INTRODUCTION

The Archaeocyatha were, geologically speaking, a very short-lived group that inhabited the carbonate-shelf and reef environments of the Early Cambrian and early Middle Cambrian seas. They are possibly the only phylum of animals to have become extinct. They were among the first to develop mineral skeletons and used calcium carbonate for this purpose. From the beginning of their study they have excited interest in their systematic position and in the nature of their soft parts, and both of these are subjects of lively controversy in current literature. The relations of the phylum to the Protista on the one hand and to the Porifera or Coelenterata on the other are by no means fully apparent; indeed, the phylum invites speculation on the nature of the soft parts.

The individual skeleton, the cup, is fundamentally an inverted cone; most cups have two fairly widely spaced walls and a central cavity, some have only one wall.

Since publication of the first edition of *Treatise,* Part E, in 1955, our knowledge of the phylum has grown perhaps more spectacularly than that of any other. The great importance placed upon it by those Russian geologists interested in the correlation of Lower Cambrian sequences throughout the USSR has resulted in an increasingly extensive literature. Archaeocyathan species have been found to be of stratigraphic and provincial value; several successive assemblages of species (or "horizons") have been distinguished. The succession of genera in the USSR is also well established and is applicable in other parts of the world.

Archaeocyathan skeletons are aesthetically pleasing and the mental reconstruction of their elegant structures from thin sections is intellectually satisfying. Indeed, for students their attractions rival those of corals.

MORPHOLOGICAL FEATURES

GENERAL FEATURES OF SKELETON

The Archaeocyatha are an extinct phylum of animals that formed calcareous skeletons, the basic form of which is an inverted cone, called the **cup.** This may be erect or curved, slowly or rapidly expanding, and may have holdfasts. **Compound** skeletons, **catenulate** or **dendroid,** are not common. Some cups are one-walled; most have two walls and a normally empty **central cavity** (Fig. 1,2). The walls are perforate and are connected across the inner space termed the **intervallum** by perforate radial longitudinal plates **(septa)** (Fig. 2), by radial **rods,** by perforate transverse plates **(tabulae),** by small, arched or sagging imperforate plates **(dissepiments),** or by radial or inclined hexagonal tubules with perforate walls. The pores of the walls may be screened or protected by various formations but only exceptionally on their intervallar surfaces.

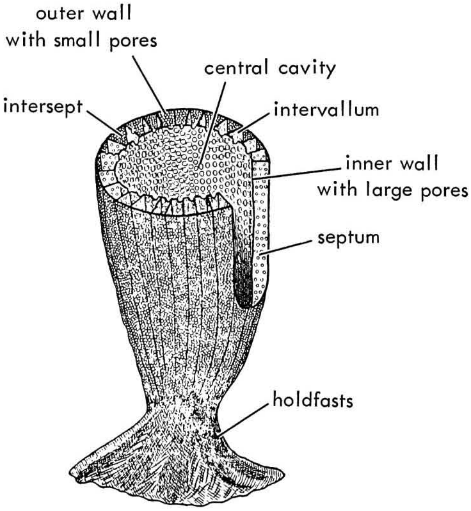


FIG. 2. Reconstruction of the skeleton of an archaeocyathan (Regulares, Ajacicyathina), a two-walled septate conical cup with central cavity and supported basally by holdfasts, ×13 (Vologdin, 1962c).

