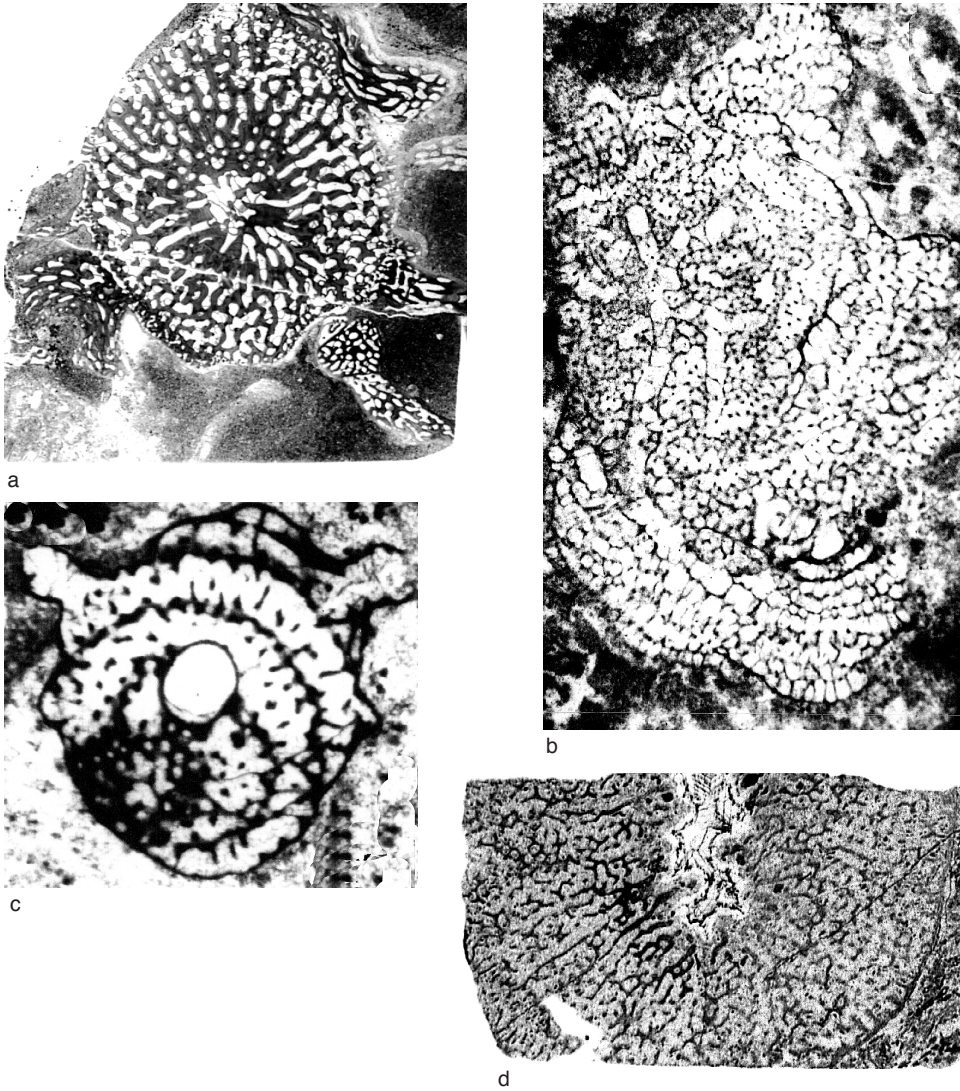
Fig. 512. *(For explanation, see facing page).*

FIG. 513. Astrorhizae and chimneys; *a,* canals in secondary skeleton, possibly replicating astrorhizal canals in original soft tissue, in central cavity of *Archaeocyathus yichangensis* YUAN & ZHANG, Toyonian, Tianheban Formation, Yichang, Hubei, China, transverse section, M85082, MNHN, ×3.3 (Debrenne, Gandin, & Zhuravlev, 1991); *b,* astrorhizal canals in primary skeleton of *Altaicyathus vologdini* (YAVORSKY), Botoman, Torgashino Formation, East Sayan, Altay Sayan, Russia, longitudinal section, 4451/52, PIN, ×10; *c,* chimneys on outer wall of *Altaicyathus* sp., Botoman, Adams Argillite, Tatonduk River, Alaska, United States, 2549, UAM, ×20; *d,* astrorhizal canals in primary skeleton of *Landercyathus lewandowskii* DEBRENNE & GANGLOFF, Botoman, Valmy Formation, Iron Canyon, Nevada, United States, oblique longitudinal section, 38115, UCMP, ×5.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

or thalamid architecture, and, among archaeocyaths, the Kazachstanicyathida (with composite architecture). They may be superposed in successive chambers, but otherwise show no regularity of arrange-ment (Fig. 513b–c, Fig. 516c). In *Korovinella* RADUGIN, pillars can bifurcate at their distal ends. Ontogenetically, pillars probably develop in a proximal direction from the chamber ceiling.

OUTER WALL TYPES

Observations on outer wall morphology by GRAVESTOCK (1984), and modifications by DEBRENNE and ZHURAVLEV (1992b), are the basis for the present account.

Simple Walls

Simple walls are united in possessing simple pores. Several subtypes are recognized.

Simple wall–Rudimentary.—In this wall type, the outer edges of intervallar elements open directly to the exterior. There may be some thickening of the marginal intervallar elements, but effectively there is no distinct outer wall. True rudimentary outer walls characterize some Dictyofavina (*Usloncyathus* FONIN, *Zunyicyathus* DEBRENNE, KRUSE, & ZHANG) and Syringocnemina (*Auliscocyathus* DEBRENNE) (Fig. 515a).

Simple wall–Basic.—Basic simple walls incorporate the marginal intervallar elements, but with additional linking lintels (Fig. 514c, Fig. 515b). This wall type is found in the Archaeocyathina only (DEBRENNE & ZHURAVLEV, 1992b).

Simple wall–Cambroid.—This is the new designation for the so-called simple wall of *Cambrocyathellus*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49). Restricted to the Loculicyathina, this simple wall subtype is most similar to the simple wall of Monocyathida, Ajacicyathida, Putapacyathida, and Capsulocyathida. It is a continuous plate pierced by simple pores. Constituent pores may be rounded, irregularly rounded, or irregularly quadrate (Fig. 515c–f).

Pore orifices may bear flat to convex diaphragms, as, for example, in *Loculicyathus membranivestites* VOLOGDIN. Stirrup pores are rare. There may be one or several pore rows per intersept, but where there is only one, pores gently zigzag along the row (Fig. 515f).

Simple wall–Anthoid.—Found only in the Anthomorphina, this is the proposed new name for so-called simple wall of *Anthomorpha*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49). It comprises transverse
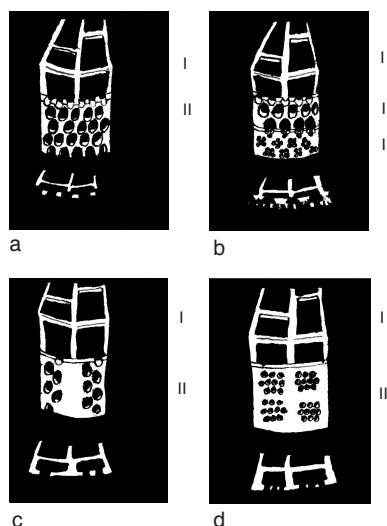

FIG. 514. Schematic reconstructions of outer walls; *a,* outer wall with simple pores in Ajacicyathida; *b,* outer wall with attached microporous sheath in Ajacicyathida; *c,* basic simple outer wall in Archaeocyathida; *d,* concentrically porous outer wall in Archaeocyathida; *I,* distal elements of intervallum; *II,* outer wall; *III,* microporous sheath (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

lintels linking adjacent pseudosepta to form a single row of slightly subquadrate large pores (Fig. 516a). In some cases, additional lintels define several poorly expressed discontinuous pore rows per intersept (Fig. 516b).

Microporous membranes superficially similar to the attached microporous sheath in Ajacicyathida can be intermittently developed (Fig. 494d). The structure of these is identical to that of membrane tabulae.

Simple wall–Altoid.—Not unlike the anthoid wall subtype, the altoid simple wall is found in Kazachstanicyathida (*Altaicyathus* VOLOGDIN and *Korovinella* RADUGIN). In this wall, lintels link the distal ends of pillars to form a continuous plate pierced by frequent polygonal pores (Fig. 516c). This is the so-called simple wall of *Altaicyathus*-type of DEBRENNE and ZHURAVLEV (1992b, p. 49).

Concentrically Porous Walls

This wall type is found in Archaeocyathina and Syringocnemina. It consists of a continuous membrane bearing irregularly
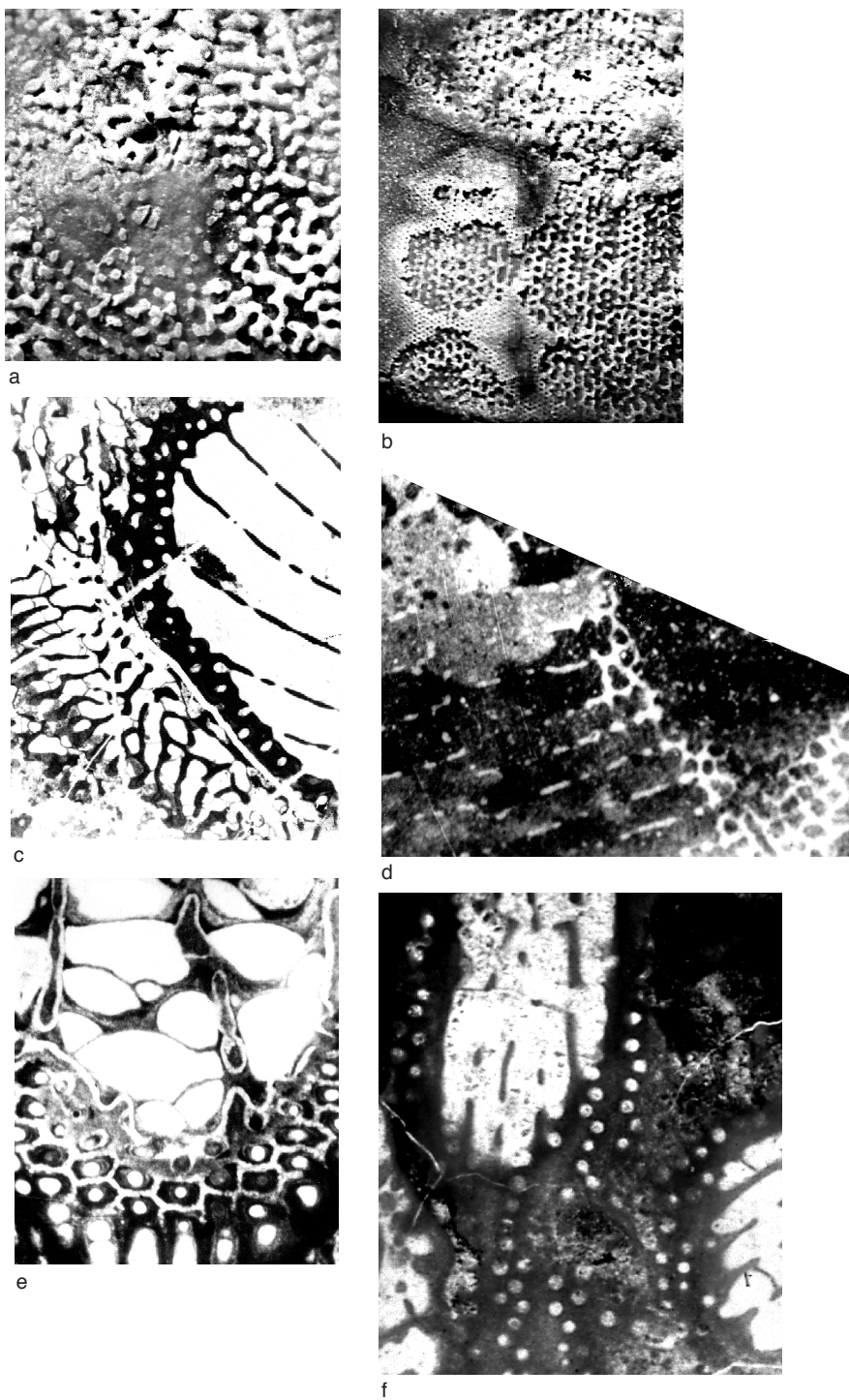
Fig. 515. *(For explanation, see facing page).*

arranged pores clustered within intervallar cells, bounded in Archaeocyathina by pseudotaeniae and synapticulae or by taeniae and linking transverse rods (Fig. 514d); and, in Syringocnemina, by individual syringes (Fig. 516e). There is no clear organization of pores into longitudinal rows.

GRAVESTOCK (1984) introduced the term centripetal for this wall type, but because that term is also used to describe wall development, the wall type is here termed concentrically porous. Prior to GRAVESTOCK (1984), this wall type was commonly described as simple, comparable to the simple outer wall in Monocyathida, Ajacicyathida, Putapacyathida, and Capsulocyathida (e.g., ZHURAVLEVA, 1960b; YAROSHEVICH, 1966), or as double (e.g., KRASNOPEEVA, 1961; OSADCHAYA & others, 1979; FONIN in VORONIN & others, 1982). Thus, some genera were described twice: with simple outer wall (*Archaeocyathus* BILLINGS, *Archaeopharetra* R. & W. R. BEDFORD) and with microporous sheath ("*Syringsella*" KRASNOPEEVA, "*Salanycyathus*" FONIN).

Compound Walls

In compound walls (GRAVESTOCK, 1984), a discontinuous porous membrane is attached to marginal intervallar cells. Two variants are accorded genus-level significance: walls with incipient subdivision of intervallar cells (Fig. 517c) and walls with completely subdivided pores (Fig. 516d, Fig. 517a).

In the first variant, thick spines arise from pore lintels but are not completely connected; in the second, the spines are completely connected to form irregular micropores. Compound walls are present in Archaeocyathina and Dictyofavina.

Pustular Walls

This wall type is known in Putapacyathida (*Chabakovicyathus* KONYUSHKOV), Loculicyathina (*Sakhacyathus* DEBRENNE & ZHURAVLEV), Archaeocyathina (*Naimarkcyathus* WRONA & ZHURAVLEV), and Syringocnemina (*Kruseicnema* DEBRENNE, GRAVESTOCK, & ZHURAVLEV). It is characterized by pustulae with a single central pore (Fig. 517d). In the last two genera, the pustulae are low cones, but in *Chabakovicyathus* KONYUSHKOV, they are hemispherical domes. Pustulae are similar to simple tumuli in Monocyathida, Ajacicyathida, and Capsulocyathida, which, however, differ in having the pore located toward the bottom.

Walls with Canals

Three types of outer wall canals are known in Archaeocyathida and Kazachstanicyathida:

1. Straight oblique canals, as in *Fragilicyathus* BELYAEVA and *Warriootacyathus* GRAVESTOCK (Fig. 517b).

2. Subdivided canals, as in *Beltanacyathus* R. BEDFORD & J. BEDFORD (Fig. 517e); these are short oblique canals with incipient or complete subdivision of external orifices by short protrusions of the canal wall. DEBRENNE and ZHURAVLEV (1992b) interpreted the outer walls of *Ataxiocyathus* DEBRENNE and *Maiandrocyathus* DEBRENNE as extreme developments of such protrusions

FIG. 515. Outer walls in Archaeocyathida; *a,* rudimentary simple outer wall in *Auliscocyathus multifidus* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, 245, PU, ×6; *b,* basic simple outer wall, *Graphoscyphia graphica* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, paralectotype, 85, PU, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* simple outer wall with rounded pores of cambroid type, *Ardrossacyathus endotheca* R. BEDFORD & J. BEDFORD, Botoman, Parara Limestone, Ardrossan, South Australia, Australia, tangential section, topotype, P32041, SAM, ×6 (Zhuravlev & Gravestock, 1994); *d,* simple outer wall with irregularly rounded pores of cambroid type, *Okulitchicyathus discoformis* (ZHURAVLEVA), Tommotian, Pestrotsvet Formation, Zhurinskiy Mys, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/59, PIN, ×20; *e,* simple outer wall with irregularly quadrate pores of cambroid type, *Neoloculicyathus sibiricus* (SUNDUKOV), Atdabanian, Pestrotsvet Formation, Oy-Muran, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/1, PIN, ×20; *f,* simple outer wall with one row of pores of cambroid type per intersept, *Cambrocyathellus proximus* (FONIN), Tommotian, Pestrotsvet Formation, Titirikteekh Creek, Lena River, Sakha (Yakutia), Russia, tangential section, 4451/5, PIN, ×20 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
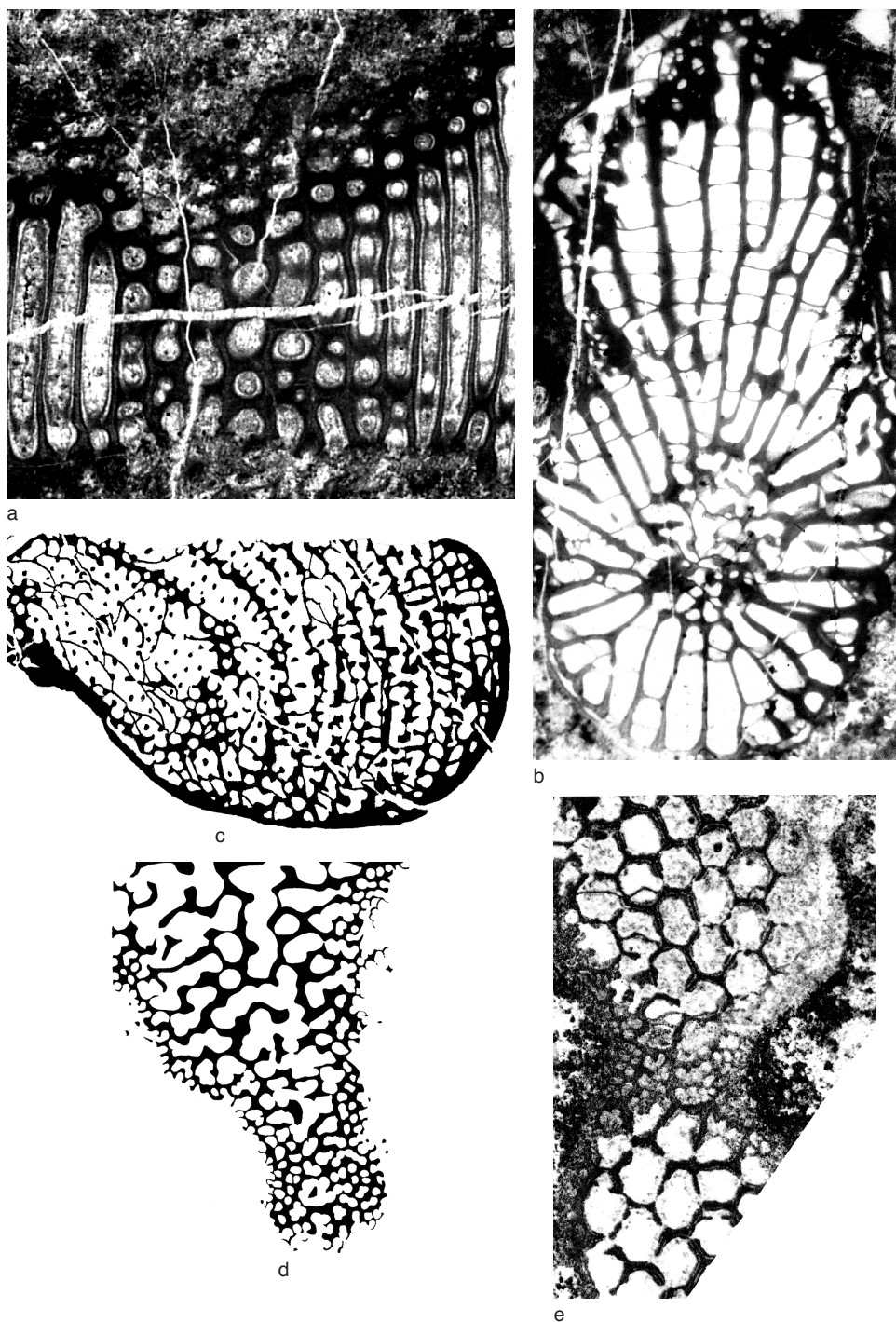
to form an additional microporous sheath with elongate irregular pores (Fig. 517f).