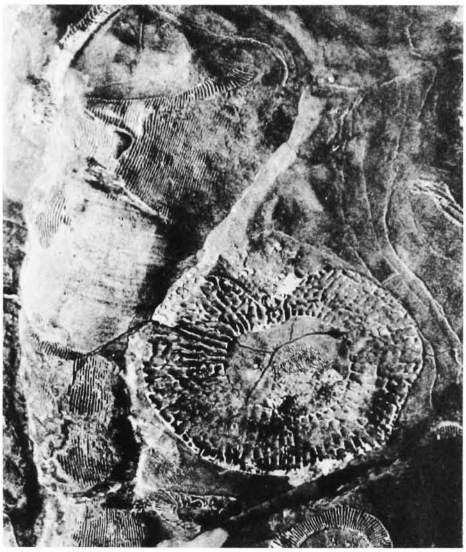


FIG. 1. Etched specimens from the Ajax Limestone, South Australia. On the left, *Thalamocyathus trachealis* (TAYLOR) with finely porous outer wall removed from most of the large elongately conical two-walled cup to display outer edges of septa; on the right, a cross section of an irregularan cup, showing inner and outer walls connected by irregularly radial septa, and empty central cavity (Taylor, 1910).

MICROSTRUCTURE

The skeletal elements of Archaeocyatha commonly consist of a very finely granular mosaic of calcite, the grains being about 0.01 or 0.02 mm. in diameter, arranged with their *c*-axes in random directions, and commonly of a uniform color. Some forms have coarser grain, others, irregular grains. Such variations are possibly due to diagenetic change. Another common diagenetic change is replacement of the calcite by silica. In a few, an alternation of bands occurs. These bands are light and dark in transmitted light, and white and more densely white in reflected light, almost certainly representing growth layering. The darker (and denser) bands may represent either greater original concentration of organic matter or possibly concentrations of finer crystalline grains, as also may spots seen in sections of a few specimens (Fig. 3).

The skeletal matter differs from that of corals in the seeming absence of acicular

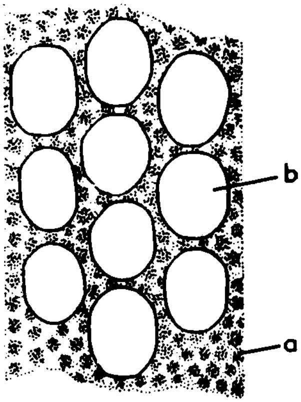


FIG. 3. Granular microstructure shown in median longitudinal section of septum of *Ajacicyathus gigantoporus* ZHURAVLEVA, ×50 [*a*, patch of denser granularity; *b*, pore] (Zhuravleva, 1960b).

crystals, though their original presence is suspected in a few species. The septa never show median dark lines such as appear where the needles of two halves of a coral septum meet, nor is there ever a dark line at the junction of one plate with another, such as forms in corals where plates having differently oriented fabrics are in contact or where one plate is formed later than another. All appearances in thin section suggest complete continuity of the skeletal elements, but this appearance conceivably may be due to recrystallization of the original. Dissepiments, which are always very thin, may form an exception to this rule of continuity, for they seem to have been formed later than those parts of septa or walls that they touch.

Although septa and walls may be analyzed as constructed of longitudinal pillars and transverse rods, the pillars do not seem to be analogous with the trabeculae of corals. No median dark axis is seen in them, and they lack any appearance of fibrosity.

All the skeletal elements except the dissepiments are perforate. In none are spicules discernible. Further, no element by itself can be considered to be a spicule, and no axial canal like that of sponge spicules has been observed.

Secondary thickening of all elements except dissepiments has been observed; such thickening is usually growth-layered. Thickening may be effected as follows. First, layers invest the outside of the outer wall; next, the inside of the outer wall and the septa are invested simultaneously; then both sides of the inner wall become coated until finally all space in the lower part of the cup may be filled; in some species all pores are closed off, but in others the pore

FIG. 4. External form in solitary Archaeocyatha (*facing page*).

1. Slenderly conical and erect form of *Dokidocyathus simplicissimus* BEDFORD & BEDFORD, ×0.3 (R. Bedford & W. R. Bedford, 1936).

2. Slenderly conical form with basal holdfasts, shown by *Tumuliolynthus karakolensis* ZHURAVLEVA, ×1 (Rozanov & Missarzhevskiy, 1966).