3. S-shaped canals, as in *Tchojacyathus* ROZANOV (Fig. 518.1) and canals with supplementary bracts, having a V-shaped appearance, as in *Chankacyathus* YAKOVLEV (Fig. 518.2).

Tabellar Walls

This wall type is known only in *Taeniae-cyathellus* ZHURAVLEVA (Archaeocyathina). It comprises longitudinal ribs linked by transverse lintels (Fig. 518.4). FONIN (1963) provided the first comprehensive description of this wall type. However, due to the common occurrence of an adherent pellis, FONIN oriented the longitudinal ribs (his tabellae) and transverse lintels (his metulae) perpendicular to their true orientation.

Aporose Walls

This outer wall is not comparable to other wall types in that it is characteristic of early ontogenetic stages in all suborders of Archaeocyathida and Kazachstanicy-athida, except Loculicyathina, which never passes through an aporose outer wall stage. One possible exception is *Chouberticyathus* DEBRENNE (Archaeocyathina) (Fig. 518.3). The aporose outer wall is usually a laminated structure, similar to epitheca of other calcified sponges.

INNER WALL TYPES

Inner walls are less diverse than outer walls, as in all orders of Archaeocyatha.

Simple Walls

Simple inner walls in Archaeocyathida and Kazachstanicyathida typically comprise a single longitudinal pore row per intersept. Forms with several pore rows per intersept are the exception. Pores may be rounded, elliptical, or subquadrate (Fig. 519a–c). Rarely, pore lintels bear spines (e.g., in *Copleicyathus* R. BEDFORD & J. BEDFORD, *Spinosocyathus* ZHURAVLEVA).

Walls with Bracts, Fused Bracts, or Pore Tubes

In Archaeocyathina and Syringocnemina, there is a structural continuum between these otherwise disparate wall types, so they are treated collectively in these suborders. Taken together, these wall types are analogous to the bracts and scales grouping in the much less morphologically plastic orders Monocyathida, Ajacicyathida, and Capsulo-cyathida (see previous section on walls with bracts or scales, p. 863). Due to the absence of septa, Putapacyathida possess an intermediate type of such structures.

Fused bracts have often been described as scales or annuli but are distinguished from these latter by their undulating outline, indicative of their constituent, semi-independent units. All formerly recognized so-called scales in this order are here regarded as fused bracts. Fused bracts are planar or S-shaped. With the exception of *Taeniaecyathellus* ZHURAVLEVA inner walls, all these variant walls possess only one longitudinal pore row per intersept.

FIG. 516. Outer walls in Archaeocyathida and Kazachstanicyathida; *a,* simple outer wall with pores of anthoid type, *Anthomorpha margarita* BORNEMANN, Botoman, Matoppa Formation, Serra Scoris, Sardinia, Italy, tangential section, M84144, MNHN, ×10; *b,* simple outer wall with pores of anthoid type, *Tollicyathus nelliae* (FONIN), Botoman, Shangan Formation, Ulug-Shangan River, Tuva, Russia, oblique transverse section, 4451/12, PIN, ×10; *c,* outer wall with simple pores of altoid type, *Altaicyathus notabilis* VOLOGDIN, Botoman, Verkhneynyrga Formation, Altay Mountains, Altay Sayan, Russia, oblique transverse section, 290/2957, TsNIGRm, ×9; *d,* compound outer wall with completely subdivided pores, *Spirillicyathus pigmentus* R. BEDFORD & J. BEDFORD, Atdabanian, Mount Scott Range, South Australia, Australia, tangential section, P21747, SAM, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* concentrically porous outer wall, *Syringocnema favus* TAYLOR, Botoman, Cymbric Vale Formation, Mount Wright, New South Wales, Australia, tangential section, FT.9487, specimen, F.83936, AM, ×4 (Kruse, 1982).
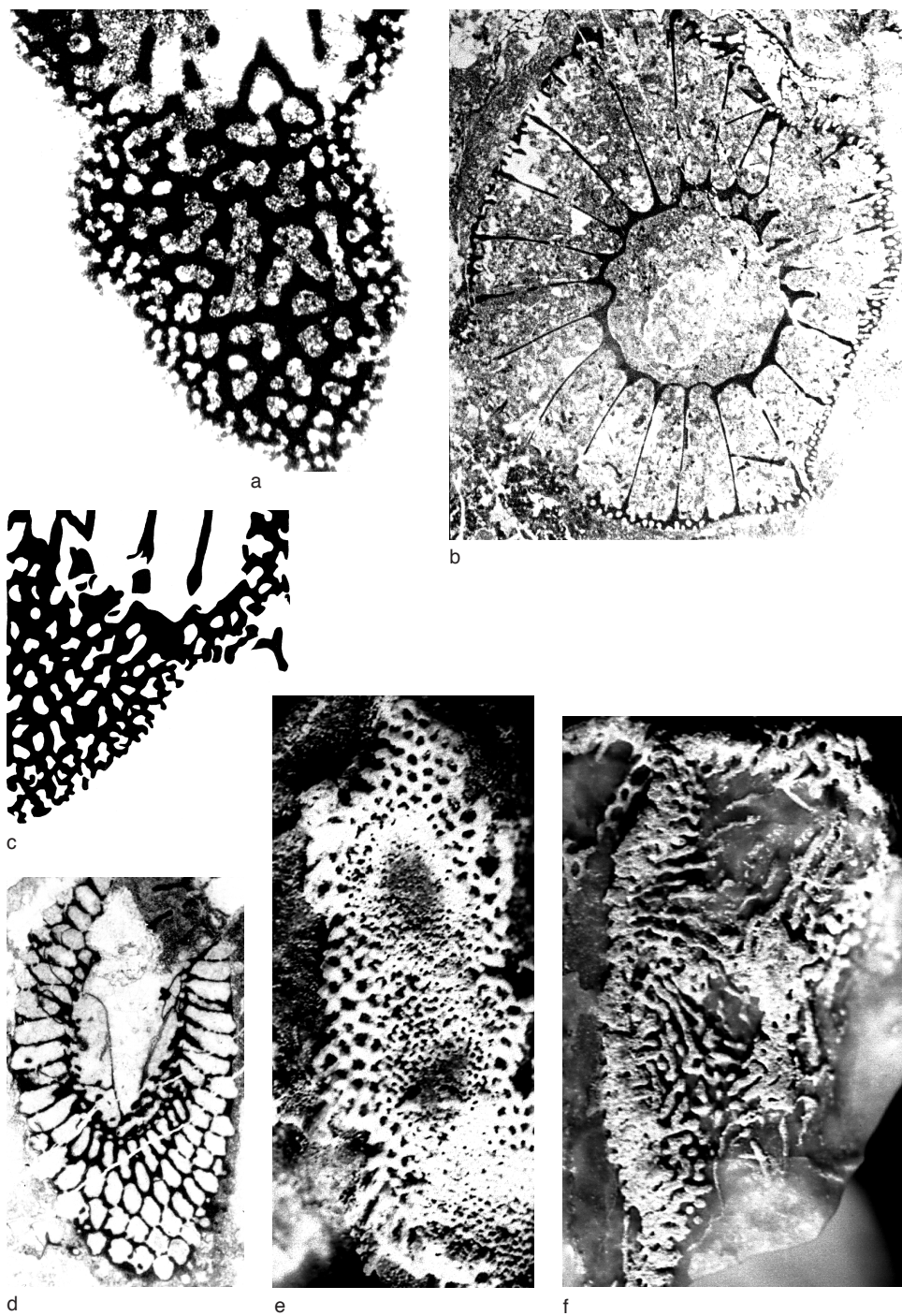
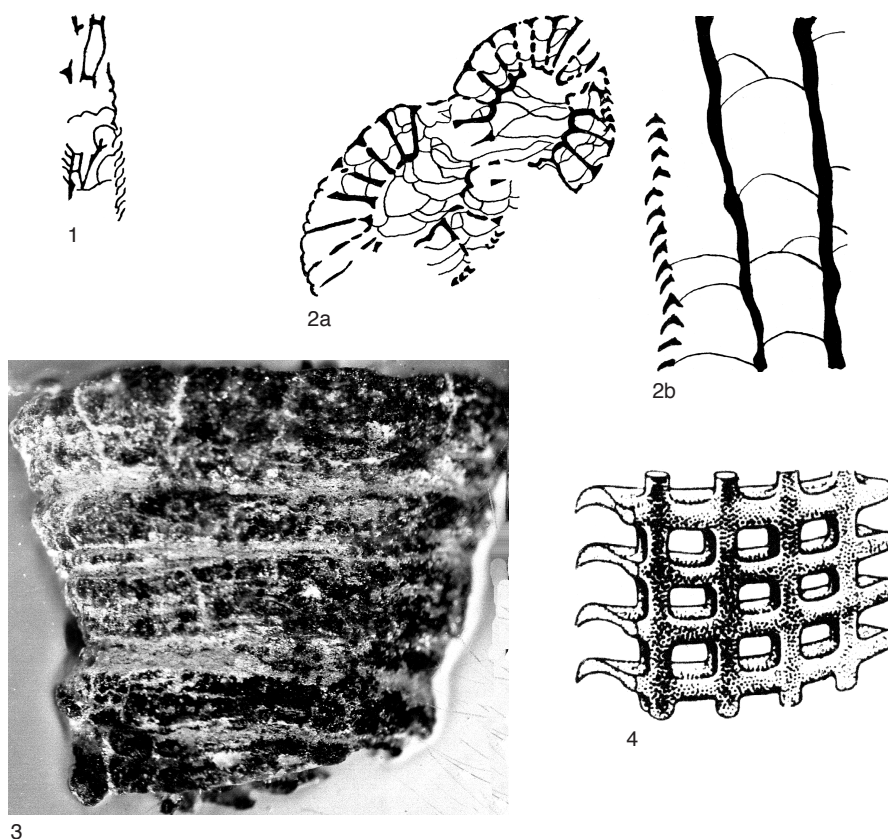FIG. 517. *(For explanation, see facing page).*

FIG. 518. Outer walls in Archaeocyathida; *1,* horizontal to upwardly projecting S-shaped canals on both walls of *Tchoja-cyathus validus* ROZANOV, Atdabanian, Uba Formation, Tyrga River, Altay Mountains, Altay Sayan, Russia, longitudinal section (outer wall to left), GIN3447/7-8, PIN, ×3.5; *2a–b,* horizontal to upwardly projecting straight canals, bearing supplementary bracts externally, on outer wall of *Chankacyathus strachovi* YAKOVLEV; *2a,* Botoman, Dmitrievka Forma-tion, Kar'ernaya Hill, Far East, Russia, transverse section, 133/52, PGU, ×3.5; *2b,* Botoman, Khanka Lake area, Far East, Russia, longitudinal section (outer wall to left), 1768-12b, PGU, ×17; *3,* imperforate (possibly rudimentary) outer wall in *Chouberticyathus clatratus* DEBRENNE, Botoman, Issafen Formation, Tizi Oumeslema, Morocco, external view of outer wall, M80272, MNHN, ×8.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *4,* schematic reconstruction of tabellar outer wall in *Taeniaecyathellus tectus* FONIN, external view, ×85 (Fonin, 1963).

FIG. 517. Outer walls in Archaeocyathida; *a,* compound outer wall with completely subdivided pores, *Copleicyathus scottensis* GRAVESTOCK, Atdabanian, Mount Scott Range, South Australia, Australia, tangential section, holotype, P21423-1, SAM, ×19 (Gravestock, 1984); *b,* horizontal to upwardly projecting straight canals in outer wall, *Warriootacyathus wilkawillinensis* GRAVESTOCK, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, transverse section, paratype, P21806-2, SAM, ×2 (Gravestock, 1984); *c,* compound outer wall with incipient subdivision of intervallar cells, *Jugalicyathus tardus* GRAVESTOCK, Atdabanian, Ajax Limestone, Mount Scott Range, South Australia, Australia, tangential section, holotype, P21747, SAM, ×7.5; *d,* pustular outer wall, *Kruseicnema gracilis* (GORDON), Botoman, Parara Limestone, Minlaton 1 drillhole, Yorke Peninsula, South Aus-tralia, Australia, oblique longitudinal section, P32047, SAM, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* subdivided canals in outer wall, *Beltanacyathus wirrialpensis* (TAYLOR), Atdabanian, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longi-tudinal section, holotype of junior synonym *ionicus* R. BEDFORD & J. BEDFORD, 86718-275, PU, ×7 (Debrenne, 1974a); *f,* subdivided canals in outer wall, *Maiandrocyathus insigne* (R. BEDFORD & W. R. BEDFORD), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, external view in longitudinal section, holotype, P986-168, SAM, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).
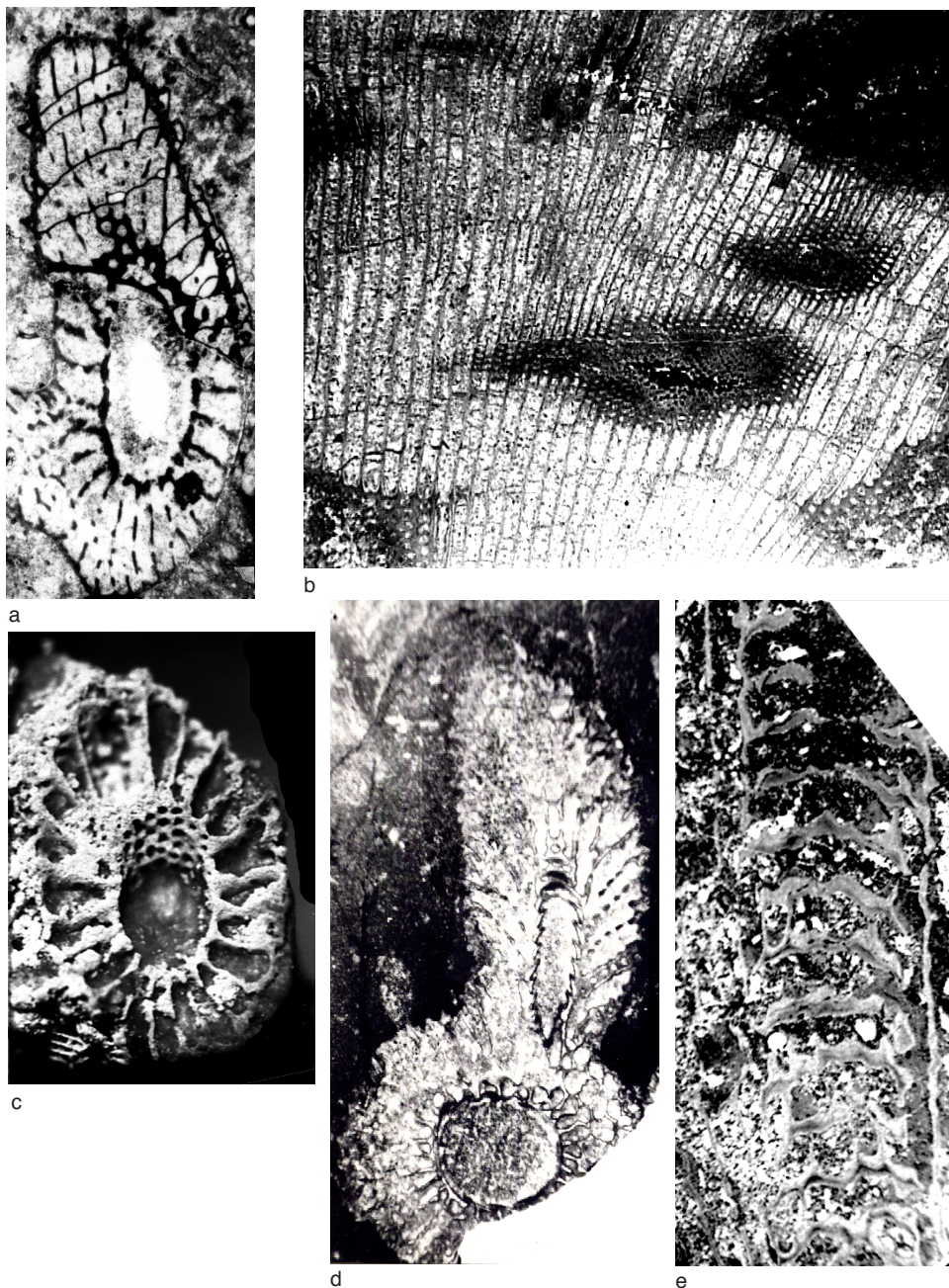
Fig. 519. Inner walls in Archaeocyathida; *a,* inner wall with rounded simple pores, *Cambrocyathellus tuberculatus* (Vologdin), Atdabanian, Salaany Gol Formation, Zuune-Arts, Tsagaan Oloom province, western Mongolia, oblique transverse section, 4451/10, PIN, ×7.5; *b,* inner wall with elliptical simple pores in *Anthomorpha margarita* Bornemann, Botoman, Matoppa Formation, Cuccuru Contu, Sardinia, Italy, tangential section, M84253, MNHN, ×5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *c,* inner wall with subquadrate simple pores, *Paranacyathus parvus* (R. Bedford & W. R. Bedford), Botoman, Ajax Limestone, Ajax Mine, South Australia, Australia, oblique transverse view, holotype, P992, SAM, ×6 (Debrenne, 1974c); *d,* annulus-like *(Continued on facing page.)*

In the present suborders, fused bracts typically develop into oblique canals during ontogeny. They may in turn fuse to form annulus-like structures (Fig. 519d). Fused and nonfused bracts and pore tubes can arbitrarily appear in the same or different cups of the same species.

Pore tubes are generally described as straight (Fig. 520a), but a minority are clearly S-shaped (e.g., in *Sigmofungia* R. BEDFORD & W. R. BEDFORD, Fig. 520b), while others are intermediate, with both types intergradational (e.g., in *Fenestrocyathus* HANDFIELD).

Walls with Canals

Inner wall canals are known only in Loculicyathina and Anthomorphina, and stirrup canals only in Anthomorphina. Canals are straight in *Shiveligocyathus* MISSARZHEVSKIY and S-shaped in *Tchojacyathus* ROZANOV.

Uniquely, the inner wall of *Eremitacyathus* ZAMARREÑO & DEBRENNE has a single continuous opening along each intersept, bounded by longitudinal plates (Fig. 520c). These openings are treated as canals.

Compound Walls

Compound inner walls bear similarity to compound outer walls. As in the latter, the pore subdivision of inner walls can be incipient (e.g., *Changicyathus* DEBRENNE & ZHURAVLEV, *Metaldetes* TAYLOR) (Fig. 520e) or complete (e.g., *Archaeosycon* TAYLOR, *Pycnoidocoscinus* R. BEDFORD & W. R. BEDFORD) (Fig. 520d).

However, some compound inner walls differ structurally from the compound outer wall. Thus, while in Metacyathoidea the inner wall pore subdivision mirrors that of the outer wall, in *Archaeosycon* and *Pycnoidocoscinus* the inner wall is formed from the superposition of wall and tabular structure.

SKELETAL MICROSTRUCTURE
PRIMARY SKELETON

The well-preserved primary archaeocyathan skeleton shows a uniformly microgranular microstructure comprising a mosaic of interlocking isometric polyhedral microgranules with randomly oriented c-axes (HINDE, 1889; TAYLOR, 1910, p. 162; HILL, 1964b). There are no spicules. HINDE (1889) described the archaeocyathan microstructure as minutely granular, and some 70 years later, ZHURAVLEVA (1960b, p. 22) reported a mosaic of grains. All these observations relied on normal thin sections, which permit a maximum magnification of about 300× only. From 1970, two new methods were introduced: polished ultrathin sections (thickness 3 µm) and scanning electron microscopy. Both techniques permit greater magnification (up to 4000×, although 2000× is generally sufficient for microstructural studies). The first result obtained by the new methods was a more precise definition of the microgranules (LAFUSTE & DEBRENNE, 1970): these are uniformly polyhedral crystallites, the surfaces of which are embossed by irregular cupules and protruberances (Fig. 521.1–2).

Surveys of various archaeocyath taxa from different regions and ranging in age from Tommotian to Botoman demonstrate a general uniformity of microstructure among the Archaeocyatha in time, space, and systematic position (Fig. 521.3–4) (DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, p. 40; KRUSE & DEBRENNE, 1989; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 60). The maximum size of microgranules is within the range of 0.5–20 µm, but more commonly 4–8 µm (KRUSE & DEBRENNE, 1989). Some difference has been observed

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FIG. 519. *(Continued from facing page).* structures developed from upwardly projecting S-shaped fused bracts on inner wall of *Syringothalamus crispus* DE-BRENNE, GANGLOFF, & ZHURAVLEV, Botoman, Poleta Formation, Westgard Pass, California, United States, oblique transverse section, B4008, UCMP, ×5 (Debrenne & Zhuravlev, 1992b); ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris); *e,* upwardly projecting straight pore tubes on inner wall of *Pycnoidocyathus sekwiensis* HANDFIELD, Botoman, Sekwi Formation, Caribou Pass, Northwest Territories, Canada, tangential section, holotype, 25384, GSC, ×4 (Handfield, 1971).
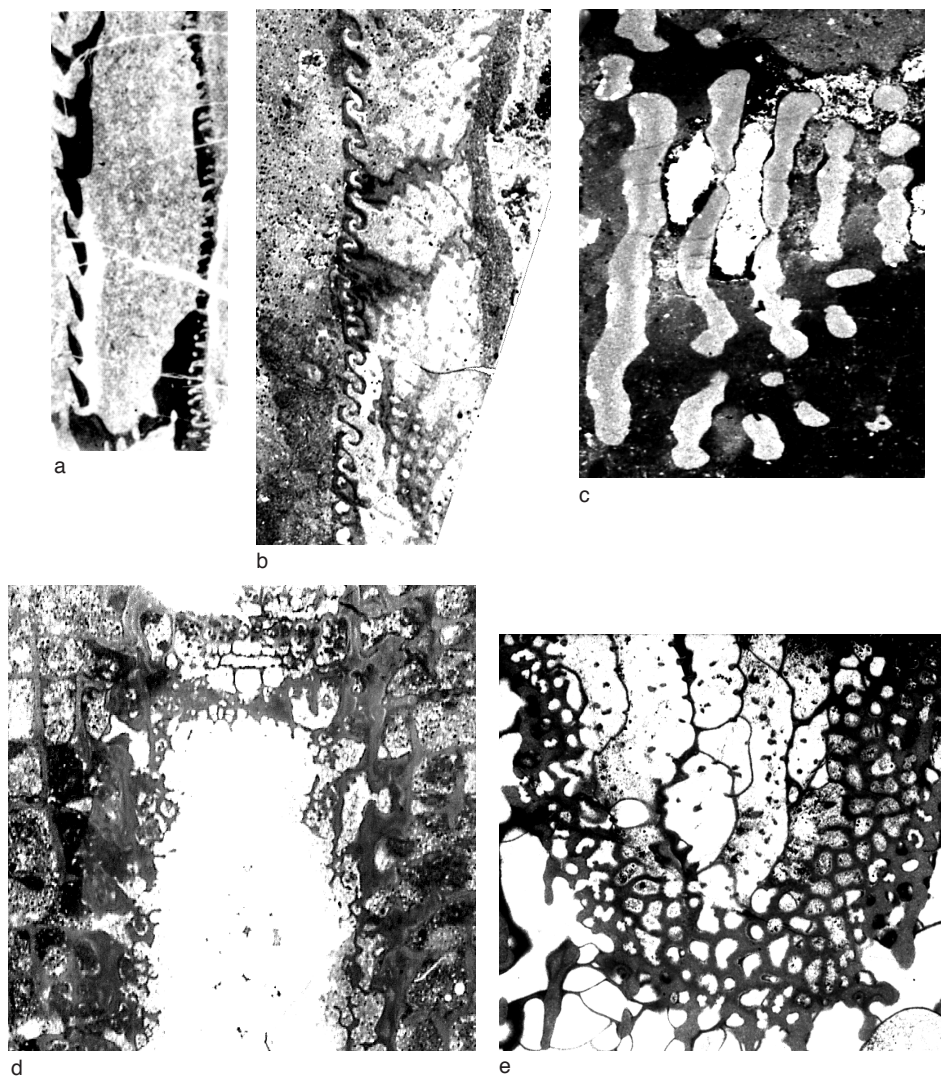
FIG. 520. Inner walls in Archaeocyathida; *a,* upwardly projecting straight pore tubes on inner wall of *Beltanacy-athus digitus* GRAVESTOCK, Atdabanian, Wilkawillina Limestone, Wilkawillina Gorge, South Australia, Australia, longitudinal section (outer wall to right), paratype, P21825, SAM, ×3 (Gravestock, 1984); *b,* upwardly projecting S-shaped pore tubes on inner wall of *Sigmofungia undata* (DEBRENNE), Botoman, Puerto Blanco Formation, Cerro Rajon, Sonora, Mexico, longitudinal section (outer wall to right), holotype, M83098, MNHN, ×5.5 (Debrenne, Gandin, & Rowland, 1989); *c,* longitudinally continuous canal-like openings in inner wall of *Eremitacyathus fissus* DEBRENNE, Atdabanian, Pedroche Formation, Las Ermitas, Cordoba, Spain, tangential section, holotype, M84016, specimen Spe 10-1a, MNHN, ×12; *d,* compound inner wall with complete pore subdivision in *Archaeosycon billingsi* (WALCOTT), Botoman, Forteau Formation, Treasure Reef, Labrador, Canada, tangential section, 62119, GSC, ×7.5; *e,* compound inner wall with incipient pore subdivision in *Metaldetes profundus* (BILLINGS), Botoman, Forteau Formaton, Mount St. Margaret, Newfoundland, Canada, tangential section, 103937, GSC, ×10 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

between Monocyathida (one-walled cups) and Ajacicyathida: component granules in the former measure 1.7 × 1.1 μm, versus 4 × 3 μm in the latter (LAFUSTE & DEBRENNE, 1982; DEBRENNE, ZHURAVLEV, & ROZANOV, 1989, pl. 10,*1–4*; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, pl. 10,*1–4*).

SECONDARY SKELETON

Investing the primary skeleton of some archaeocyath cups is a later-formed secondary skeleton, termed stereoplasm by VORONIN (1963). Although observed occasionally in other suborders, it is most characteristic of the Archaeocyathina. The secondary skeleton envelops the external surface of the cup (Fig. 511, Fig. 521.2), either as a thin sheet (pellis), as thicker encrustations of the cup apex (radicatus), or otherwise protruding from the cup (buttresses) (Fig. 522). Within the cup, it infills spaces between primary skeletal elements, as bubblelike vesicles in the intervallum and/or central cavity (Fig. 521.3), or as tubular structures (tubuli) in the central cavity (Fig. 494d, Fig. 513a). There is continuity between exostructures, endostructures, and intervallar structures. Secondary skeleton is typically laminated, indicating repeated episodic accretion. It has no fixed morphology and is no longer accorded taxonomic significance.

Secondary skeleton in archaeocyaths was apparently of dual origin. On the one hand, it was initiated while the archaeocyath was still alive, forming canals similar to the crypts of *Merlia normani* KIRKPATRICK. On the other hand, while the cells responsible for this process die, early diagenesis may modify the secondary skeleton even as the organism continues to function normally in the upper part of the cup. Microstructural differences delimit the early diagenetic skeleton (REITNER & ENGESER, 1987).

LAFUSTE and DEBRENNE (1977) were the first to document the microstructure of the secondary skeleton, in *Archaeocyathus atlanticus* BILLINGS from Labrador. Like the primary skeleton, the secondary skeleton is microgranular, but finer than the former, in the

size range of 0.5–4 μm, but commonly 2–3 μm. Slight variations in microgranule size define the laminations. Additionally, rims of palisading crystallites, 0.75 × 2.0 μm in size, were identified by these authors, separating the primary and secondary skeletons of *Archaeocyathus atlanticus* BILLINGS from the same area. Less distinct palisades were observed between individual laminations of the secondary skeleton. Palisades were also present in *Archaeosycon billingsi* (WALCOTT) from the same locality (DEBRENNE & JAMES, 1981).

Vesicles are an aspect of the secondary calcareous skeleton characteristic of many sessile organisms, namely sponges, corals, rudists, bryozoans, brachiopods (e.g., *Richthofenia* KAYSER), and some cirripedes (SEILACHER & SEILACHER-DREXLER, 1986). The widespread occurrence of vesicles in cups of Archaeocyathida (Fig. 521.3) is considered to be indicative of the progressive withdrawal of the living matter toward the distal end of the cup with growth (VOLOGDIN, 1962a; ZIEGLER & RIETSCHEL, 1970), by analogy with the living *Vaceletia crypta* (VACELET), with the soft body being restricted to the uppermost millimeters of the cup (DEBRENNE & VACELET, 1984). A similar ratio of skeleton to living tissue is observed in many extant nonspiculate skeleton-bearing sponges and Mesozoic stromatoporoids (WOOD, 1987). Conversely, Ajacicyathida and Putapacyathida are generally devoid of vesicles, suggesting that the living matter occupied virtually the entire cup throughout growth in these orders (DEBRENNE, 1991).

Of the diverse functions proposed for the secondary skeleton (see DEBRENNE & ZHURAVLEV, 1992b, p. 56–57), those relating to anchoring a cup to the substrate (buttresses; GRAVESTOCK, 1983) and sealing vacated portions of a cup (vesicles) seem the best founded. The secondary skeleton also prevents the introduction of parasitic organisms and epibionts into dead parts of the skeleton, heals injuries to the skeleton, and may assist in the regulation of water flow through the skeleton. When secondary layers fill skeletal injuries, no gaps are observed between them and the
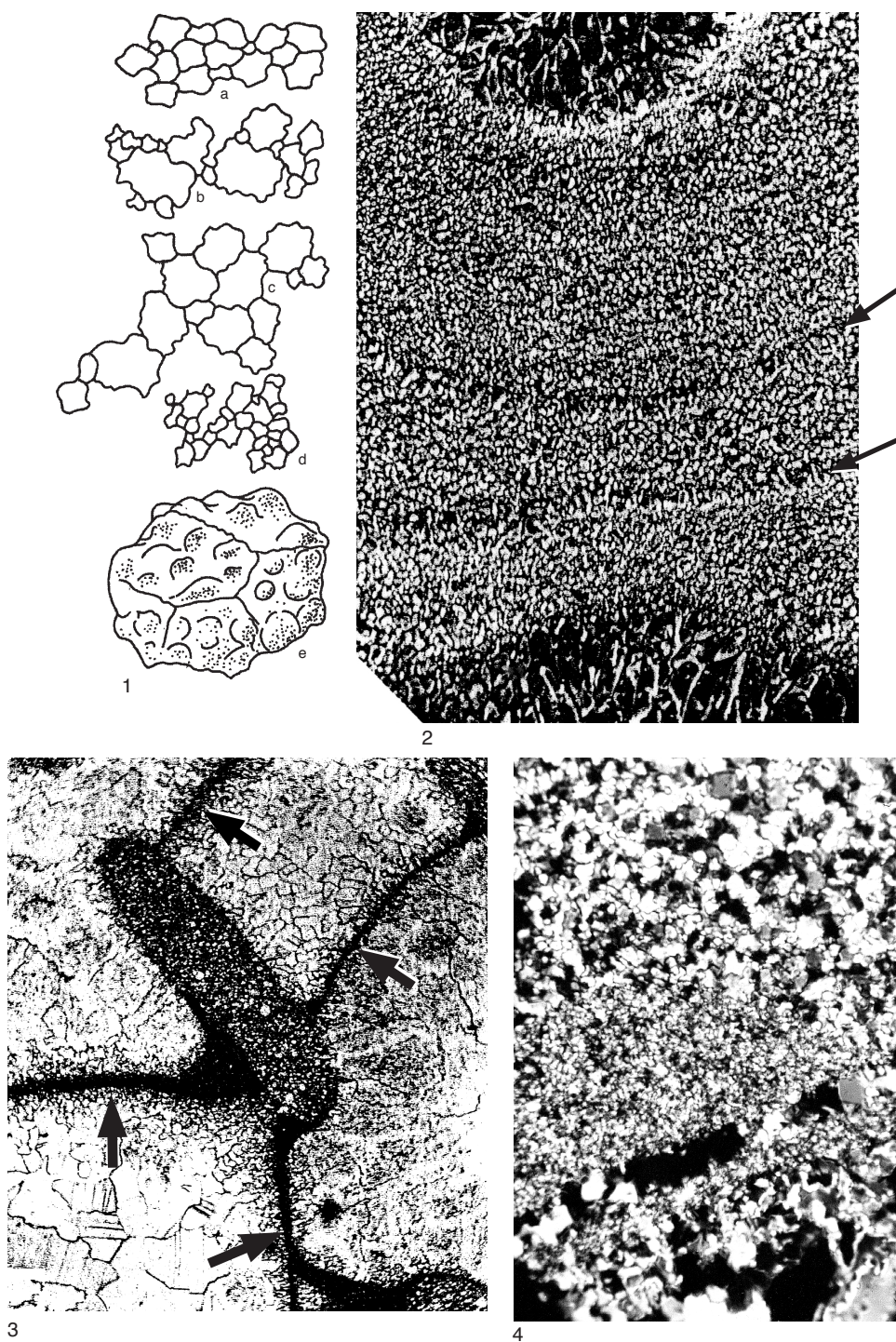
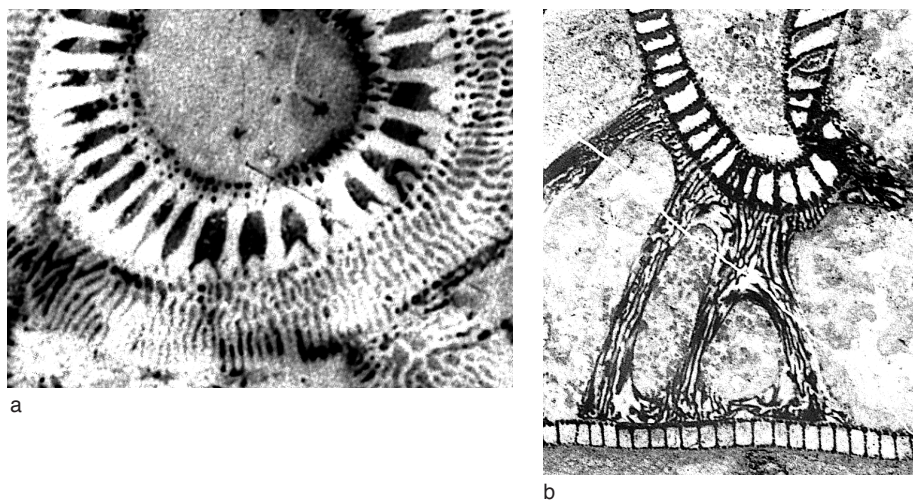FIG. 521. *(For explanation, see facing page).*

FIG. 522. Buttresses; *a,* successive development of exocyathoid and tersioid buttresses upon a *Somphocyathus coralloides* TAYLOR cup, Atdabanian, Wilkawillina Limestone, Wirrealpa, South Australia, Australia, transverse section, 86673-376, PU, ×5; *b,* tersioid buttresses upon a *Polycoscinus cymbricensis* (KRUSE) cup (top) abutting a *Coscinoptycta convoluta* (TAYLOR) cup (bottom), Botoman, White Point Conglomerate, Emu Bay, Kangaroo Island, South Australia, Australia, transverse section, M82007-9, MNHN, ×7 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

primary skeleton (DEBRENNE & ROZANOV, 1978). These functions imply facultative secretion by the host cup, and not by any foreign organism. They were evidently responsible for the development of complex exocyathoid structures. Exocyathoid structures look superficially like independent archaeocyathan cups, but their contiguity with the parent cup may be interpreted as a process of anchoring the cup on the substrate, as demonstrated by GRAVESTOCK (1983) (Fig. 522).

Putative archaeocyathan spicules (triactines, tetractines) in archaeocyaths from Atdabanian reefs of Australia, figured and discussed by REITNER (1992, p. 293, pl. 59,*1–10*; REITNER & MEHL, 1995),

were discounted as archaeocyathan by DEBRENNE and ZHURAVLEV (1992b), who emphasized that such spicules invariably occur within the secondary skeleton. In fact, any fine allochthonous material from the immediate environment may be incorporated into the archaeocyathan secondary skeleton: these authors illustrated trilobite fragments likewise trapped in this manner (DEBRENNE & ZHURAVLEV, 1992b, pl. 35,*2*) in Toyonian reefs of China to demonstrate that the so-called archaeocyathan spicules are adventitious. No undoubted spicules have been recorded from the primary skeleton of archaeocyaths. In other groups of calcified sponges,

FIG. 521. Archaeocyathan microstructure; *1a–e,* microstructure in ultrathin section, ×1700; *a, Archaeolynthus* TAYLOR; *b, Nochoroicyathus* ZHURAVLEVA (Debrenne, 1983); *c,* primary skeleton of *Archaeocyathus* BILLINGS; *d,* secondary skeleton of *Archaeocyathus* (Lafuste & Debrenne, 1977); *e,* schematic reconstruction of microgranule comprising archaeocyathan skeleton (Debrenne, 1983); *2,* primary skeletal element of a taenia (center) limited by secondary palisading tissue (*arrows*) and further invested above and below by laminae of secondary thickening (stereoplasm) with fine-grained external limit; coarsely crystalline darker areas at top and bottom are cement, *Archaeocyathus atlanticus* BILLINGS, Botoman, Forteau Formation, Mount St. Margaret, Newfoundland, Canada, SEM image of transverse section, 62107, GSC, ×200 (Debrenne & James, 1981); *3,* portions of taeniae (primary skeleton; center, top right and bottom right) invested by secondary vesicles (dark; *arrows*); cavities occluded by calcite spar mosaic (pale), *Archaeocyathus atlanticus* BILLINGS, Botoman, Forteau Formation, Taylors Gulch, Labrador, Canada, transverse section, M83136, MNHN, ×70; *4,* same, contact of coarser-crystalline primary taenia (above) and finer-crystalline secondary vesicle (below), ultrathin transverse section, ×350 (Lafuste & Debrenne, 1977).

the spicules are incorporated into the primary skeleton as they are secreted in the earliest stage of biomineralization (WENDT, 1980). The apparent absence of genuine spicules among archaeocyaths favors comparison with the Demospongiae, as Calcarea and Hexactinellida invariably possess spicules, whereas demosponges can construct a calcareous or keratose nonspiculate skeleton (e.g., *Vaceletia* PICKETT, Pacific population of *Astrosclera* LISTER, Dictyoceratida, Dendroceratida) (VACELET, 1979b).

BIOMINERALIZATION AND DIAGENESIS

The uniformity of archaeocyathan microstructures implies some measure of organic matrix-mediated mineralization (LOWENSTAM, 1981), whereby mineral nucleation and growth occur in contact with a precursor organic template (DEBRENNE & VACELET, 1984). Matrix mediation is suggested by the reactions of archaeocyathan cups in close proximity, the younger of which tend to distort in response to their encroachment upon the older; this implies an initially unmineralized growing edge. In support of this, BRASIER (1976) observed that archaeocyaths in the Wilkawillina Limestone (South Australia) were often distorted where juveniles had attached, suggesting that the disturbed portion of the organism was originally elastic. This hypothesis is preferred to the so-called biologically induced mineralization assumed by some authors (LOWENSTAM, 1981; BARSKOV, 1984), which results in component crystal habits similar to those produced by inorganic precipitation. In the case of the Archaeocyatha, the presence of embossed surfaces is in favor of organic secretion, as mineral precipitation generates only planar surfaces; the interlocking granules, despite the fact that axes have random orientation, are therefore most probably the result of an organic matrix-mediated process, albeit at a primitive stage.