3. Cylindrical form of *Sigmocoscinus sigma* BEDFORD & BEDFORD, ×0.7 (R. Bedford & W. R. Bedford, 1936).

4. Curved conical form of *Kotuyicyathus kotuyikensis* ZHURAVLEVA, ×1 (Zhuravleva, 1960b).

5. Transversely annulated, annulation not involving inner wall, as seen in *Pycnoidocyathus synapticulosus* BEDFORD & BEDFORD, ×0.3 (R. Bedford & W. R. Bedford, 1936).

6. Transversely annulated type, annulations involving inner wall, as shown by *Orbicyathus mongolicus* VOLOGDIN; *6a*, ext. view, ×2; *6b,c*, tang. sec. of two rings, ×4 (Vologdin, 1937b).

7. Longitudinally ribbed and fluted externally, with basal holdfasts, exemplified by *Beltanacyathus ionicus* BEDFORD & BEDFORD, ×0.3 (R. Bedford & J. Bedford, 1936).

8. Conical, suddenly expanding form of *Paranacyathus subartus* ZHURAVLEVA, ×0.7 (Zhuravleva, 1960b).

9. Broadly conical form of *Cryptoporocyathus junicanensis* ZHURAVLEVA, ×5 (Zhuravleva, 1960b).

10. Subspherical form of *Fransuasaecyathus subtumulatus* ZHURAVLEVA, ×5 (Zhuravleva, 1960b).

11. Bowl-shaped form, with irregular longitudinal folds affecting both walls, shown by *Coscinoptycta convoluta* (TAYLOR), ×0.7 (Taylor, 1910).

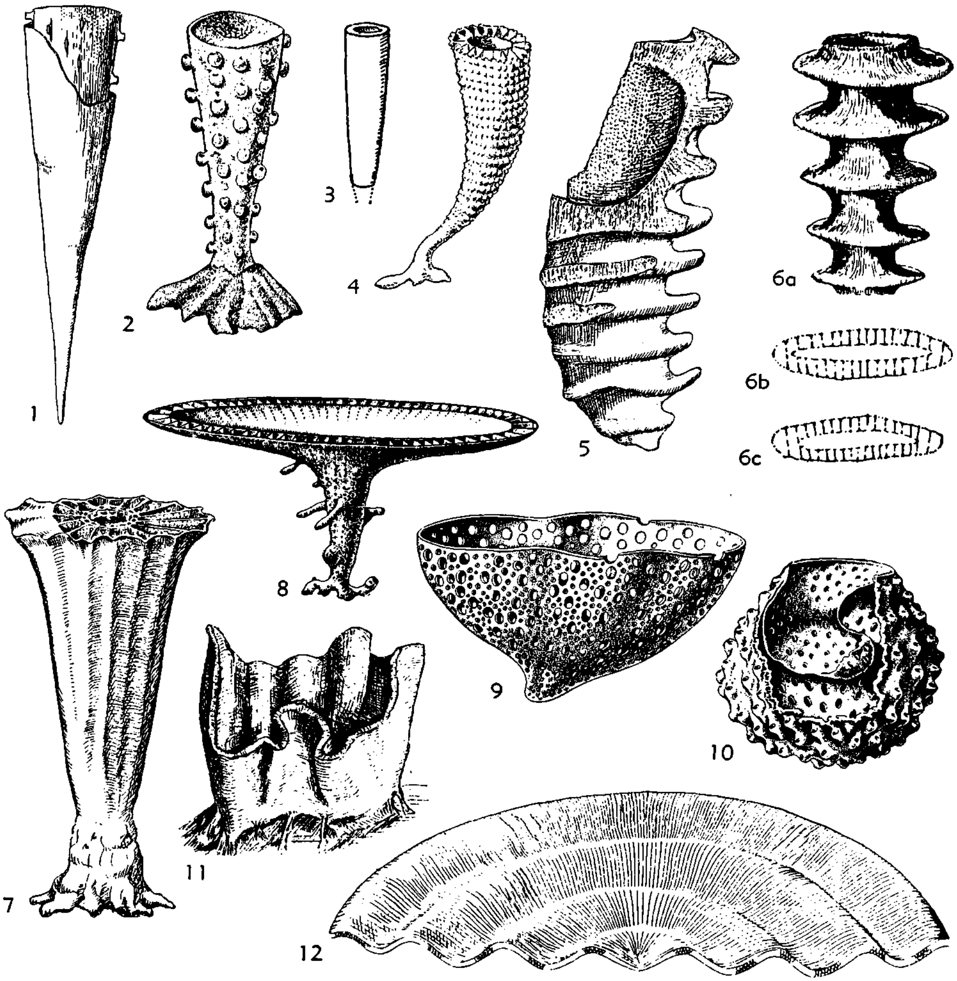
12. Discoid form, with concentric waves (cut in half diametrically), seen in *Okulitchicyathus discoformis* (ZHURAVLEVA), ×0.16 (Zhuravleva, 1960b).