Microgranular microstructures are shared by several fossil groups: cribricyaths, some calcareous algae, probable calcified cyanobacteria (*Renalcis* VOLOGDIN and others), some foraminifers, some calcified sponges and hydrocorals (FENNINGER & FLAJS, 1974; FLAJS, 1977; JONES, 1979; ROZANOV, 1979; WENDT, 1979, 1984; ROZANOV & SAYUTINA, 1982; BOYKO, 1984). In all these groups, granules differ in size and shape, being much smaller and less embossed than in archaeocyaths. No conclusions can be drawn concerning possible affinities between these groups on the basis of microstructure alone. The microgranular structure is a primitive one and may have given rise to a variety of more elaborate secretion products in the course of evolution.

Altogether, this microstructure is finer than that expected from the neomorphism of aragonite, so an original calcitic mineralogy is assumed. Comparative petrographic study of Labrador reef fabrics and faunas by JAMES and KLAPPA (1983) led these authors to conclude that archaeocyaths were probably originally of magnesium calcite composition. This conclusion is supported by the common occurrence of microdolomite inclusions in the skeleton, an increased magnesium content, synsedimentary marine epitaxial fibrous cement developed in optical continuity with skeletal elements, and less altered carbon and oxygen isotope signatures (BRASIER & others, 1994; ZHURAVLEV & WOOD, 2008).

BIOLOGY OF ARCHAEOCYATHA

INFERRED CHOANOCYTES

The presence of choanocyte chambers in archaeocyaths can only be indirectly demonstrated. BALSAM and VOGEL (1973) pioneered the empirical study of archaeocyathan functional morphology using generalized metal models in flume tanks. These authors, and subsequently ZHURAVLEV (1989, 1993) and SAVARESE (1992, 1995), concluded that the archaeocyathan cup was admirably suited to passive filtration. Due to the velocity gradient induced within the cup, water

entered the cup through the outer wall pores, passed through the intervallum, and exited via the inner wall pores and central cavity. This is the water flow direction in sponges. Hypotheses suggesting a passive ingress of water into the cup through the central cavity or intervallum and its egress through the outer wall (VOLOGDIN, 1962a; ZHURAVLEVA, 1974c) are inconsistent with the principles of hydrodynamics.

The absence of septa in sponges was one of the major arguments of OKULITCH and DE LAUBENFELS (1953) against the assignment of archaeocyaths to Porifera. However, ZIEGLER and RIETSCHEL (1970) noted that the presence of septa only means that the water flow did not stream diffusely through the soft tissue, but was channelled. This proposal has been confirmed by SAVARESE (1992), who found that his septate models did not leak fluid from the outer wall, enhancing the excurrent fluid flow through the central cavity. Thus, certain Devonian and Triassic thalamid sponges also developed septalike structures (OTT, 1974; PICKETT & RIGBY, 1983). It is thus clear why the intervallar rods of dokidocyathine archaeocyaths are arranged in regular longitudinal rows (GRAVESTOCK, 1984; DEBRENNE & ROZANOV, 1985; ZHURAVLEV, 1989) rather than arbitrarily: they form a structure which is indeed a septum with a single longitudinal row of pores.

In summary, the archaeocyathan skeleton was to some degree suited to passive filtration—although, as in extant sponges with nonspiculate skeletons, this need not exclude active filtration and, indeed, given the now established poriferan nature of the group, choanocytes are inferred to be present.

An auxiliary observation, favoring the presence of choanocyte chambers in archaeocyaths, concerns forms having an outer wall consisting of an attached microporous sheath mantling funnel-shaped pores. As in extant demosponges, only a choanocyte chamber system could prevent the blockage of such a porous structure by external particles (RIGBY & POTTER, 1986).

IMMUNE RESPONSES

Archaeocyaths display a wide range of skeletal reactions in response to the proximity of other species (BRASIER, 1976; DEBRENNE & ZHURAVLEV, 1992b, 1994; WOOD, ZHURAVLEV, & DEBRENNE, 1992) (Fig. 523). These are comparable with the allograph, autograph, and xenograph immune behaviors of demosponges (VAN DE VYVER & BUSCEMA, 1985; ILAN & LOYA, 1990). The development of archaeocyathan secondary calcareous laminations might be analogous to the formation of a collagen barrier between demosponge bodies (VAN DE VYVER & BUSCEMA, 1985).

Partial atrophy and maintenance of spatial separation due to juvenile attachment or proximity to adjacent adult cups (KRUSE, 1990a) have been recognized to be more pronounced among the Ajacicyathida than the Archaeocyathida or Kazachstanicyathida, that is, there is a spectrum of allogenic incompatibility in the class (WOOD, ZHURAVLEV, & DEBRENNE, 1992). The greater incompatibility demonstrated by the Ajacicyathida hinders mutual encrustation, and thereby greatly limits the ability of ajacicyathides to construct rigid reef framework. Conversely, allogenic reactions are minimal among the Archaeocyathida and Kazachstanicyathida, and these orders played a much greater bioconstructional role in reefs.

These inferences alone cannot be used as a definitive argument in favor of the taxonomic proximity of archaeocyaths and demosponges; data on immune responses in calcified sponges are lacking, thus precluding comparison. Furthermore, the comparison of secondary calcareous skeleton with collagen barriers can only be a working hypothesis at present. Nevertheless, it is interesting to note the similarities in interspecific interactions within the two groups.

ASEXUAL REPRODUCTION IN CHAETETID ARCHAEOCYATHS

The modularity of chaetetid archaeocyaths results from two processes: in
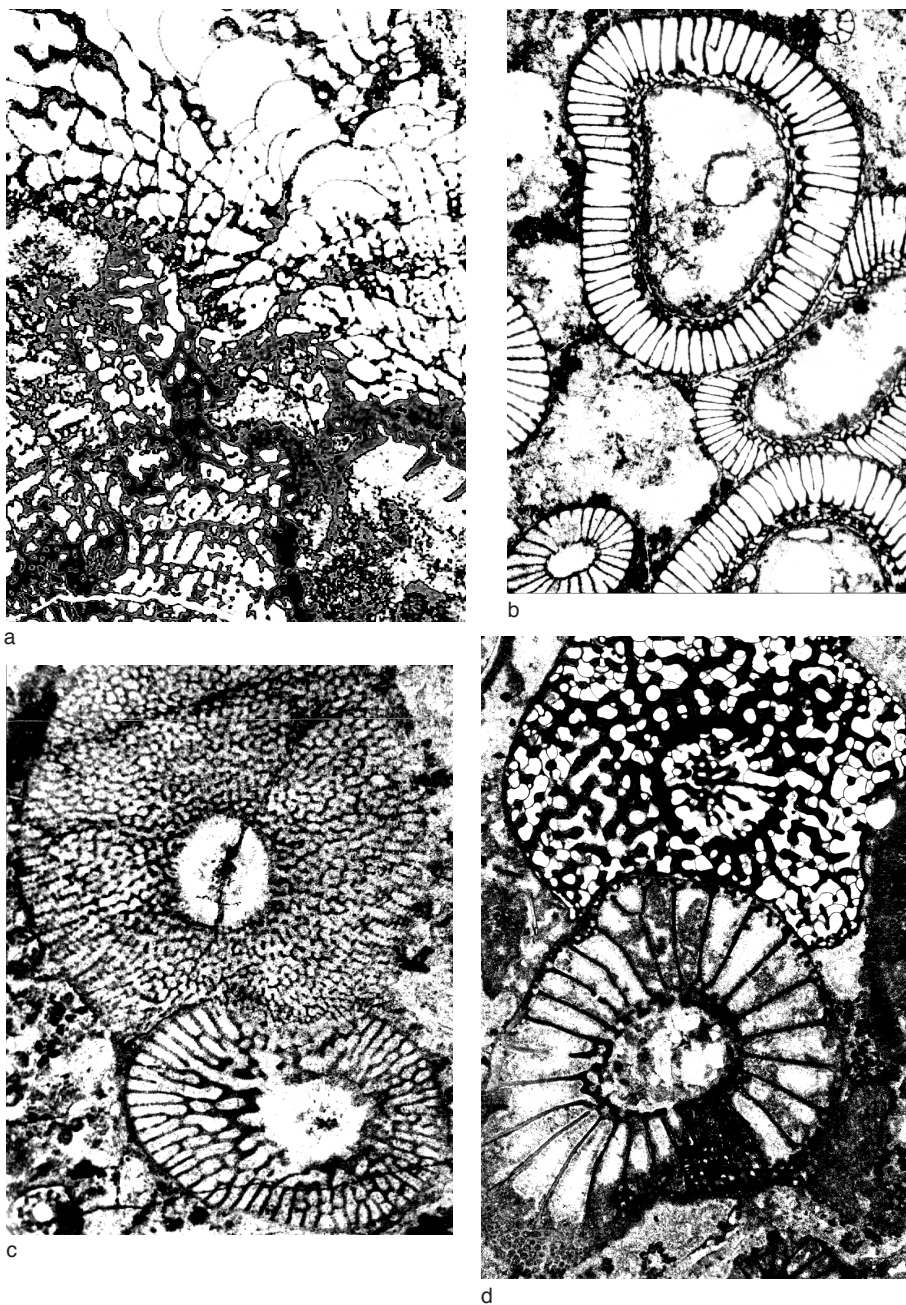
Fig. 523. Modularity and immune responses; *a,* intercalicular budding on surface of skeleton of *Gatagacyathus mansyi* Debrenne & Zhuravlev, Botoman, Poleta Formation, Mount Lida, Nevada, United States, oblique longitudinal section, M83138, MNHN, ×10 (Debrenne & Zhuravlev, 1994); *b,* interaction of modules in pseudocerioid *Sajanocyathus ussovi* Vologdin, Botoman, Verkhnemonok Formation, West Sayan, Altay Sayan, Russia, transverse section, 4451/55, PIN, ×2.7; *c,* interaction of *Keriocyathus arachnaius* Debrenne & Gangloff (Archaeocyathida; top) and *Siderocyathus duncanae* Debrenne & Gangloff (Ajacicyathida; bottom), *(Continued on facing page).*

Gatagacyathus DEBRENNE & ZHURAVLEV, by external budding evolving into a branching modular form (Fig. 523a); and in *Usloncyathus* FONIN (Fig. 510.1) and *Zunyicyathus* DEBRENNE, KRUSE, & ZHANG (Fig. 495d), by the separation of new aquiferous units within a thin sheath of soft tissue covering the skeleton (DEBRENNE & ZHURAVLEV, 1994). In chaetetid sponges, two similar budding modes have been noted by WEST and CLARK (1983): calicular longitudinal fission and addition of new calicles at the periphery. A third mode of asexual reproduction is observed in most chaetetid archaeocyaths: the arising of small buds connected with a single calicle. The cavity of the parent calicle extends into the atrium of the offspring bud and the parent calicle's facets become the bud's inner wall, as in *Zunyicyathus grandis* (YUAN & ZHANG), *Gatagacyathus mansyi* DEBRENNE & ZHURAVLEV, *Usloncyathus araneosus* (GRAVESTOCK), *U. obtusus* (GRAVESTOCK), and *Zunyicyathus pianovskajae* (ZHURAVLEVA) (ZHURAVLEVA & others, 1970, p. 45; DEBRENNE, KRUSE, & ZHANG, 1991; DEBRENNE & ZHURAVLEV, 1994). This process may correspond to the intercalicular budding of WEST and CLARK (1983). In living chaetetid demosponges, peculiar buds are connected with certain calicles (VACELET, 1991; VACELET & others, 1992). These buds are spectacular in *Acanthochaetetes wellsi* HARTMAN & GOREAU (REITNER, 1991a; WOOD, 1991a). A similarity in skeletal structure of chaetetid archaeocyaths and chaetetid demosponges, together with an even greater similarity in the nature of their budding, suggests the presence of crypt cells in some archaeocyaths.

SYMBIONTS

Microscopic ovoid and rodlike bodies, 0.25 mm in diameter, observed in samples from early Cambrian reefs of Sardinia, were interpreted by CAMOIN, DEBRENNE, and GANDIN (1989) as bacteria and bacterial aggregates. They occur within all three major components of these bioconstructions: archaeocyaths, calcimicrobes, and sediment. As bacteria, they have been considered responsible for the precipitation of the micritic sedimentary matrix (BURNE & MOORE, 1987), as well as participating in the calcification of archaeocyathan skeleton. Within archaeocyathan skeletons, the putative bacteria are generally clustered, but within interskeletal spaces (pores or loculi) cemented by calcite spar, they are generally isolated and only rarely clustered.

The observation of putative bacteria within the skeletal elements of archaeocyaths might suggest a symbiotic relationship similar to that practiced by many extant sponges (VACELET, 1975). However, precise studies by SURGE and others (1997) of carbon stable isotope ratios in archaeocyathan skeletons collected from shallow-water and deep-water bioherms in the Ajax Limestone (South Australia) showed no significant variation in isotope ratio within either category of bioherm, but they did reveal a significant difference between shallow and deep samples. The observed difference parallels the upward increase in $\delta^{13}C$ in present oceans. These authors concluded that the archaeocyathan skeleton was precipitated in equilibrium with seawater and that archaeocyaths therefore did not possess photosymbionts. This need not preclude the presence of chemotrophic or heterotrophic symbionts.

Evidence for the presence of photosymbionts is necessarily indirect: the so-called thin-tissue syndrome and the lack of correlation between archaeocyathan abundance and high nutrient supply, as indicated, for example, by phosphate-enriched strata (COWEN, 1988;

FIG. 523. *(Continued from facing page).*
Botoman, Valmy Formation, Iron Canyon, Nevada, United States, transverse section, collection number not known, UCMP, ×6.8; *d,* interaction of *Archaeocyathus* sp. (Archaeocyathida; top) and *Tegerocyathus edelsteini* (VOLOGDIN) (Ajacicyathida; bottom), Toyonian, Torgashino Formation, East Sayan, Altay Sayan, Russia, transverse section, 4451/73, PIN, ×4.5 (Debrenne & Zhuravlev, 1992b; ©Publications Scientifiques du Muséum national d'Histoire naturelle, Paris).

ROWLAND & GANGLOFF, 1988; TALENT, 1988; ROWLAND & SHAPIRO, 2002; cf. WOOD, ZHURAVLEV, & DEBRENNE, 1992; WOOD, 1995, 1999). Many archaeocyaths did possess a large skeletal surface area mantled by a thin veneer of soft matter amenable to photosymbionts. However, such forms tended to be mud dwellers favoring turbid waters, presumably inimical to photosymbionts (ZHURAVLEVA, 1972a; KRUSE, ZHURAVLEV, & JAMES, 1995; ZHURAVLEV, 2001c). Similarly, the plot of archaeocyathan generic diversity through time matches that of phosphatic-shelled genera (lingulates+tommotiids+mobergellans+protoconodonts), suggesting that there is indeed a positive correlation between archaeocyathan diversity and phosphate input (ZHURAVLEV, 2001b).

SYSTEMATICS OF ARCHAEOCYATHA

HISTORY OF CLASSIFICATION

The first major step in archaeocyathan studies was by BORNEMANN (1884, 1886, 1891a, 1891b). In contrast to North American discoveries up to that time, the material he collected in Sardinia from 1868 onward was plentiful and well preserved. BORNEMANN distinguished most of the fundamental skeletal elements. His interpretations of their nature and significance in some ways foreshadowed modern concepts (longitudinal radial partitions, now Ajacicyathina; horizontal partitions, now Coscinocyathina; vegetative stages as the basis of different Archaeocyathina), which are the basis of the present systematics (DEBRENNE, 1996, p. 35). Importantly, he recognized the distinctiveness of the group in creating a separate class, Archaeocyathinae, ostensibly allied to sponges and cnidarians (BORNEMANN, 1884).

TAYLOR (1910) was the first to organize genera into families to create the beginnings of an archaeocyath systematics. These families were based on differences in intervallar structures, now the basis for subordinal categories, such as Dokidocyathina (his Dictyocyathidae), Ajacicyathina (Archaeocy-

athidae), Archaeocyathina (Spirocyathidae), Syringocnemina (Syringocnemidae), and Coscinocyathina (Coscinocyathidae).

Subsequently, archaeocyathan systematics were strongly influenced by OKULITCH (1935b, 1943), VOLOGDIN (1936, 1937b, 1940a, 1940b), and the BEDFORDS (R. BEDFORD & W. R. BEDFORD, 1934, 1936; R. BEDFORD & J. BEDFORD, 1936, 1937, 1939). Archaeocyaths were recognized as a subphylum of the Porifera and divided into classes Regulares and Irregulares, based on differences in skeletal ontogeny. Concurrently, TING (1937) and SIMON (1939) viewed the group as merely a superfamily in the suborder Tetracladina of siliceous sponges. Their opinion derived from the observation that some Australian archaeocyaths were silicified and that *Archaeocyathus minganensis* BILLINGS had spicules. That species, however, is a true Ordovician anthaspidellid sponge, the type species of the genus *Archaeoscyphia* (HINDE, 1889). They also criticized those systematists who followed TAYLOR (1910); in their opinion, wall structures, and not intervallar structures, should form the framework for archaeocyathan systematics.

Developments up to the early 1950s were summarized by OKULITCH (1955a).

It was ZHURAVLEVA's (1960b, p. 48–51) classification that laid the basis for the modern systematics of so-called regular archaeocyaths (Monocyathida, Ajacicyathida, Tabulacyathida [=Putapacyathida, p. 1019], Capsulocyathida). She applied ontogenic principles and demonstrated from the order of appearance and complication of skeletal structures that intervallar elements had hierarchical primacy over outer wall structures that, in turn, had primacy over inner wall structures. Thus, suborders were established on intervallar features, superfamilies on outer wall features, and families on inner wall features. This scheme was further developed by DEBRENNE (1964, p. 112–117), HILL (1965, p. 46–49; 1972, p. 50–103) and ROZANOV (1973, p. 85–86). Only KRASNOPEEVA (1953, 1978) persisted with systematics in the style of TING, while KONYUSHKOV

(1978) attempted to construct a system based on purely theoretical ideas concerning the integration of soft tissue in various archaeocyathan groups. ROZANOV (1973) introduced VAVILOV'S (1922) principle of homologous variability, which facilitated the recognition of features of equal weight in related lineages (ROZANOV & MISSARZHEVSKIY, 1966, p. 73; ROZANOV, 1973, p. 80).

The taxonomy of so-called irregular archaeocyaths (Archaeocyathida, Kazachstanicyathida) has proven more difficult, due to the abundance of secondary calcareous skeleton, which tends to obscure primary features, as well as to the lesser diversity of skeletal features in this group. At least five independent schemes have been established (see DEBRENNE & ZHURAVLEV, 1992b, tables 7–8). KRASNOPEEVA (1953, 1969, 1980) considered that all Irregulares possess intervallar tubes (class Syringoidea), whereas all one-walled archaeocyaths represented the initial stages of development of two-walled cups. ZHURAVLEVA (1960b, p. 267–315), by analogy with her Regulares scheme, distinguished among the Irregulares: one-walled cups (order Rhizacyathida), two-walled cups (Archaeocyathida), and forms with tubular intervallum (Syringocnematida). The Archaeocyathida were subdivided into forms without tabulae (Archaeocyathina) and with tabulae (Archaeosyconiina). This proposal was adopted in the *Treatise on Invertebrate Paleontology* classification of HILL (1972, p. 103–130), with the nomenclatural change of Rhizacyathida to Thalassocyathida. DEBRENNE (1970a, 1974a) employed the combination of intervallar elements and attempted to establish homologous series, as in the Regulares. Later, FONIN (1981, 1985, p. 35) and GRAVESTOCK (1984, p. 23) used skeletal ontogenetic data, but they arrived at different results.