openings may remain free; sinuous canal-like spaces opposite them and through the secondary thickening enable them to maintain communication with the environment.

The secondary thickening may be lamellar, lamellar-granular, granular, or of columnar calcite, and is distinct from the nonorganic clear columnar calcite deposited during diagenesis.

EXTERNAL FORM

The calcareous skeletons of both solitary and colonial Archaeocyatha are known. The skeleton of an individual is termed a cup. Of solitary cups, the great majority are slenderly conical (Fig. 4,*1-2*), especially in the class Regulares; most slender cones are erect or suberect, but some are curved (Fig. 4,*4*), the curvature normally decreasing during growth; some become cylindrical in the adult stage (Fig. 4,*3*). Periodic expansions of the intervallum may affect both walls in parallel or only the outer wall, and there may be transverse or annular (Fig. 4,*5-6*) or longitudinal (Fig. 4,*7*) flutings that may affect only the inner wall around the central cavity. Broadly conical and saucer-shaped cups are not common (Fig. 4,*8-9,11*). Some large bowl-shaped cups with narrow intervallar rims have irregular longitudinal folds in their rims



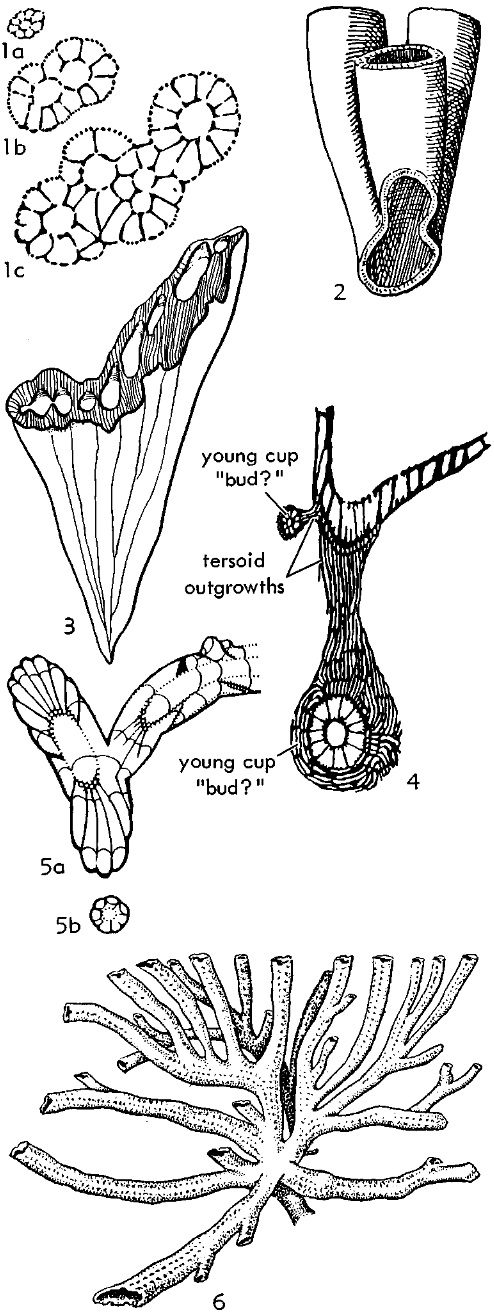


FIG. 5. External form in colonial Archaeocyatha.——*1a-c.* Massive; serial sections through colony of *Ajacicyathus sanaschticolensis* VOLOGDIN, ×3 (Vologdin, 1937b).——*2.* Dendroid; increase by opposed indenting of intervallum, in *"Archaeocyathus" aequitriens* BEDFORD & BEDFORD, ×0.7 (R. Bedford & J. Bedford, 1937).——*3.* Catenulate; *Salairocyathus (Polystillicidocyathus) erbosimilis* DEBRENNE, ×1.5 (Debrenne, 1959b).——*4.* Pseudocolony? Linkage of cups by tersioid outgrowths (Taylor, 1908).——*5.* Dendroid, new cup arising from intervallum; *5a,* oblique thin section, and *5b,* transv. sec. of *Loculicyathus frondosus* VOLOGDIN, ×2.5 (Vologdin, 1962c).——*6.* Dendroid form of *Archaeolynthus polaris* (VOLOGDIN), ×0.7 (Zhuravleva, 1960b).

(Fig. 4,*11*); others have irregular dents. Discoid cups, in which the angle of the cone is approximately 180° are found in a few species (Fig. 4,*12*); the discs may be concentrically waved. A small number of species, especially in two-walled cups without septa, have subspherical, hemispherical, or irregularly bulbous cups that may not be attached to substrates (Fig. 4,*10*). In the Irregulares, expansions and contractions may be very irregular, and in many, fingerlike protrusions occur. The shape of the older part of the cup may be hidden under outgrowths of tubular, heel-like, or irregular form that acted as holdfasts. In many one-walled cups (and in a few two-walled cups) the upper edge arches over the cavity, leaving only a small orifice.

The colonial habit is rare, and form of colonies is less varied than in corals. In a **catenulate colony** the cups are contiguous in a row or chain and the outer wall fails to develop between neighbors (Fig. 5,*3*); a few cups in such a colony may have no central cavity. In a **massive colony** cups are massed together without outer walls between them, but each has its own central cavity (Fig. 5,*1*). In a **dendroid colony** each individual cup is a branch isolated from the others except at its point of origin in either the inner or the outer wall (Fig. 5,*2*,*5-6*). In some Irregulares, the buds originate from the outer part of the intervallum and the outer wall. A few species of Irregulares have fingerlike projections of the central cavity that cause the intervallum to bulge outward beyond the normal conical outline to form wider projections of the intervallum (Fig. 5,*2*). Lateral outgrowths from one or more cups may surround neighboring cups of the same species, giving the appearance of a colony (Fig. 5,*4*).

OUTGROWTHS FROM CUP

Lateral expansions affecting a sector or the whole circumference of the archaeocyathan cup are quite common and fall into two groups.

Group I consists of expansions from the intervallum in which are skeletal elements usually similar to those in the original intervallum. Among included types are the following: 1) **Slender, tubular processes,** commonly of the width of an interseptal space, hollow or crossed by dissepiments (Fig. 6,*15*). These are commonest in the Irregulares. 2) **Tersiae, or tersioid processes;** these are fingerlike, as wide as several interseptal spaces; they contain septa, and dissepiments, normally somewhat thicker than those of the cup from which they originate (Fig. 6,*1,5*). They form in many genera of Irregulares and in a few Regulares. 3) **Intervallar expansion in width,** near the base of the cup, acting as a holdfast, with the form of a talon, a pedestal, or a heel (Fig. 6,*4*). 4) **Exocyathoid expansions;** these are formed by the growth of an additional intervallum, in sectors or circumferentially, the septa of the addition being continuous or discontinuous with those of the original intervallum (Fig. 6,*3,6*). When the expansion is external the outer wall may be repeated; expansions into the central cavity (Fig. 6,*7,11,14*) are less readily relatable to the septa and perhaps may be complex outgrowths of the inner wall. Exocyathoid expansions normally appear to have had an adherent function, and occur in both Regulares and Irregulares (Fig. 6,*13*). Those of Coscinocyathina have been called labyrinthomorph (Fig. 6,*9*), those of some Regulares exocyathoid, and those of some Irregulares metaldetimorph (Fig. 6,*8*). Originally, separate generic names were given to these three types.