As archaeocyaths are generally studied using thin sections, or incomplete silicified or dolomitized cups, overestimation of the taxonomic value of certain features can become inevitable. The suborders Globosocyathina and Nochoroicyathina were proposed on this basis. The former was established on oblique thin sections of Monocyathida with peltae (Fig. 507.1), whereas the latter was described from occasional thin sections intersecting pectinate tabulae. At the same time, all regular septate archaeocyaths with porous tabulae were assigned to a single suborder, Coscinocyathina, independently of skeletal ontogeny. It was subsequently demonstrated that such archaeocyaths represented at least two different groups (now suborders Erismacoscinina and Coscinocyathina of the orders Ajacicyathida and Capsulocyathida, respectively). In the ontogeny of Erismacoscinina, tabulae appeared after septa and were independent of the cup wall, whereas in the Coscinocyathina, the cup is distinguished by a thalamid architecture with later development of septa (ZHURAVLEV, 1986a). The tabula presence/absence problem in irregular taenial archaeocyaths creates even more difficulties. In some cases, as in *Metacyathellus caribouensis* (HANDFIELD) or *Pycnoidocoscinus serratus* (KAWASE & OKULITCH) as redescribed from Canada by ZHURAVLEV (in VORONOVA & others, 1987, p. 38, 40), tabulae are scarce and similar in construction to the outer wall. The chance of missing such structures in transverse thin section is therefore great, and consequently pairs of twin genera have been established, for example, *Sigmofungia-Palmericyathellus*, *Metaldetes-Metacoscinus*, and *Archaeocyathus-Claruscyathus*, the synonymy of which need to be confirmed. As well, forms with frequent tabulae do not constitute a single discrete group: in *Altaicyathus* VOLOGDIN, cup development begins with a spherical chamber with pillars, while in *Korovinella* RADUGIN, it begins with a one-walled cup with tabula, differences that substantiate the distinction of Kazachstanicyathina and Altaicyathina. On the other hand, in *Paracoscinus* R. BEDFORD & W. R. BEDFORD and similar forms, tabulae appear later than the other intervallar elements, and cup development is similar to that in typical Archaeocyathida and comparable with that in Ajacicyathida.

A further problem is the interpretation of juvenile taenial archaeocyaths. For example, HILL (1972, p. 131–132) doubted the reality of *Rhizacyathus* R. BEDFORD & J. BEDFORD as an independent genus, whereas GRAVESTOCK (1984, p. 40) demonstrated from Australian material that many one-walled or even two-walled irregular cups were juveniles of various genera of Irregulares. Indeed, while mature one-walled regular archaeocyaths are readily distinguishable from one-walled juvenile stages of two-walled regular species, all described one-walled, and even some two-walled irregular archaeocyaths, are identical in size and morphology to the initial stages of the Irregulares present in the same locality.

All these inconsistencies were recognized during a major revision of the archaeocyaths by DEBRENNE, ZHURAVLEV, and ROZANOV (1989; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990; DEBRENNE & ZHURAVLEV, 1992b), which allowed these authors to compile a completely new systematics for irregular archaeocyaths and to significantly rework the systematics of regular archaeocyaths. Their scheme is adopted here with further modification. Their revision has led to the rejection of the customary subdivision of archaeocyaths into (sub)classes Regulares and Irregulares, now superseded by six orders, based on structural differences and skeletal ontogeny: Monocyathida, Ajacicyathida, Putapacyathida, Capsulocyathida, Archaeocyathida, and Kazachstanicyathida. The two most diverse orders are Ajacicyathida and Archaeocyathida, approximately corresponding to the former subdivision into Regulares and Irregulares, respectively.

CURRENT PRINCIPLES OF CLASSIFICATION

The present archaeocyathan systematics are based on three principal datasets: (1) skeletal ontogeny; (2) morphological functional analysis; and (3) limits of homologous variability. The ontogenetic observations allow the determination of the order of appearance of skeletal elements and of stabilization of adult features, and thence, in accordance with principles of heterochrony, the use of these data for the establishment of the taxonomic hierarchy. Morphological functional analysis, coupled with paleoecological observations, provides the basis for the discrimination of genotypic from phenotypic features. Finally, knowledge of the series of homologous variability allows us to establish those features of equal taxonomic weight in different evolutionary lineages, and even to forecast the features of taxa that could conceivably exist. Data on skeletal microstructure and paleogeographic and stratigraphic distribution are consistent with the systematics derived on the three above-mentioned criteria.

Skeletal Ontogeny

Archaeocyathan skeletons preserve much information on the ontogeny of individual species. As ontogenetic patterns are recapitulated in the stratigraphic distribution of related species and genera, their significance is assured. The intensive study of archaeocyathan skeletal ontogeny commenced as early as BORNEMANN (1886) and was continued by TAYLOR (1910, p. 82), the BEDFORDS (R. BEDFORD & W. R. BEDFORD, 1934, 1936; R. BEDFORD & J. BEDFORD, 1936, 1937, 1939), OKULITCH (1935b, 1943, p. 32), VOLOGDIN (1957a, 1959b) and especially by ZHURAVLEVA (1960b, p. 40) and ROZANOV (1973, p. 27). These data were summarized and supplemented by significant new observations, especially on Capsulocyathida, Archaeocyathida, and Kazachstanicyathida, by DEBRENNE, ZHURAVLEV, and ROZANOV (1989, p. 80; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 65; DEBRENNE & ZHURAVLEV, 1992b, p. 76). The following generalizations are applicable to archaeocyathan skeletal ontogeny.

1. There are three major types of skeletal ontogeny among two-walled archaeocyaths:

a. The septal type begins with a juvenile conical cup resembling one-walled archaeocyaths (Monocyathida) and proceeds via the initial development of a centripetal inner wall, open below the lowermost rods

of the septa supporting it, and by the initial parts of the septa, irrespective of their adult morphology, bearing a single longitudinal row of pores. The septal type is restricted to the orders Ajacicyathida and Archaeocyathida. In succeeding ontogeny, the distinction between these two orders appears: multiporous septa begin to develop in ajacicyathides, but multiporous taeniae in archaeocyathides. The initial multiporous septa in the ajacicyathide suborders Ajacicyathina and Erismacoscinina are always retiform. Archaeocyathide taeniae can persist until maturity or evolve into pseudosepta (as in Loculicyathina and Anthomorphina), into a pseudotaenial or dictyonal network (Archaeocyathina), or into calicles (Dictyofavina). In turn, calicles can be reorganized into syringes (Syringocnemina).

b. The second type of skeletal ontogeny is the thalamid type, in which the juvenile cup is subspherical in shape, the inner wall is of invaginal type and is a continuation of the outer wall, and the inner wall is closed at the base. Such juvenile cups characterize the order Capsulocyathida.

c. The Kazachstanicyathida have their own distinctive type of ontogeny: initial chambers are empty (Kazachstanicyathina) or contain pillars (Altaicyathina), and the entire skeletal ontogeny is limited to the successive accretion of similar chambers.

The nature of cup ontogeny in the order Putapacyathida is still uncertain.

2. The relative rapidity of stabilization of outer wall features was greater than for other skeletal elements. In late Atdabanian and Botoman forms, the outer wall could acquire the characteristic structures of a given species even at the one-walled stage in Ajacicyathina, before the appearance of tabulae in Erismacoscinina, and before the appearance of septa in Coscinocyathina.

Characteristics of first-order intervallar elements (septa, plate, and segmented tabulae) are established earlier than those of the inner wall. Exceptionally, in forms with aporose septa and a complex outer wall,

mostly of late Atdabanian and Botoman age, the sequence is reversed due to heterochrony.

Overall, stabilization of cup features thus occurred in the following sequence: outer wall—intervallar elements of the first order—inner wall.

Intervallar elements of the second order (pectinate and membrane tabulae, synapticulae, and spines) could appear at any stage after the initiation of development of the first-order intervallar elements, this varying even in different individuals of the same species. Pectinate tabulae could appear after all other elements had acquired the features characteristic of species.

The shapes of cup elements (pore outlines, additional elements on the inner wall) typical of a given species of Ajacicyathida or Capsulocyathida were stabilized earlier than the size of those elements.

Spines or bracts always preceded fused bracts, scales, annuli, or canals developed on the inner wall in adult forms (ROZANOV, 1973; GRAVESTOCK, 1984; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 67–74).

3. The secondary calcareous skeleton, as well as traces of the aquiferous system (astrorhizae, exaules, tubuli), could appear irregularly at any stage of development but always after the primary calcareous skeleton.

These morphogenetic observations suggest that, on the basis of architecture, archaeocyaths can be subdivided into the presently accepted six orders. Aspects of intervallar development allow further division into the twelve aforementioned suborders. As the order of stabilization of cup elements during ontogeny suggests the primacy of outer wall features over inner wall features, outer wall structure defines the superfamily level, and inner wall structure defines the family level.

Functional Morphology

BALSAM and VOGEL (1973) pioneered the empirical study of archaeocyathan functional morphology using generalized metal models of the archaeocyathan skeleton in flume tanks. They concluded that the porous,

upright skeleton was admirably suited to passive filtration in ambient flow and that water must enter the cup through the outer wall pores, pass to the central cavity via the inner wall pores, and ultimately exit the osculum at the top of the central cavity. Further research on fossil material (ZHURAVLEV, 1989, 1993; DEBRENNE & ZHURAVLEV, 1992b, p. 96, 1994, 1996; WOOD, ZHURAVLEV, & DEBRENNE, 1992; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; ZHURAVLEV & WOOD, 1995) and with models (SIGNOR, SAVARESE, & DENNY, 1989; SAVARESE, 1992, 1995) has focused on the significance of specific skeletal elements in archaeocyathan functional morphology.

These results have led to the synonymy of many species, genera, and higher taxa, which were found to reflect phenotypic variations only. The two former major archaeocyathan subdivisions, the classes Regulares and Irregulares, were rejected as they proved to represent two generalized archaeocyathan adaptations only. It has been postulated that the majority of the former regular archaeocyaths (Monocyathida and Ajacicyathida) were adapted mainly to soft, shifting substrates and low ambient energy (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; DEBRENNE & ZHURAVLEV, 1996) and/or turbidity (ZHURAVLEV, 1999a). Ajacicyathide cups were relatively material-efficient structures (SIGNOR, SAVARESE, & DENNY, 1989) and so facilitated more rapid growth. In contrast, the bulk of former irregular archaeocyaths (Archaeocyathida) were presumably restricted to lithified substrates and high ambient energy (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; RIDING & ZHURAVLEV, 1995; DEBRENNE & ZHURAVLEV, 1996). According to ZHURAVLEV and WOOD (1995), the two thalamid orders (Capsulocyathida and Kazachstanicyathida) were, with few exceptions, obligate cryptobionts. Together with ontogenetic data that indicate closer relationships between Monocyathida, Ajacicy-

athida, and Archaeocyathida, a subdivision according to adaptive strategies does not permit a Regulares-Irregulares distinction.

The archaeocyathine adaptation to lithified substrates and high ambient energy prompted strong development of the secondary calcareous skeleton in order to anchor the cup. Aspects of the secondary skeleton that served this function, such as an elaborated radicatus, secondary thickenings, and buttresses, were in the past overstated as criteria for the establishment of genera (e.g., *Retecyathus* VOLOGDIN, a junior synonym of *Archaeocyathus* BILLINGS with less developed secondary thickenings) and even orders (e.g., Somphocyathida, established for Ajacicyathida with buttresses). In addition, observations show that secondary calcareous skeleton served to cicatrize damaged skeleton, isolate extraneous bodies on the growing surface, seal off abandoned parts of the cup, and protect from neighboring organisms (DEBRENNE & ZHURAVLEV, 1992b, p. 62).

On a smaller scale, features such as cup shape, modularity, septal and tabular porosity, orientation of inner wall elements, presence of synapticulae and pectinate tabulae, number of wall pores per intersept, development of double inner walls, and stirrup pores were analyzed in order to clarify their systematic significance as generic criteria.

Among these, platelike cup shape and outer wall transverse bulging were found to lack generic significance, as the first relates to substrate softness, and the second depends on the degree of development of segmented tabulae. Nevertheless, the mutual longitudinal (e.g., *Orbiasterocyathus* ZHURAVLEVA) or transverse folding of both walls (e.g., *Orbicyathus* VOLOGDIN) warrants generic status, as this generates two cup shapes that maintain a constant locular volume during growth and thus maintain the outer-inner wall pore area ratio. In some genera, this ratio may be regulated by the development of longitudinal outer wall plication (as, for example, in *Rozanovicoscinus* DEBRENNE).

In contrast, outer wall transverse bulging (as in *Batschykicyathus* ZHURAVLEV) did not maintain this ratio. A thalamid wall, however, which is also expressed in outer and inner wall bulging, does not represent a single feature and must be treated together with the entire set of features of the thalamid architecture.

As modular organization confers many ecological advantages in reef-building settings, such as indeterminate growth leading to larger size, greater powers of regeneration, and the ability to encrust and gain secure attachment to substrates, modularity was one of the main pathways of archaeocyathan evolution (WOOD, ZHURAVLEV, & DEBRENNE, 1992). As such, it developed independently and repeatedly in all major archaeocyathan lineages (suborders). Some atypical budding types, such as intercalicular budding, suggest close affinities between archaeocyaths and demosponges (DEBRENNE & ZHURAVLEV, 1994). Although certain types of modular organization and development are restricted to particular archaeocyathan suborders, the same features are widespread among other sponges and even other sessile animals. Consequently, only species can be defined with certainty by this feature.

Archaeocyathan models must be treated with caution as they do not take account of soft tissue mantling the skeleton. Nonetheless, such models provide some constraints on functional morphology. Thus, flume experiments with archaeocyathan skeletal models predict that archaeocyaths with completely porous septa would filter more effectively under low current speeds, while those with aporose septa would be advantaged under high free-stream velocities (SAVARESE, 1992). Such a conclusion is confirmed by ecological observations: archaeocyathan communities living in low-energy environments were dominated by individuals with porous septa (e.g., deeper facies of the Pestrotsvet Formation, Siberian Platform [ZHURAVLEV, 1986a]; upper Sellick Hill Formation, South Australia

[DEBRENNE & GRAVESTOCK, 1990]), while those that developed in high-energy environments are dominated by species with aporose septa (e.g., reef-core facies of Pestrotsvet Formation, Siberian Platform [ZHURAVLEV, 1986a]; oncoid archaeocyathan rudstone of Salaany Gol Formation, Mongolia [WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993]). The restriction of the latter to warmer waters with normal salinity (DEBRENNE & ZHURAVLEV, 1996) may also be explained by the greater filtration rates correlated with increased water temperature, as observed among extant sponges (RIISGARD, 1993). Septal porosity thus indicates two modes of adaptation: archaeocyaths possessing completely porous septa are generalists, while those with aporose septa are specialists. Septal porosity is thus a genotypic rather than a phenotypic feature and may be used as a generic criterion if all individuals of the same species consistently show the same type of septal porosity. However, the advantage of aporose septa in tall cups encountering higher ambient currents may lead to a loss of septal porosity during ontogeny. In such cases (ROZANOV, 1973, p. 38, 70; GRAVESTOCK, 1984, p. 37), this feature would have intraspecific value only. Further, in some ajacicyathines with inner walls of communicating canals, the enhanced soft tissue communication thereby provided apparently compensated for a reduction of porosity in the septa. The majority of such genera thus either lack septal pores (e.g., *Ethmophyllum* MEEK, *Stephenicyathus* ZHURAVLEV) or possess a transitional porosity varying between the porous and aporose states in different populations (e.g., *Formosocyathus* VOLOGDIN, *Irinaecyathus* ZHURAVLEVA, *Tegerocyathus* KRASNOPEEVA).

Similarly, a temperature gradient is observed in the distribution of genera possessing pectinate tabulae, which are restricted to warmer waters, whereas synapticulate genera are more eurythermic (ZHURAVLEVA, 1981; DEBRENNE & ZHURAVLEV, 1996). This mutual paleogeographic substitution of synapticulae and pectinate tabulae is further confirmation of the homology of these elements, which,

while functionally interchangeable, are not completely identical. Possibly, synapticulae add some rigidity to the skeleton, as they are present only in archaeocyaths with coarsely porous septa or similar structures.

The number of pore rows per intersept is another feature that reflects the differing functions of the outer and inner walls. Thus, a general trend to (1) reduce the mutual friction between currents outflowing the intervallum; and (2) to increase the speed of the cental cavity outflow in order to avoid water recycling; would and did lead to the dominance of a uniporous interseptal state of the inner wall. Thus, among 187 genera of Ajacicyathina and Erismacoscinina listed by Debrenne, Rozanov, and Zhuravlev (1990, table 9), genera with a uniporous inner wall comprise 58% of the total. Chronologically, this ratio increased from 0% in the early Tommotian to 67% in the middle Toyonian. The transition from the multiporous interseptal state of the inner wall to the uniporous state is thus a significant functional threshold for the archaeocyathan filtration system that warrants use as a generic criterion. However, the number of pore rows per intersept of the outer wall has no effect on current inflow, and so this feature lacks generic value. For the inner wall, stirrup pores and canals were significant only if there were no additional intervening pores.

Many other features of the inner wall, such as the shape of the primary elements (annuli and canals) and the development of fused bracts and fused ethmophylloid-type canals, presumably served to increase the initial velocity of the cumulative exhalant jet. The progressive development of such structures was among the major evolutionary trends in Ajacicyathida and Coscinocyathina (Zhuravlev, 1993). However, in Archaeocyathida, whose aquiferous system was restricted to the uppermost few millimeters of the soft tissue, the same elements probably play a protective function only, and intraspecific variability in the development of spines,

bracts, and even fused bracts is observed (Debrenne & Zhuravlev, 1992b, p. 55).

Another trend is revealed by the appearance on the inner wall of various structures (spines, narrow bracts) that probably served a protective function. Their presence is the rule rather than the exception, and taxonomically, such structures, attached to otherwise simple pores, should be grouped as elements of the simple inner wall type. Subsidiary elements (spines, bracts, annuli, and microporous membranes) covering the primary elements on the central cavity side typically present a high intraspecific variability (Zhuravleva, 1960b, p. 160; Repina & others, 1964, p. 214) and could be considered of equivalent significance.

The orientation of spines and narrow bracts and the development of modified bracts, canals, scales, and annuli upon them would be expected to reduce mutual friction between currents (Zhuravlev, 1993). However, the significance, and thus the taxonomic value of the shape of these structures, is difficult to evaluate without the testing of models.

Homologous Variability

The principle of homologous (parallel) series in hereditary variability was advanced by Vavilov (1922). He proposed that the variability of related taxa is not merely an arbitrary set of traits, but a repetition of the same limited set of features. Thus, species of the one genus have similar series of variability, genera of the one family potentially contain a parallel set of species bearing the same features, and so on. The principle implies the operation of genetic constraints on morphological variability, which are shared among allied genera or families. It means that the number of possible features in a given group of organisms is limited, so that the whole set of characters of a yet undiscovered form can be predicted.

Vavilov's Principle was successfully applied to regular archaeocyathan genera by Rozanov (Rozanov & Missarzhevskiy, 1966, p. 73; Rozanov, 1973, p. 50, 1974), and the history of this application is documented by

DEBRENNE, ZHURAVLEV, and ROZANOV (1989, p. 77; DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, p. 89). Archaeocyaths provide an excellent example of VAVILOV's concept: the first of ROZANOV's tables of homologous variability (ROZANOV & MISSARZHEVSKIY, 1966, fig. 45) forecast many genera of regular archaeocyaths, which were subsequently discovered in various localities and described by different specialists. A corresponding table of homologous variability for irregular archaeocyaths was first given by DEBRENNE and ZHURAVLEV (1992b, table 5).

Homologous features include the diverse types of outer and inner walls and intervallar structures. For example, a pustular outer wall occurs in Loculicyathina, Archaeocyathina, Syringocnemina, and Putapacyathida, while a somewhat similar tumulose outer wall is known in Monocyathida, Dokidocyathina, Ajacicyathina, Erismacoscinina, and Capsulocyathina. Similarly, inner walls with scales or fused bracts are known in all suborders (except Coscinocyathina) of two-walled archaeocyaths, and so on.