Group II consists of expansions of dense skeletal tissue applied outside the outer wall. They are found basally only, at a cup height of 2 to 5 mm. and always have an adherent function. Types distinguished are as follows: 1) **Dense skeletal tissue without canals or spaces,** commonly seen in small, slenderly conical Regulares (Fig. 6,*12*). 2) **Dense skeletal tissue pierced by canals** proceeding from the pores of the outer wall and parallel with the outer surface of the mass (Fig. 6,*2*). 3) **Dense skeletal tissue laminate,** the laminae parallel to the outer surface of the mass being separated by similar parallel spaces (Fig. 6,*10*). This type is rare.

SIZE OF CUP

The diameter of the overwhelming majority of archaeocyathan cups ranges from 10 to 20 or 25 mm. The height is normally proportional to the diameter; and for the above diameter, the height may be 80 to 150 mm. Some species, especially one-walled, or two-walled cups without septa, never attain an adult diameter greater than 1.5 to 3 mm., though nearly all one-walled forms have a diameter of 4 to 6 mm. at a height of 15 to 25 mm. The maximum diameter known is 500 to 600 mm. in the disc-shaped *Okulitchicyathus* where the cup has the relative minimum height of 6 to 10 mm. The maximum known height is 250 to 300 mm. Microscopic forms regarded by VOLOGDIN as planktonic archaeocyathans are here considered to be probably not referable to the phylum.

Small forms were prevalent on the Siberian Platform when the phylum first appeared in Early Cambrian (Sunnaginian) times, and again in Tolbachanian (Botomian) times when, it is thought, the seas became highly enriched in magnesium salts. Maximum size of Archaeocyatha individuals both in height and diameter, as well as abundance, is attained in strata containing bioherms, but the largest species are found in the interbiohermal pockets. Species with small adult diameters accompany the large species in strata with bioherms.

OUTER WALL

The outer wall of two-walled Archaeocyatha is homologous with the single wall of one-walled Archaeocyatha. It shows considerable diversity of structure, though less than that of the inner wall (Fig. 7,8). Present knowledge indicates that the outer wall is imperforate at the extreme base, or tip, of the cup. It then becomes simply porous. In cups with complex pores in adult stages this simply porous stage lasts only fleetingly.

Simply perforate, thin walls are fairly

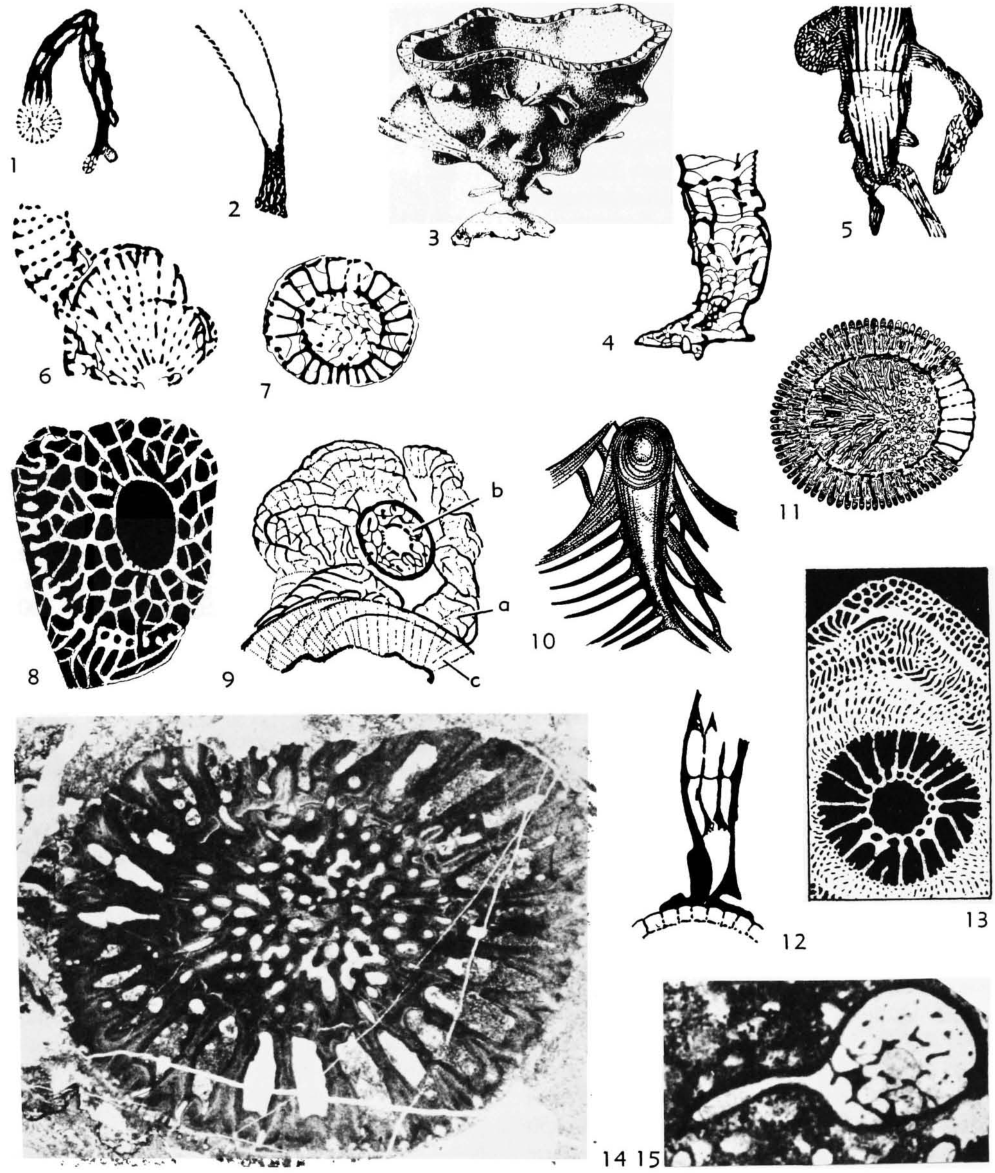


Fig. 6. Outgrowths from the cup.

1. Tersioid process in *Robustocyathus robustus* Zhuravleva, ×2.5 (Zhuravleva, 1960b).

2. Holdfast of dense skeletal tissue without canals of *Tumuliolynthus tubexternus* (Vologdin), ×4 (Zhuravleva, 1949).

3. Unconformable intervallar segment and irregular processes in *Paranacyathus subartus* Zhuravleva, ×1 (Zhuravleva, 1960b).

4. Expansion in width of intervallar space to form adherent talon in *Bicyathus bateniensis* (Vologdin), ×3 (Vologdin, 1959c).

5. Tersioid processes in *Paranacyathus* sp., ×2.5 (Zhuravleva, 1959b).

6. Exocyathoid processes, one doubling the intervallum and outer wall, and the other unconformable; thin section, ×3 (Zhuravleva, 1960b).