Homologous series can be established through recurrences. The concept of recurrences (DEBRENNE & ZHURAVLEV, 1992b, p. 87), or repeating polymorphic sets, was introduced by MEYEN (1988) under the term refrains. According to MEYEN, the existence of recurrences can be attributed to a certain inherited genotypic unity. In the case of archaeocyaths, recurrences can be represented by identical vectors corresponding to a certain order in the appearance of structures during skeletal ontogeny; for example, simple pores, then bracts, then canals on the inner wall in a set of related archaeocyathan lineages. Thus, the structures belonging to the same recurrence are homologous.

The table of homologous variability may serve as a key for the determination of genera, as a prognosis of taxa that may conceivably exist and as a basis for the estimation of the systematic value of a character. This does not mean that every empty cell of the table will eventually be occupied, but that any new form found and described will be accommodated within such a table. Such consistency permits the construction of taxonomic keys (KERNER, VIGNES LEBBE, & DEBRENNE, 2011).

Innovations in Archaeocyathan Taxonomy

Archaeocyathan taxonomy (see Archaeocyatha systematics descriptions, p. 923–1084) takes account of developments up to and including the most recent revision, that of DEBRENNE, ZHURAVLEV, and KRUSE (2002). Two significant taxonomic innovations are additionally introduced here.

Role of supplementary wall features.— DEBRENNE, ZHURAVLEV, and KRUSE (2002) introduced the concept of supplementary features in walls comprising a combination of different wall types. These authors applied it mainly among ajacicyathine genera bearing walls with canals, most notably the Ethmocyathidae (inner wall with noncommunicating canals) and Sajanocyathidae (inner wall with communicating canals) among the Bronchocyathoidea (outer wall with simple pores), and the Ethmophylloidea (outer wall with canals). Studies of several of these genera had disclosed that some taxa did not possess straight or V-shaped canals as commonly described, but in fact bore a combination of straight canals with terminal bracts. These bracts were termed supplementary by DEBRENNE, ZHURAVLEV, and KRUSE (2002).

In the systematic descriptions of the Archaeocyatha (p. 923–1084), this concept is extended consistently to combination walls of all types, not only those with component bracts. In any wall comprising two different wall types, the fundamental wall type is the element adjacent to the intervallum, whereas the supplementary wall type is the constituent facing the exterior (on outer walls) or the central cavity (on inner walls). The fundamental wall type remains the family-level criterion; the supplementary elements are of genus-level significance only.

The major outcomes of this innovation are the following.

1. In Ajacicyathina, synonymy of Hupecyathelloidea (outer wall with canals and independent microporous sheath) with Ethmophylloidea, the independent microporous sheath of the former is now treated as supplementary. Hupecyathellidae becomes a junior subjective synonym of Carinacyathidae.

2. In Erismacoscinina, synonymy of Lunulacyathoidea (outer wall with spinose screen and bracts or scales) with Polycoscinoidea (outer wall with attached microporous sheath), the bracts or scales of the former are now treated as supplementary. Lunulacyathidae becomes a junior subjective synonym of Polycoscinidae.

3. In Erismacoscinina, synonymy of Schumnyicyathoidea (outer wall with noncommunicating canals and attached microporous sheath) with Porocoscinoidea (outer wall with noncommunicating canals), the attached microporous sheath of the former is now treated as supplementary. Schumnyicyathidae becomes a junior subjective synonym of Tatijanaecyathidae.

Tabulacyathida versus Putapacyathida.— VOLOGDIN (1956) erected the order Tabulocyathida (subsequently corrected by HILL [1972] to Tabulacyathida) based on his tabulate, nonseptate genus *Tabulacyathus* VOLOGDIN, 1932. Subsequently, DEBRENNE, ZHURAVLEV and ROZANOV (1989); DEBRENNE, ROZANOV, and ZHURAVLEV (1990); and DEBRENNE (1991) retained Tabulacyathina as a suborder within the Ajacicyathida. The taxon was restored to ordinal status by DEBRENNE, ZHURAVLEV, and KRUSE (2002).

Regrettably, in erecting the nominate genus *Tabulacyathus* and its type species *T. taylori,* VOLOGDIN (1932, p. 30–33, fig. 24 and pl. 7,*3*) figured two specimens in the type series of *T. taylori* but failed to designate either as holotype. Furthermore, as subsequently established by ZHURAVLEVA, KONYUSHKOV, and ROZANOV (1964, p. 124–126), the two specimens figured by VOLOGDIN (1932) were of different taxa. These authors designated the specimen figured by VOLOGDIN (1932, fig. 24) with a tabular outer wall as "holotype"

(i.e., lectotype, in accordance with Article 74 of the International Code of Zoological Nomenclature, ICZN, 1999), and KONYUSHKOV (in ZHURAVLEVA, KONYUSHKOV, & ROZANOV, 1964, p. 102–104) assigned the second specimen (with plate tabulae between independent walls) to his new genus and species *Galinaecyathus lebedensis.*

DEBRENNE, ZHURAVLEV, and ROZANOV (1989, p. 67–68) and DEBRENNE, ROZANOV, and ZHURAVLEV (1990, p. 94) reported that the designated lectotype of *T. taylori* is "more or less" similar to *Altaicyathus notabilis* VOLOGDIN (1932, p. 27), described from the same locality in the same publication. If the identification of these two species were to be accepted, *Tabulacyathus* and Tabulacyathidae should be transferred to Altaicyathina and synonymized with *Altaicyathus* and Altaicyathidae, respectively. Hence, on the basis of page precedence and a claimed better accord with the original generic diagnosis, these authors invalidly argued for the lectotype designation to be reversed and diagnosed their Tabulacyathina accordingly.

From examination of the type material of *T. taylori* in 1990, A. YU. ZHURAVLEV concludes that the lectotype could represent any of several similar taxa. Consequently, *Tabulacyathus* (together with its derivatives Tabulacyathidae and Tabulacyathida) is here removed from the order formerly named Tabulacyathida and treated as a *nomen dubium.*

The ordinal taxon Putapacyathida VOLOGDIN (1961) now embraces the remaining genera formerly united in Tabulacyathida.

EVOLUTIONARY TRENDS

The major temporal trends in archaeocyathan evolution were: (1) oligomerization (increase in size of outer wall pores within fixed limits)—compensation (formation of microporous sheaths, thus decreasing pore sizes)—renewed oligomerization (ROZANOV, 1973, p. 62); (2) increased modularity (WOOD, ZHURAVLEV, & DEBRENNE, 1992); (3) reduction of septal porosity (GRAVESTOCK,

1984; Wood, Zhuravlev, & Debrenne, 1992); (4) development of annular and oblique upwardly projecting structures on the inner wall (Zhuravlev, 1993); and (5) transition from a multiporous interseptal state of the inner wall to a uniporous state. These are all consistent with the evolution of archaeocyaths as filter feeders (Zhuravlev, 1989, 1993; Savarese, 1992).

BIOSTRATIGRAPHY

The first archaeocyathan zonation was proposed by Vologdin (1940b, 1957a, 1957b, 1961), based mainly on faunas of the Altay Sayan Fold Belt of Siberia. Unfortunately, his schemes were supported neither by evolutionary patterns within the group nor by an accurate lithostratigraphy.

The archaeocyathan zonation of Zhuravleva (1960b), based on the relatively continuous lower Cambrian sections of the Siberian Platform, was honed by Zhuravleva, Korshunov, and Rozanov (1969); Rozanov and others (1969); and Varlamov and others (1984) to form the basis of the current archaeocyathan zonation for Siberia. This comprehensive scheme, and its associated stages, are the only ones officially approved in the former USSR and now in Russia (Spizharskiy & others, 1983; Spizharski & others, 1986; Astashkin & others, 1991). The scheme comprises four lower Cambrian stages, in ascending order: Tommotian (with three archaeocyath zones), Atdabanian (four zones), Botoman (one zone at the base), and Toyonian (one medial zone).

Tommotian

Tom.1. *Nochoroicyathus sunnaginicus* Zone
Tom.2. lower *Dokidocyathus regularis* Zone
Tom.3. upper *Dokidocyathus regularis* Zone
Tom.4. *Dokidocyathus lenaicus–Tumuliolynthus primigenius* Zone

Atdabanian

Atd.1. *Retecoscinus zegebarti* Zone
Atd.2. *Carinacyathus pinus* Zone
Atd.3. *Nochoroicyathus kokoulini* Zone
Atd.4. *Fansycyathus lermontovae* Zone

Botoman

Bot.1. *Carinacyathus squamosus–Botomocyathus zelenovi* Zone
Bot.2. unzoned
Bot.3. unzoned

Toyonian

Toy.1. unzoned
Toy.2. beds with *Irinaecyathus grandiperforatus*
Toy.3. unzoned

This Siberian Platform zonation is supplemented by archaeocyathan zonations developed for other regions of the former USSR in accordance with the then prevailing national stratigraphic rules. Such local zones (lonas) were established for the Russian Far East and Altay Sayan, so that the Botoman and Toyonian stages each have three zones (Repina & others, 1964; Zhuravleva, Repina, & Khomentovskiy, 1967; Borodina & others, 1973; Okuneva & Repina, 1973; Belyaeva & others, 1975; Osadchaya & others, 1979; Belyaeva, 1988; Astashkin & others, 1995).

The composite Siberian scheme does not take account of evolutionary events within monophyletic lineages of the group, or even of the complete stratigraphic ranges of constituent taxa. Its component zones are Oppel zones *sensu* Hedberg (1976), that provide convenient, relatively rich fossil assemblages that are easily traceable between sections. Some zone boundaries were subsequently recognized as markers of significant evolutionary events within the group (Rozanov, 1973). Thus, for example, the base of the first Atdabanian zone represents the mass appearance of archaeocyaths with complex walls, and the base of the first Botoman zone was thought to mark the rise of a variety of advanced wall types (e.g., attached microporous sheaths on the outer wall, communicating canals on the inner wall). Some of these proposals were subsequently confirmed, whereas others were not. Nevertheless, by default, the Siberian scheme became the reference zonation for determining the ages of faunas in other regions of the globe up to the 1980s. It remains the most comprehensive archaeocyathan zonation available, and the Siberian

Platform zonation is the basis for the listed age ranges of individual genera in the present Archaeocyatha, Cribricyatha, and Radiocyatha systematic sections.

In the 1980s and 1990s, early Cambrian archaeocyathan zonations based on the same approaches were proposed for other regions, namely Australia (GRAVESTOCK, 1984; ZHURAVLEV & GRAVESTOCK, 1994), Spain (PEREJÓN, 1984, 1994), North America (VORONOVA & others, 1987; MANSY, DEBRENNE, & ZHURAVLEV, 1993; MCMENAMIN, DEBRENNE, & ZHURAVLEV, 2000), Morocco (DEBRENNE & DEBRENNE, 1995), and Mongolia (ZHURAVLEV, 1998). In China, several discrete archaeocyathan assemblages are recognized (YUAN & ZHANG, 1981; YUAN & others, 2001; YANG & others, 2005).

Although archaeocyathan zonations now embrace the principal regions of archaeocyathan distribution, they are still primarily of regional use only. From the very beginning, the number of zones has exceeded their correlation potential. Interprovincial correlation is still effected at the genus level; there are no species in common between the principal areas of archaeocyathan development, namely the Siberian Platform (including Kolyma Uplift) and the bordering part of the Russian Far East (Yudoma–Maya Depression and Shevli terrane); Altay Sayan together with Mongolia and Transbaikalia; South Urals; Kazakhstan; Central-East Asia (Tajikistan, Uzbekistan, and Tarim of China); Morocco; Spain-Germany-Poland (BIAŁEK & others, 2007); France, together with southwestern Sardinia; South China; Laurentian part of present North America and Koryakia; and Australia and Antarctica with South African, Falkland Islands (STONE, THOMSON, & RUSHTON, 2012), and Argentine (GONZÁLEZ & others, 2013) allochthonous clasts.

Nevertheless, the value of archaeocyaths as index fossils remains, in that within any one region the archaeocyathan assemblages maintain the same species composition within the same lithofacies, irrespective of distance. Thus, a correlation of Australia and Antarctica, eastern and western Laurentia, or Altay Sayan and Mongolia is available at the zonal level (DEBRENNE & KRUSE, 1989; WRONA & ZHURAVLEV, 1996; ZHURAVLEV, 1998; MCMENAMIN, DEBRENNE, & ZHURAVLEV, 2000), whereas other lower Cambrian fossil groups thus far provide only a tentative correlation within these same regions (THEOKRITOFF, 1982; PALMER & REPINA, 1993; PALMER & ROWELL, 1995; LANDING & BARTOWSKI, 1996; LANDING, 1998). Furthermore, certain distinct, stratigraphically restricted archaeocyathan genera are useful for correlation of lower Botoman strata between such remote regions as Western Europe, southern China, and Australia (*Rudanulus, Porocoscinus*); as well as Altay Sayan, Mongolia, and Laurentian North America (*Krasnopeevaecyathus, Polythalamia, Claruscoscinus, Altaicyathus*); western Europe, Altay Sayan, and Australia (*Aptocyathus*); and Australia and North America (*Sigmofungia, Pseudosyringocnema*). Early Atdabanian assemblages in Morocco, western Europe, Kazakhstan, Altay Sayan, and Mongolia are characterized by *Urcyathus, Retecoscinus, Agyrekocyathus,* and *Usloncyathus*, and allied species of *Tegerocyathus, Archaeocyathus,* and *Pycnoidocyathus* are present in middle Toyonian strata worldwide. In general, at least three archaeocyathan assemblages—early Atdabanian, early Botoman, and middle Toyonian—are useful for global correlation of lower Cambrian strata (especially in conjunction with other fossil groups).

Regrettably, regional zonations are not necessarily comprehensively applicable within their own geographic ambit, due to lithofacies variation among archaeocyathan assemblages. This is illustrated particularly in the key Lena-Aldan River area of the southeastern Siberian Platform, where correlation between lithofacies has proven difficult. Whereas species composition, and even proportions of individuals, may vary little for hundreds of kilometers within the same lithofacies, correlation between adjacent lithofacies only a few kilometers apart may

be impossible. This pattern is particularly well expressed during the late Tommotian–early Atdabanian interval, where a transitional phase of especially rapid turnover is evident within reef paleocommunities. The rapidity of this reorganization was related to the dispersion of reef biota into a variety of environments from extremely shallow, agitated waters to relatively deep, calm conditions below fair-weather wave base. Eventually, such communities had no species in common. As a result, two different archaeocyathan zones were established for the base of the Atdabanian stage in the area of its type section, and correlation of these is still under debate. Thus, even similar archaeocyath genera are rare in *Dictyosycon-Khasaktia* boundstone developed in the *Leptosocyathus polyseptus* Zone, as compared to *Renalcis-Epiphyton* mudmounds of the *Retecoscinus zegebarti* Zone (ZHURAVLEVA, KORSHUNOV, & ROZANOV, 1969; VARLAMOV & others, 1984; ZHURAVLEV & NAIMARK, 2005). Other early Cambrian animal groups, for example, trilobites (PALMER, 1998; PEGEL, 2000; ÁLVARO & others, 2003), were probably similar in this respect.

Correlation difficulties are compounded in the mobile belts of the Altay Sayan and Mongolia. From the beginning, it has been suggested that archaeocyathan assemblages containing the simplest genera should be the oldest, independently of any lithofacies restriction (ROZANOV & MISSARZHEVSKIY, 1966). As a result, assemblages that include forms with attached microporous sheath, inner wall communicating canals, and other complicated cup elements have been assigned to younger horizons. Thus, for example, an assemblage of morphologically complex taxa (*Alataucyathus jaroschevitschi*, *Tabulacyathellus bidzhaensis*, *Pretiosocyathus subtilis*) from the Salaany Gol Formation of Mongolia has been treated as latest Atdabanian or even early Botoman (VORONIN & others, 1982; ASTASHKIN & others, 1995). However, subsequent analysis of Mongolian reef taxa, as well as new data on continuous sections in the Altay Sayan (Tuva,

East Sayan, Kuznetsk Alatau) and Transbaikalia, have revealed a rich species pool already present by the earliest Atdabanian stage in these regions as well (ZHURAVLEVA & others, 1997a, 1997b; OSADCHAYA & KOTEL'NIKOV, 1998; ZHURAVLEV, 1998; DYATLOVA & SYCHEVA, 1999). The aforementioned *Alataucyathus jaroschevitschi–Tabulacyathellus bidzhaensis–Pretiosocyathus subtilis* assemblage in these mobile belts has proven to be earliest Atdabanian.

It is noteworthy that taxonomic disparity among the environmentally much more heterogeneous paleocommunities of the Altay Sayan, Russian Far East, and Mongolia is greater than that among their less diverse Siberian Platform counterparts (ZHURAVLEV & NAIMARK, 2005). These regions spanned a number of different volcanic arcs (West Sayan, Altay, Far Eastern Gerbikan–Nel'kan River area), accretionary wedges, microcontinents, and seamounts (East Sayan, Kuznetsk Alatau), whereas on the Siberian Platform, reef communities occupied a relatively simple, ramplike margin of a broad, epeiric platform (SUKHOV, 1997; KHERASKOVA & others, 2003). Comparison of community and taxonomic diversity for the Siberian Platform and these mobile belts reveals that seascape heterogeneity, significantly more varied in the latter, was the underlying determinant. Thus, in the Altay Sayan and Russian Far East, different zonations were applied to lithologically different Botoman successions, such as carbonate (East Sayan, Kuznetsk Alatau), volcanic-carbonate (Tuva), and volcanic-siliciclastic-carbonate (Altay, West Sayan) (OSADCHAYA & others, 1979).

Analogous dissimilarity of archaeocyathan assemblages, even within the same basin, has also been noted in the Stansbury Basin of South Australia, where Atdabanian-Botoman archaeocyaths of Yorke Peninsula are totally different from the coeval fauna of Fleurieu Peninsula (DEBRENNE & GRAVESTOCK, 1990; ZHURAVLEV & GRAVESTOCK, 1994; GRAVESTOCK & others, 2001), and in the Ossa-Morena tectonosedimentary zone

of Iberia, where seven Ovetian (Atdabanian-?Botoman) archaeocyathan biostratigraphic zones established by Perejón (1984, 1994); and Perejón and Moreno-Eiris (2006) could, to a certain extent, represent coeval paleocommunities developing in different environments.

The influence of lithofacies needs to be taken into account also with respect to other early Cambrian fossil groups, including trilobites, acritarchs, mollusks, hyoliths, and small skeletal fossils (Zhuravlev, 1995; Palmer, 1998). Considered in isolation, any one group can provide a basis for a provisional correlation chart only. Global correlation charts based purely on archaeocyath, trilobite, or acritarch assemblages differ as a result (Debrenne & Zhuravlev, 1992b, fig. 43; Vidal, Moczydłowska, & Rudavskaya, 1995, fig. 9; Geyer & Shergold, 2000; Zhuravlev & Riding, 2001; Shergold & Geyer, 2003). Archaeocyathan assemblages are thereby commonly regarded as relatively young, whereas trilobite assemblages are assumed to be relatively old, and acritarch assemblages, significantly older. For example, some trilobite assemblages from the Holyoake Range of Antarctica have been correlated with Atdabanian assemblages of the Siberian Platform, whereas archaeocyaths from the same localities have been interpreted as Botoman (Debrenne & Zhuravlev, 1992b; Palmer & Rowell, 1995). The underlying problem is that none of these assemblages has a definite analogue on the Siberian Platform, and reliance on such broad entities as the superfamily Fallotaspidoidea or suborder Syringocnemina cannot yield precise correlation.

Robust correlation requires a synthesis of data from several fossil groups.

In the current provisional global chronostratigraphic scheme (Peng & Babcock, 2011), archaeocyaths range through the Terreneuvian Series (Stage 2) to Cambrian Series 2 (Stage 4) interval, and single species are restricted to each of Cambrian Series 3 (Guzhangian Stage) and the Furongian Series (Paibian Stage).

PALEOECOLOGY

Archaeocyaths were adapted to a narrow range of temperature, salinity, and depth, but, in concert with calcimicrobes, were among the earliest widespread metazoan reef builders.

TEMPERATURE

Archaeocyaths were stenothermal organisms, corresponding to intertropical climatic conditions (Zhuravleva, 1981; Debrenne & Courjault-Radé, 1994). Paleogeographic reconstructions indicate that the regions farthest from the paleoequator were Morocco and southern Europe to the south, and possibly Yangtze (southern China) and an enigmatic (nonconfirmed) locality in Korea to the north (Courjault-Radé, Debrenne, & Gandin, 1992, fig. 1). The Moroccan–southern European and Chinese archaeocyathan assemblages are characterized by (1) low generic diversity; (2) a predominance of morphologically simple, solitary forms with highly porous septa (*Nochoroicyathus* Zhuravleva) or additionally with plate tabulae (*Erismacoscinus* Debrenne), even during late Atdabanian–Botoman time; (3) an almost complete lack of forms with aporose septa during the Atdabanian-Botoman; (4) the absence of forms with pectinate tabulae; and (5) a prevalence of forms with synapticulae (*Afiacyathus* Voronin, *Sibirecyathus* Vologdin) (Perejón, 1984; Debrenne & Gandin, 1985; Debrenne & Jiang, 1989; Debrenne, Gandin, & Debrenne, 1993; Yang & others, 2005; Perejón & Moreno-Eiris, 2006).

SALINITY

Archaeocyaths were stenohaline organisms. Increased salinity impoverished archaeocyathan communities; only the simplest forms, with simple walls and porous septa, tolerated more saline conditions. Archaeocyaths could survive in lime muds deposited during brief salinity decreases, although not in evaporitic environments.

Such a trend has been observed on the Siberian Platform, particularly in the *Cari-*

nacyathus pinus Zone (Atdabanian). Along the Lena River, westward shallowing and associated salinity increase is accompanied by a drastic drop in species diversity and changes in the distribution of archaeocyathan skeletal features (Debrenne & Zhuravlev, 1996, fig. 1).

The same salinity intolerance is observed in South Australia in the direction of the formerly lagoonal northern Lake Torrens area (upper Andamooka Limestone), by comparison with the correlative marine Wirrealpa Limestone in the Flinders Ranges.

Siberian and Australian archaeocyathan communities inhabiting equivalent high-salinity environments comprise species of the same genera (*Nochoroicyathus* Zhuravleva) with similar morphological features (highly porous septa and spinose walls), despite the great distance separating these regions. Taxonomic similarity among archaeocyathan communities was thus dependent upon environmental as well as phylogenetic and dispersive factors.

BATHYMETRY

The depth zonation proposed by Zhurav-leva and Zelenov (1955)—cited in the revision of Part E of the *Treatise on Invertebrate Paleontology* (Hill, 1972, fig. 26) and still occasionally quoted—of archaeocyathan growth between 10 and 100 m depth is no longer accepted for normal archaeocyathan-calcimicrobial buildups. The use of calcimicrobes as depth indicators was rejected by Riding (1975) on the basis of uncertainties in both growth limits and taxonomic affinities of the claimed calcimicrobial depth indicators.

Archaeocyaths were stenobathic organisms. They lived anchored in soft substrates in intertidal to subtidal zones but probably did not occupy the subphotic zone. Their preference for shallow water is evidenced by (1) their development mainly in carbonate-dominated lithofacies; (2) their common association with ooid and bioclast limestones; (3) their association with siltstone and quartz arenite exhibiting oscillation and interference ripples and other tidal-

flat features, indicating nearshore settings; (4) their common occurrence interbedded with a variety of hemispheroidal stromatolites and oncoids (Rowland, 1981; Wood, Zhuravlev, & Chimed Tseren, 1993; Perejón & others, 2000; Hicks & Rowland, 2009; Gandin & Debrenne, 2010); and (5) the coexistence of macroboring organisms in Labrador patch reefs (James & Kobluk, 1978).

On the Siberian Platform, there is a progressive basinward disappearance and eventual termination of archaeocyaths in bioherms. In the Tommotian stage, only solitary *Archaeolynthus* Taylor and *Nochoroicyathus* Zhuravleva have been reported from the outer shelf facies (Khomentovskiy & Karlova, 1986; Pel'man & others, 1990). The Atdabanian distal assemblage was more diverse, as it reflects the general archaeocyathan diversification at that time. *Propriolynthus* Okuneva, *Batschykicyathus* Zhuravlev, *Nochoroicyathus* Zhuravleva, *Tumulocyathus* Vologdin, *Geocyathus* Zhuravleva, *Jakutocarinus* Zhuravleva, *Japhanicyathus* Korshunov, *Fansycyathus* Korshunov & Rozanov, and *Coscinocyathus* Bornemann were present, for example, in the middle Atdabanian (*Carinacyathus pinus* Zone) in the facies seaward of a carbonate barrier. But again, this assemblage was poor by comparison with the reef belt proper and deeper backreef facies; it completely lacked any modular or irregular forms. Additionally, the distal archaeocyathan assemblage was restricted mainly to biohermal cavities. Archaeocyaths were completely absent from the deepest buildups, which were stromatactis-bearing mudmounds (Zhuravlev, 2001c).

From the abundance of spicules (hexactinellide, calcarean, and heteractinide), it seems that basinward, spiculate sponges dominated over calcified sponges during the early Cambrian (Debrenne & Zhuravlev, 1996). In the Flinders Ranges of South Australia (James & Gravestock, 1990), on the Siberian Platform, and in Mongolia (Zhuravlev, 2001c; Zhuravlev & Naimark,

2005), these spicule-archaeocyath assemblages appear to be restricted to deeper water settings. Elsewhere in South Australia, isolated bioherms in the upper Sellick Hill Formation and lower Fork Tree Limestone were deposited in deep water on a mildly unstable ramp adjoining a shallow shelf (ALEXANDER & GRAVESTOCK, 1990). They contain an oligotypic fauna dominated by ajacicyathides, with extensive development of exocyathoid buttresses (DEBRENNE & GRAVESTOCK, 1990). This community appears relatively undifferentiated in comparison to the coeval shallower water community in the uppermost Kulpara Formation and lowermost Parara Limestone (ZHURAVLEV & GRAVESTOCK, 1994).

The striking characteristic of these deeper communities is the extreme development of secondary skeletal structures in practically all species. A similar behavior has been observed in the deepest bioherms of the Tommotian stage of the Siberian Platform (KRUSE, ZHURAVLEV, & JAMES, 1995), but in archaeocyathide archaeocyaths (*Dictyocyathus* BORNEMANN) only.

Toward the shallower limit of the archaeocyathan depth range, episodic erosional events can be demonstrated for archaeocyathan settings in only a few cases: the Punta Manna Member of the Nebida Formation, Sardinia (SELG, 1986; DEBRENNE, GANDIN, & PILLOLA, 1989) and the upper Tommotian portion of the Tyuser Formation, Khara-Ulakh Mountains, Siberian Platform (ZHURAVLEVA, 1966). In the latter, a distinctive archaeocyathan strategy consists of *Dictyocyathus* BORNEMANN encrusting the biohermal surface (DEBRENNE & ZHURAVLEV, 1996, fig. 2).

WATER ENERGY AND TURBIDITY

As passive filter feeders, archaeocyaths were more adapted to habitats with reduced turbulence and increased currents and nutrient supply, as are extant calcified sponges (WILKINSON & EVANS, 1989). The dominance of certain morphological features within some archaeocyathan communities might be due to local environmental conditions such as turbulence, detrital input, or volcanic ashfall (PRATT & others, 2001; ZHURAVLEV, 2001c).

Clathrate outer walls, associated with complex inner walls, have been ascribed to volcanogenic facies (e.g., Verkhnemonok Formation of West Sayan; Ust'toka unit of Dzhagdy Range, Russian Far East; Cymbric Vale Formation of New South Wales, Australia) (REPINA & others, 1964; BELYAEVA & others, 1975; KRUSE, 1982). However, where present in these facies, archaeocyaths are preserved in pure limestone. Although *Botomocyathus* ZHURAVLEVA, the most widespread clathrate genus, was typical of Siberian Platform areas where volcanic rock was totally absent, a significant input of siliciclastic and sometimes of tuffaceous particles, combined with agitated water conditions, characterized many of these areas.

Putapacyathida also show an association with volcanogenic facies (West Sayan and New South Wales) (DEBRENNE, ROZANOV, & ZHURAVLEV, 1990, table 9).

Other types of complex outer and inner walls (e.g., in *Ethmophyllum* MEEK, *Sekwicyathus* HANDFIELD, *Aulocricus* DEBRENNE, *Cordilleracyathus* HANDFIELD) were, with few exceptions, typical of Laurentia, especially throughout the Cordillera. A significant terrigenous input has been noted for most localities there (MORGAN, 1976; DEBRENNE, GANDIN, & ROWLAND, 1989; MOUNT & SIGNOR, 1992; MANSY, DEBRENNE, & ZHURAVLEV, 1993). These complex outer wall systems [downwardly oriented bract, intrapore spine(s), or V-shaped canal] could be interpreted as a resistant screen preventing the clogging of pores by terrigenous particles.

In the Achchagyy Tuoydakh–Churan profile along the Lena River, Siberia, modular forms and species with sparsely porous to aporose septa were evidently more frequent in shallower platform areas with greater current activity. In contrast, species with compound outer and inner walls were dominant eastward, in deeper environments

with gentler ambient currents. Seemingly, the compound outer wall enhanced the inhalant flow by narrowing the pore area, while complex inner walls enhanced the initial velocity of the exhalant water jet, reducing the possibility of recycling the used water (DEBRENNE & ZHURAVLEV, 1996, fig. 1).

ARCHAEOCYATHAN INTERACTIONS

Archaeocyathan skeletons display a variety of reactions in response to the proximity of other species (BRASIER, 1976; KRUSE, 1990a; DEBRENNE & ZHURAVLEV, 1992b, p. 163, 1994; WOOD, ZHURAVLEV, & DEBRENNE, 1992). These range from a simple intraspecific competition between two individuals with antagonistic rejection and atrophy of the weaker (Ajacicyathida-Ajacicyathida; Fig. 523b), to an acute rejection and resorption (Archaeocyathida-Ajacicyathida). The competitive superiority of the Archaeocyathida over the Ajacicyathida was presumably due to the former's possession of a more mobile aquiferous system (DEBRENNE & ZHURAVLEV, 1992b, p. 99), related to their morphofunctional dissimilarity in distribution of soft tissue. On contact, the archaeocyathide cup overgrew the ajacicyathide and usually completely suppressed it by ultimately obscuring it with secondary thickening (Fig. 523c–d).

Archaeocyathides were more compatible with each other in both conspecific and interspecific interactions than were other orders. Their relationships may be interpreted as mutualism. In Archaeocyathida-Archaeocyathida interactions, secondary skeletal layers were generally developed on both individuals in the immediate area of contact. Complete fusion could be achieved in the interaction of several branching units of the same archaeocyathide modular form.

The dominance of solitary forms among the Ajacicyathida is the consequence of their high degree of individualization, which is itself tied to the pattern of soft tissue distribution in the cup. Being passive filter feeders using an elaborate skeletal sieve system, ajacicyathides could presumably pump at fairly low exhalant and inhalant velocities. Consideration of similar extant sponges (REISWIG, 1971) shows that such forms were resistant to the occlusion of their incurrent system. Among the Archaeocyathida, the sealing of all basal ostia by secondary skeleton was also a response to high sedimentation rates in order to prevent sediment infiltration into the choanoderm (DEBRENNE & ZHURAVLEV, 1992b, p. 62; KRAUTTER, 1994).

Modular archaeocyathides and dendritic renalcid calcimicrobes (*Gordonophyton* KORDE, *Tubomorphophyton* KORDE) evidently outcompeted solitary ajacicyathides, but even the modular archaeocyathides were locally subdued by the renalcids. In turn, ajacicyathides, as well as their superiors, were able to outcompete chambered and tubular renalcids and stromatolite-associated noncalcified microbes (ZHURAVLEV, 2001c).

Massive modular Kazachstanicyathida were especially successful, because of the considerable flexibility of their aquiferous system (DEBRENNE & ZHURAVLEV, 1992b, pl. 38,5).

BIOCONSTRUCTION

The bioconstructional capacity of archaeocyaths has been documented in many recent works, representing all regions and spanning their appearance in the Tommotian to their virtual demise in the Toyonian (ZHURAVLEVA, 1960b, p. 59, 1966, 1972a; JAMES & KOBLUK, 1978; JAMES & KLAPPA, 1983; GANDIN & DEBRENNE, 1984, 2010; ROWLAND, 1984; ROWLAND & GANGLOFF, 1988; DEBRENNE, GANDIN, & ROWLAND, 1989; JAMES, KOBLUK, & KLAPPA, 1989; REES, PRATT, & ROWELL, 1989; JAMES & GRAVESTOCK, 1990; DEBRENNE, GANDIN, & ZHURAVLEV, 1991; KENNARD, 1991; KRUSE, 1991; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; KRUSE, ZHURAVLEV, & JAMES, 1995; RIDING & ZHURAVLEV, 1995; KRUSE & others, 1996; ZHURAVLEV, 1996, 2001c; WOOD, 1999; COPPER, 2001; PRATT & others, 2001; ROWLAND & SHAPIRO, 2002;

KIESSLING, FLÜGEL, & GOLONKA, 2003). The resultant bioconstructions (meter-scale mounds) all had the same basic plan and can be categorized into component domains occupied by associations of lime mud, archaeocyaths, renalcid calcimicrobes, and/or cement. Whereas the frame-building capacity of solitary archaeocyaths was low, modular archaeocyaths did produce genuine framework, particularly in the later early Cambrian. Additionally, both types provided substrate for the frame-building renalcids and/or cement, as well as furnishing additional opportunities for cavity development.

Calcimicrobial-archaeocyathan bioconstructions may be termed reefs *sensu lato*, but most are strictly bioherms, having topographic relief and biogenic framework, but of uncertain capacity for wave resistance. The majority probably grew in mesotrophic to mildly eutrophic waters, with the relative dominance of archaeocyaths or renalcids and other associated organisms determined by nutrient and terrigenous siliciclastic input, wave energy, sedimentation rate, and depth (WOOD, ZHURAVLEV, & DEBRENNE, 1992; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993). Sedimentologically, archaeocyathan reefs were similar to later Phanerozoic reefs in possessing synoptic relief, synsedimentary cements, and growth-framework cavities housing cryptobionts (JAMES & KLAPPA, 1983; KRUSE, ZHURAVLEV, & JAMES, 1995; ZHURAVLEV & WOOD, 1995). Among the archaeocyaths, Ajacicyathida were highly competitive, and their incompatibility often involved spatial separation between adjacent cups, preventing them from becoming good binders (DEBRENNE & ZHURAVLEV, 1992b, p. 164; WOOD, ZHURAVLEV, & DEBRENNE, 1992). Their elaborate skeletal sieve system allowed them to proliferate on mud substrates, in habitats with low turbulence and a high sedimentation rate, where the probability of pore clogging was high (WOOD, ZHURAVLEV, & DEBRENNE, 1992; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993). They populated the imme-

diate periphery and the internal cavities of reefs where calcareous mud is dominant (DEBRENNE, GANDIN, & DEBRENNE, 1993). In contrast, in Archaeocyathida and Kazachstanicyathida, the development of secondary skeleton, distal localization of living tissue, and greater integration favored modularity over individualization and hence a greater tolerance to the proximity of other species. This enhanced their bioconstructional capability as binders and bafflers (WOOD, ZHURAVLEV, & DEBRENNE, 1992). Such capacities allowed the archaeocyathides to constitute up to 99% of the total archaeocyathan population in some bioherms (DEBRENNE, GANDIN, & GANGLOFF, 1990).

Within early Cambrian reefs, the two groups engaged in competition for space, with resultant suppression of weaker individuals (DEBRENNE & ZHURAVLEV, 1992b; WOOD, ZHURAVLEV, & DEBRENNE, 1992; KRUSE, ZHURAVLEV, & JAMES, 1995; ZHURAVLEV & WOOD, 1995; ZHURAVLEV, 1996). Direct overgrowth of one organism by another led to incomplete or even pathological development of the primary skeleton, extreme production of secondary skeleton, especially along mutual contacts, and/or dwarfing or complete immuration of the weaker competitor.

Together with archaeocyaths, coralomorphs (e.g., *Cysticyathus* ZHURAVLEVA, *Hydroconus* KORDE), radiocyaths, cribricyaths, and especially renalcid calcimicrobes (e.g., *Renalcis* VOLOGDIN, *Epiphyton* BORNEMANN) were common constituents in early Cambrian reefs. Archaeocyath-coralomorph and archaeocyath-radiocyath interactions show no hierarchy. All these organisms used each other as a substrate.

Exceptionally, cribricyaths appear to have considerably disrupted archaeocyathan growth (DEBRENNE & ZHURAVLEV, 1992b, pl. 38,6), suggesting that cribricyaths facultatively behaved as parasites on archaeocyaths. This observation contradicts the view that cribricyaths may have been a type of archaeocyathan larva (ZHURAVLEVA &

OKUNEVA, 1981; BELYAEVA, 1985; BELYAEVA & ZHURAVLEVA, 1990).

The relationship between archaeocyaths and renalcid calcimicrobes was more varied. Renalcids were tiny, dendritic (*Epiphyton* BORNEMANN, *Gordonophyton* KORDE, *Tubomorphophyton* KORDE), chambered (*Chabakovia* VOLOGDIN, *Renalcis* VOLOGDIN, *Tarthinia* DROZDOVA), fanlike (*Bija* VOLOGDIN), or tubular (*Batinevia* KORDE, *Girvanella* NICHOLSON & ETHERIDGE, *Razumovskia* VOLOGDIN) calcareous organisms. Their simple morphology and common facultative occurrence in reef cavities imply that they were calcified bacteria, probably cyanobacteria (RIDING, 2001). Conversely, their distinct microgranular microstructure, typical of eukaryotes (ROZANOV & SAYUTINA, 1982), the appearance of obligate cryptobionts (ZHURAVLEV & WOOD, 1995), and the lack of vital effects on carbon isotopic values (SURGE & others, 1997) do not favor a cyanobacterial assignment.

All these factors tended to displace the ajacicyathides toward marginal, at times harsh, environments (extremely shallow, deep, agitated, or turbid).

This engendered three principal associations: modular archaeocyaths and *Gordonophyton-Tubomorphophyton* occupying optimal niches; solitary ajacicyathides and *Renalcis-Tarthinia* in intermediate locales; and skeletal and nonskeletal stromatolites in marginal settings (ZHURAVLEV, 2001c).

Branching forms (e.g., *Cambrocyathellus* ZHURAVLEVA) were mainly bafflers, whereas encrusting (e.g., *Retilamina* DEBRENNE & JAMES) and massive examples (e.g., *Korovinella* RADUGIN) were binders. Colonization by encrusting and massive archaeocyaths required a hard substrate.

Reefs were either dominantly renalcid calcimicrobial or (rarely) dominated by metazoans (ZAMARREÑO, 1977; GANDIN & DEBRENNE, 1984; SELG, 1986; STEPANOVA, 1986; DEBRENNE, GANDIN, & ROWLAND, 1989; REES, PRATT, & ROWELL, 1989; DEBRENNE & GRAVESTOCK, 1990; JAMES &

GRAVESTOCK, 1990; WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993; MORENO-EIRIS, 1994). Indeed, historically, Tommotian archaeocyaths initially invaded purely calcimicrobial reefs, which had first proliferated in the preceding basal Cambrian Nemakit–Daldynian stage.

Reefs were presumably initiated during episodes when mud input slowed or ceased, allowing localized cementation or stabilization of seafloor mud (KRUSE, ZHURAVLEV, & JAMES, 1995; RIDING & ZHURAVLEV, 1995; ROWLAND & SHAPIRO, 2002). The large monospecific domains that formed the bulk of many biohermal communities suggest that archaeocyathan larvae were of viviparous origin, as they apparently did not travel far after release. This reproductive strategy is typical of sponges and other sessile organisms subject to high disturbance (AYLING, 1980; HOPPE, 1988).

The early Cambrian reef ecosystem was largely composed of generalists and opportunistic filter- and suspension-feeders, which were dependent upon a relatively high supply of nutrients. Many reefs were dominated by only one or two archaeocyathan species, implying that these communities were the result of rapid colonization and subsequent growth from one or a few larval spat falls (WOOD, ZHURAVLEV, & CHIMED TSEREN, 1993). Such trophic organization is similar to some other Paleozoic reefs, but contrasts fundamentally with some Mesozoic and most Cenozoic (both fossil and living) reefs, which are dominated by mixo- and phototrophs adapted to low-nutrient conditions (WOOD, 1993, 1995, 1999).

ZHURAVLEV (2001c) has proposed an ecological succession for these early Cambrian reefs: (1) settlement on muddy substrate of solitary ajacicyathides tolerant of turbid conditions (pioneer stage); (2) encrusting of resulting floatstone-rudstone by modular archaeocyaths to produce framework (stabilization stage); (3) strengthening of framework by binding *Renalcis* VOLOGDIN and occupation of reef cavities by an array of monocyathides, capsulocyathides, cribricyaths, and

boring organisms (diversification stage); (4) either via intrinsic reef growth or extrinsic sea level fall, growth into the marginal peritidal or surf zone, with development of a species-impoverished, commonly monospecific, archaeocyathan community (e.g., *Protopharetra*-"*Paranacyathus*" community in the Poleta Formation at Stewart's Mill, Nevada, United States; ROWLAND & SHAPIRO, 2002). Despite their small size, a number of early Cambrian reefs represent such complete ecological successions. Others were initiated and dominated by calcimicrobes, with archaeocyaths as subordinate dwellers contributing only modestly to reef construction.

Cryptic cavities have provided archaeocyaths with a hard substate since their inception. Cavities and cavity dwellers have been described in reefs (KOBLUK & JAMES, 1979), among them a large variety of archaeocyaths, some of which are thought to have been obligate cryptobionts, e.g., thalamid forms such as *Polythalamia* DEBRENNE & WOOD (Capsulocyathida) and *Altaicyathus* VOLOGDIN (Kazachstanicyathida), and archaeocyaths of chaetetid organization, such as *Usloncyathus* FONIN (ZHURAVLEV & WOOD, 1995).

Cryptic niches are not limited to reefs. A remarkable cryptic community in the Ovetian (Atdabanian) Pedroche Formation of southern Spain comprises archaeocyaths and other cryptobionts encrusting the walls and ceilings of crevices formed during synsedimentary fracturing of Neoproterozoic andesite (VENNIN & others, 2003). These cavity dwellers additionally represent the earliest known metazoan rocky community.

It may be that archaeocyathan-calcimicrobial competitive interactions, in which dendritic renalcids were dominant, contributed to the eventual near-total elimination of archaeocyaths from the Cambrian reef biota in the Toyonian stage (ZHURAVLEV, 1996).

PALEOBIOGEOGRAPHY

Global archaeocyathan distribution was fundamentally controlled by the availability and mutual proximity of normal-marine carbonate depositional tracts. Resulting biogeographic patterns were influenced by rapid tectonic changes, particularly those accompanying rifting (LIEBERMAN, 1997; ZHURAVLEV & MAIDANSKAYA, 1998; DEBRENNE, MAIDANSKAYA, & ZHURAVLEV, 1999), as well as by evolution within the group, leading to the frequent appearance of short-lived, specialized, endemic taxa (NAIMARK & ROZANOV, 1997).

Among global paleogeographic reconstructions proposed for the early Cambrian (e.g., ROZANOV, 1984; ZONENSHAIN, KUZMIN, & KONONOV, 1985; SCOTESE & MCKERROW, 1990; COURJAULT-RADÉ, DEBRENNE, & GANDIN, 1992; KIRSCHVINK, 1992; MCKERROW, SCOTESE, & BRASIER, 1992; STOREY, 1993; DALZIEL, DALLA SALDA, & GAHAGAN, 1994; TORSVIK & others, 1996; KIRSCHVINK, RIPPERDAN, & EVANS, 1997; LIEBERMAN, 1997; SMITH, 2001; GOLONKA, 2002; MEERT & LIEBERMAN, 2008; RINO & others, 2008), those that best fit the archaeocyathan distribution portray a post-supercontinental world (Rodinian or Pannotian) with the major epicontinental basins within the intertropical zone. The inferred pathways of archaeocyathan migration, coupled with the use of the Jaccard similarity coefficient applied to the total local Cambrian faunas, calculated for Nemakit-Daldynian–early Tommotian, early Atdabanian, and late Atdabanian–Botoman intervals, support those paleogeographic reconstructions suggesting the existence of East and West Gondwana in the early Cambrian, as proposed by MOORES (1991) and KIRSCHVINK (1992), with their subsequent collision by the late early Cambrian (CAWOOD, 2005; PAULSEN & others, 2007), the rifting of Laurentia from the Australian-Antarctic margin, and the drift of suspect terranes toward Siberia (DEBRENNE, MAIDANSKAYA, & ZHURAVLEV, 1999). Terrane theory, with the prospect of more complex models incorporating suspect terranes and drifting microcontinents (CONEY, JONES, & MONGER, 1980), provides further options

for the reconstruction of archaeocyathan paleobiogeography.

Archaeocyaths appeared within the transitional Anabar–Sinsk tract of the Siberian Platform at the beginning of the Tommotian stage and had dispersed to the Altay Sayan Fold Belt (East Sayan and Kuznetsk Alatau) and Far East (Shevli Basin) only by the very end of this stage. The Siberian Platform, the first center of archaeocyathan diversification (ROZANOV, 1980), was located at low latitudes, mostly south of the paleoequator and was geographically inverted relative to its present position (COCKS & TORSVIK, 2007).

A longstanding puzzle has been the relatively late appearance of archaeocyaths in suitable lithofacies in Altay Sayan, Transbaikalia, Mongolia, and other nearby areas, together with the organization of archaeocyathan assemblages in distinct circumplatformal belts according to age and composition. Three sets of terranes are currently recognized in the archaeocyath-bearing regions of present Central Asia: Kazakhstan terrane group (Kazakhstan-Turkmenistan-Tajikistan-Kyrgyzstan), Altay Sayan–Transbaikalia-Mongolia terranes, and Far East terranes (KHAIN & others, 2003; KHERASKOVA & others, 2003; SENNIKOV & others, 2004; COCKS & TORSVIK, 2007; GORDIENKO & others, 2007). Overall, Central Asia is a complex of accretionary (Altay, Sayans, Transbaikalia, Mongolia, Kazakhstan) and collisional terranes (northern China, southern Mongolia, Dzhungaria, southern Tien Shan, northern Pamir). Their appearance has been linked to the postulated development of several paleooceans (ZONENSHAIN, KUZMIN, & KONONOV, 1985; KHERASKOVA & others, 2003), of which the earliest Paleoasian Ocean was probably never wide. Intense tectonism, including volcanism, took place in the latest Ediacaran and earliest Cambrian along the northern periphery of East Gondwana, where a rift-to-drift transition involved a number of Central Asian microcontinents (e.g., Zavkhan, Tuva-Mongolia, South Gobi, North Tien Shan). Tectonic and sedimentological analyses

suggest that these blocks drifted from northwestern East Gondwana toward Siberia during that interval (KHERASKOVA & others, 2003; COCKS & TORSVIK, 2007). Paleomagnetic and paleontological data have further confirmed and constrained this scenario (ZHURAVLEV & MAIDANSKAYA, 1998; METELKIN & KAZANSKIY, 2002; MIKHAL'TSEV, KAZANSKIY, & SENNIKOV, 2002).

Other regions were not suitable for archaeocyathan colonization at that time, with phosphate-rich sedimentation prevailing in northern peri-East Gondwana terranes (Yangtze, Mongolia, and Kazakhstan) and West Gondwana (West Africa and Iberia [PARRISH & others, 1986; VIDAL, MOCZYDŁOWSKA, & RUDAVSKAYA, 1995; CULVER & others, 1996]), extensive evaporite basins in subequatorial parts of Siberia (Turukhansk-Irkutsk-Olekma tract) and northern West Gondwana (Oman–southern Iran–Saudi Arabia, northern Pakistan [WOLFART, 1983; ASTASHKIN & others, 1991]), and mainly fluviatile and deltaic siliciclastic sediments elsewhere (HOLLAND, 1971, 1974; GANDIN, MINZONI, & COURJAULT-RADÉ, 1987; ROZANOV & ŁYDKA, 1987; COOK, 1988; LANDING & others, 1988; FRITZ & others, 1991; BORDONARO, 1992; PILLOLA & others, 1994).

During the first half of the Atdabanian Stage, when marine transgression generated widespread carbonate sedimentation in the Altay Sayan Fold Belt, Mongolia, Iberia, Germany, Poland, Morocco, and Australia (SHERGOLD & others, 1985; MORENO-EIRIS, 1987; ASTASHKIN & others, 1991, 1995; ELICKI, 1995; GEYER, LANDING, & HELDMAIER, 1995; BIAŁEK & others, 2007; ÁLVARO & others, 2010), archaeocyaths of Siberian affinity (e.g., *Sibirecyathus* VOLOGDIN, *Geocyathus* ZHURAVLEVA, *Retecoscinus* ZHURAVLEVA, *Capsulocyathus* VOLOGDIN, *Dictyocyathus* BORNEMANN) reached western Europe (Normandy, Spain) and Morocco, where a new center of diversification developed and endemic forms appeared. ROZANOV's (1984) and MCKERROW, SCOTESE, and BRASIER's (1992) paleogeographic reconstructions

showing a close proximity of Siberia to the northern West Gondwana margin are consistent with a postulated Siberian-Euro-Moroccan archaeocyathan dispersal pathway. Avalonia was unsuitable for archaeocyaths due to its temperate location (Landing & MacGabhann, 2010).

By the terminal Atdabanian and initial Botoman stages, continued transgression had finally initiated carbonate accumulation and hence archaeocyathan proliferation on Yangtze, Australia, and Laurentia. Archaeocyaths migrated along the northern periphery of West Gondwana from the European-Moroccan center of diversification, and via Mongolia and Kazakhstan, to populate Yangtze. (Note that archaeocyaths reported from intervening Sinai and Iran by Omara [1972], Basahel and others (1984), Mel'nikov and others [1986], and Lasemi and Amin-Rasouli [2007] should be discounted, as the Iranian so-called archaeocyaths are eocrinoids, spiculate demosponges, microbialites, and ooids, whereas the Sinai material could be the enigmatic, tubelike *Cloudina* Germs. As well, putative Himalayan archaeocyaths have proved to be microstromatolites [Debrenne, Gangloff, & Zhuravlev, 1990]). A number of genera, for example, *Rasetticyathus* Debrenne, *Porocoscinus* Debrenne, *Rudanulus* Debrenne, and *Spirillicyathus* R. Bedford & J. Bedford, were restricted or almost exclusive to Yangtze, western Europe–Morocco, and/or Australia (Debrenne & Jiang, 1989). By the end of the Botoman Stage, archaeocyaths had dispersed from Australia to Antarctica, where some 50% of species were in common with the former (Debrenne & Kruse, 1986, 1989; Wrona & Zhuravlev, 1996; Kruse & Shi in Brock & others, 2000).

Australia became one of the principal Botoman centers of diversification (Rozanov, 1980; Debrenne & Zhuravlev, 1992b, fig. 40c). Archaeocyathida with outer wall canals (*Warriootacyathus* Gravestock) and subdivided canals (*Beltanacyathus* R. Bedford & J. Bedford, *Ataxiocyathus* Debrenne, *Maiandrocyathus* Debrenne), as

well as erismacoscinines with attached microporous sheath (*Polycoscinus* R. Bedford & J. Bedford), were restricted entirely to this center of diversification. A possible independent center of diversification, the Russian Far East, was proposed by Belyaeva (1987). Some centers of diversification are also characterized by the presence of peculiar forms difficult to place in the classification system, for example, *Eremitacyathus* Zamarreño & Debrenne in Spain, *Retilamina* Debrenne & James in North America.

By the late Atdabanian, the Cordilleran margin of Laurentia crossed the paleo-equator, providing suitable conditions for archaeocyathan settlement. At the same time, Laurentia and Siberia moved toward each other, facilitating faunal migration. The first Laurentian archaeocyaths probably originated from Australian stock: *Metaldetes* Taylor, *Metacyathellus* Debrenne & Zhuravlev, *Sigmofungia* R. Bedford & W. R. Bedford, and *Pycnoidocoscinus* R. Bedford & W. R. Bedford are known only from these two regions (Mansy, Debrenne, & Zhuravlev, 1993). By the end of the Botoman Stage, the distance between Laurentia and Siberia was not great, facilitating migration of common genera and perhaps even species (*Tegerocyathus* Krasnopeeva, *Krasnopeevaecyathus* Rozanov, *Polythalamia* Debrenne & Wood, *Claruscoscinus* Handfield). Laurentia, in turn, became a center of diversification (Rozanov, 1980; Debrenne & Zhuravlev, 1992b, fig. 40c).

Further northward movement of Laurentia allowed archaeocyaths and other reef-building organisms to spread to the Appalachian margin, while simultaneously they were significantly reduced along its Cordilleran margin (Debrenne, Maidanskaya, & Zhuravlev, 1999; McMenamin, Debrenne, & Zhuravlev, 2000).

Early Cambrian transgression attained its maximum in the Botoman Stage, leading to the relative isolation of those regions inhabited by archaeocyaths. Archaeocyathan endemicity was thus greatest at that time. The

percentage of endemic genera in the various centers of diversification was 22% in Europe-Morocco, 21% in Australia-Antarctica and 38% in Laurentia (DEBRENNE & ZHURAVLEV, 1992b, p. 96). Similarly, archaeocyathan gamma diversity, which expresses the degree of provinciality, was highest in the Botoman and indicates that geographic isolation was among the major factors controlling archaeocyathan diversification. A further factor was environmental heterogeneity, as revealed by beta diversity analysis. Again, beta diversity was highest in the Botoman (ZHURAVLEV & NAIMARK, 2005, fig. 2a, 3). On this collective basis, an early Cambrian paleogeographic division, based on archaeocyaths, into Afro-Siberian-Antarctic and American-Koryakian provinces was suggested (ZHURAVLEV, 1986a) and since employed by other authors (GANGLOFF, 1990; DEBRENNE & ZHURAVLEV, 1992b, fig. 40d). This broad division has been confirmed by cluster analysis of more current generic distribution data, by which KRUSE and SHI (in BROCK & others, 2000) recognized two archaeocyathan realms, Eurasian and Lauraustral, the former embracing Siberia-Mongolia, Central–East Asia, and Europe-Morocco provinces, and the latter the Australia-Antarctica and North America–Koryakia provinces.

Intraprovincial lithofacies-based subdivision has been proposed by OSADCHAYA (1979) for the Altay Sayan Fold Belt. She recognized carbonate-, mixed siliciclastic-carbonate-, and mixed volcanic-carbonate-dominant provinces, the last two of which have recognizable counterparts in Mongolia (ZHURAVLEV, 1998).

The appearance of new centers of diversification does not seem to be associated only with regional isolation; the high Botoman endemism is also due to the rapid diversification of certain superfamilies (e.g., Ethmophylloidea in Laurentia, and Polycoscinoidea and Beltanacyathoidea in Australia). In addition, diverse and distinct genera appeared in both regions among the Metacyathoidea. All these superfamilies were characterized by complicated outer wall structures, which might have provided an improved screen, preventing the clogging of pores by particles, as discussed above. Thus, inferred unsuitable conditions might have increased the specialization rate within these taxa and consequently contributed to endemicity.

On the whole, the Atdabanian–Botoman witnessed the greatest extent of carbonate platforms in the entire early Cambrian, facilitating extensive calcimicrobial-archaeocyathan reef building within the belt extending 30° to either side of the paleoequator (DEBRENNE & COURJAULT-RADÉ, 1994).

The middle Botoman peak of the early Cambrian transgression was marked by extensive accumulation of black shale and black, thin-bedded limestone in low latitudes: Siberia, some microcontinents of the Altay Sayan Fold Belt, Transbaikalia, Russian Far East, Kazakhstan, Iran, Turkey, South Australia, Yangtze (CHEN & others, 1982; SHERGOLD & others, 1985; ASTASHKIN & others, 1991, 1995; HAMDI, 1995). These deposits reflected an anoxic-dysoxic event adversely affecting archaeocyathan communities (ZHURAVLEV & WOOD, 1996). Seemingly, archaeocyaths survived this event in refugia, some of which were island arcs, in West Sayan and Tuva of the Altay Sayan Fold Belt, the Dzhagdy Basin of the Russian Far East, Kazakhstan, and some regions of Australia, where the most complete Botoman record of archaeocyathan assemblages is preserved. The late Botoman archaeocyathan fauna included abundant Erbocyathoidea, Tercyathoidea, Claruscoscinidae, and Kazachstanicyathida.

The late Botoman–Toyonian probably coincides with the major early Cambrian regression, variously termed in different regions the Hawke Bay, Daroca, or Toyonian regression. The Toyonian sedimentary record is characterized by widespread *Skolithos* piperock in Iberia, Morocco, eastern Laurentia, and other intertidal siliciclastic tracts of Baltica, the Midde East, and Laurentia. Sabkha conditions prevailed over large areas of Siberia, Australia, and Yangtze (PALMER & JAMES, 1980; BERGSTRÖM &

AHLBERG, 1981; BRANGULIS & others, 1986; COOK, 1988; MEL'NIKOV & others, 1989; ASTASHKIN & others, 1991; FRITZ & others, 1991; MCCOLLUM & MILLER, 1991; MANSY, DEBRENNE, & ZHURAVLEV, 1993; GOZALO & others, 2007; LASEMI & AMIN-RASOULI, 2007; ÁLVARO & CLAUSEN, 2008). Together with the preceding anoxic-dysoxic event, this regression decimated the archaeocyaths and other invertebrate reef dwellers by substantially reducing the shallow marine platform area.

During the middle Toyonian, low-diversity archaeocyathan communities consisting mainly of surviving *Tegerocyathus* KRASNOPEEVA, *Archaeocyathus* BILLINGS, and *Pycnoidocyathus* TAYLOR species became widespread (DEBRENNE & ZHURAVLEV, 1992b, fig. 40d).

A general foundering of carbonate and mixed-sedimentary ramps at the beginning of the middle Cambrian (Amgan stage) led to the virtual extinction of the archaeocyaths. This foundering was expressed in the accumulation of deeper-water (including black) shale in the Siberia, northern Mongolia–Transbaikalia, Russian Far East, and Kazakhstan terranes (ASTASHKIN & others, 1991, 1995; KHERASKOVA & others, 2003). The postulated transition from coldhouse to greenhouse conditions during the late early to late middle Cambrian was probably also a major factor in this extinction (ZHURAVLEV & WOOD, 2008; LANDING & MACGABHANN, 2010; LANDING, 2011). Prior emission of greenhouse gases from the Botoman-age Kalkarindji continental flood basalt province of northern Australia offers a potential trigger for this warming (GLASS & PHILLIPS, 2006; HOUGH & others, 2006). In addition, drift of the European-Moroccan margin of Gondwana toward higher, temperate latitudes, beyond the limits of carbonate development (COURJAULT-RADÉ, DEBRENNE, & GANDIN, 1992), no doubt hindered the reestablishment of archaeocyathan populations within this region. The same probably held true for Australia, due to a counterclockwise rotation of Gondwana (KIRSCHVINK, 1992). Thus, Antarctica alone remained in low paleolatitudes, so furnishing both known species of post–early Cambrian archaeocyaths (DEBRENNE, ROZANOV, & WEBERS, 1984; WOOD, EVANS, & ZHURAVLEV, 1992).