7. Outgrowths into central cavity; dissepiments common in the Regulares. They may be described as **perforate,** when the area occupied by wall tissue is greater than that occupied by the pores (Fig. 7,*1*,*10*); or **retiform,** when the pores are so closely spaced that the wall is netlike (Fig. 7,*11*). The pores may be rounded, oval, polygonal, or chinklike in outline (Fig. 7,*10*,*11*,*12*), or, as in many Irregulares, they may be irregular in outline and in arrangement (Fig. 7,*2*). Commonly pores are arranged in longitudinal rows, one to eight such rows to an intersept (Fig. 9). The pores of neighboring rows may be opposite (Fig. 7,*20*) or alternate (Fig. 7,*10*). In many species the wall tissue between the rows, especially in the midline of the intersept, is thicker than that between the pores of a row, giving the appearance of a low longitudinal rib, projecting either outward or inward or both. Spines may project from the tissue between four pores. The lower lip of a pore may be produced like a spine (Fig. 7,*17*), or like an uncurved or only slightly curved scale (Fig. 7,*13*), or as a bract with a concave upper surface like a half cupule; or the upper lip may be produced into a peak like the projection from the brim of a man's cap. From the whole rim of a large pore, a domelike tumulus may develop, pierced by one opening or by many smaller ones (Fig. 7,*18*); a smooth tumulus with one opening is a simple tumulus and the opening may be central or on the upper or lower surface (Fig. 7,*19*; 8,*2*). A tumulus with many pores is commonly knobby, a small pore piercing each knob.

Where simply porous walls are thick, length of the pores may be greater than their diameter so that they may be called **pore-canals** (Fig. 7,*15*). Where the skeletal tissue between these pore-canals is thin, or formed of louvre-like or resupinate plates, the pore-canals may be termed pore-tubes. Pore-canals and pore-tubes commonly are circular but may be hexagonal in section (Fig. 7,*3*), and are arranged in opposite or alternate longitudinal rows, one to four to an interseptal space. They may be straight and perpendicular to the wall surfaces, oblique, or geniculate, either V- (Fig. 7,*4*) or inverted V-shaped. The outer upper or lower lip of the pore-canal or pore-tube may be produced into a peak or a bract (Fig. 7,*5*). Pore canals that branch outward, giving finer porosity on the outer surface of the wall than on the inner one, are known in *Cryptoporocyathus* (Fig. 7,*22*). The description "with branching pores" earlier was used for a wall with a finely porous outer (supplementary) sheath (Fig. 7,*14*).

Some external walls consist only of a series of troughed or S-shaped annuli applied at regular short intervals to the outer ends of the septa (Fig. 7,*16*) or of rows of scales forming annuli (Fig. 7,*7*).

Walls may be developed with an external sheath. The sheath is commonly perforate, and its perforations are always

FIG. 6. *(Continued from facing page.)*

and rods? in *Loculicyathus* sp., ×3 (Krasnopeeva, 1960).

8. Exocyathoid expansion from an irregularan cup, thin section, ×2; *"Metaldetimorpha" yorkei* BEDFORD & BEDFORD (R. Bedford & J. Bedford, 1937).

9. Exocyathoid expansion [*a*, *"Labyrinthomorpha tolli"* VOLOGDIN, associated with *b*, *Protopharetra laxa* BORNEMANN, and *c*, *Coscinocyathus dianthus* BORNEMANN], thin section, ×5 (Vologdin, 1959c).

10. Dense, laminate, basally adherent skeletal tissue, *Tumulocyathus* sp., ×40 (Zhuravleva, 1960b).

11. Outgrowths into central cavity, lined by secondary thickening interpreted by VOLOGDIN as calcified soft parts, *Ajacicyathus demboi* VOLOGDIN, transv. sec., ×10 (Vologdin, 1962d).

12. Holdfast formed of dense skeletal tissue in *Loculicyathus salairicus* VOLOGDIN, ×3 (Vologdin, 1962b).

13. Exocyathoid expansion forming holdfast for *Beltanacyathus ionicus* BEDFORD & BEDFORD, thin section, ×2 (R. Bedford & J. Bedford, 1937).

14. Outgrowths into central cavity, lined by secondary thickening, in *Robustocyathus robustus* (VOLOGDIN), interpreted by VOLOGDIN as calcified soft parts, ×?4 (Vologdin, 1962b).

15. Slender tubular process with dissepiment in *Protopharetra polymorpha* BORNEMANN, ×2 (Zhuravleva, 1960b).

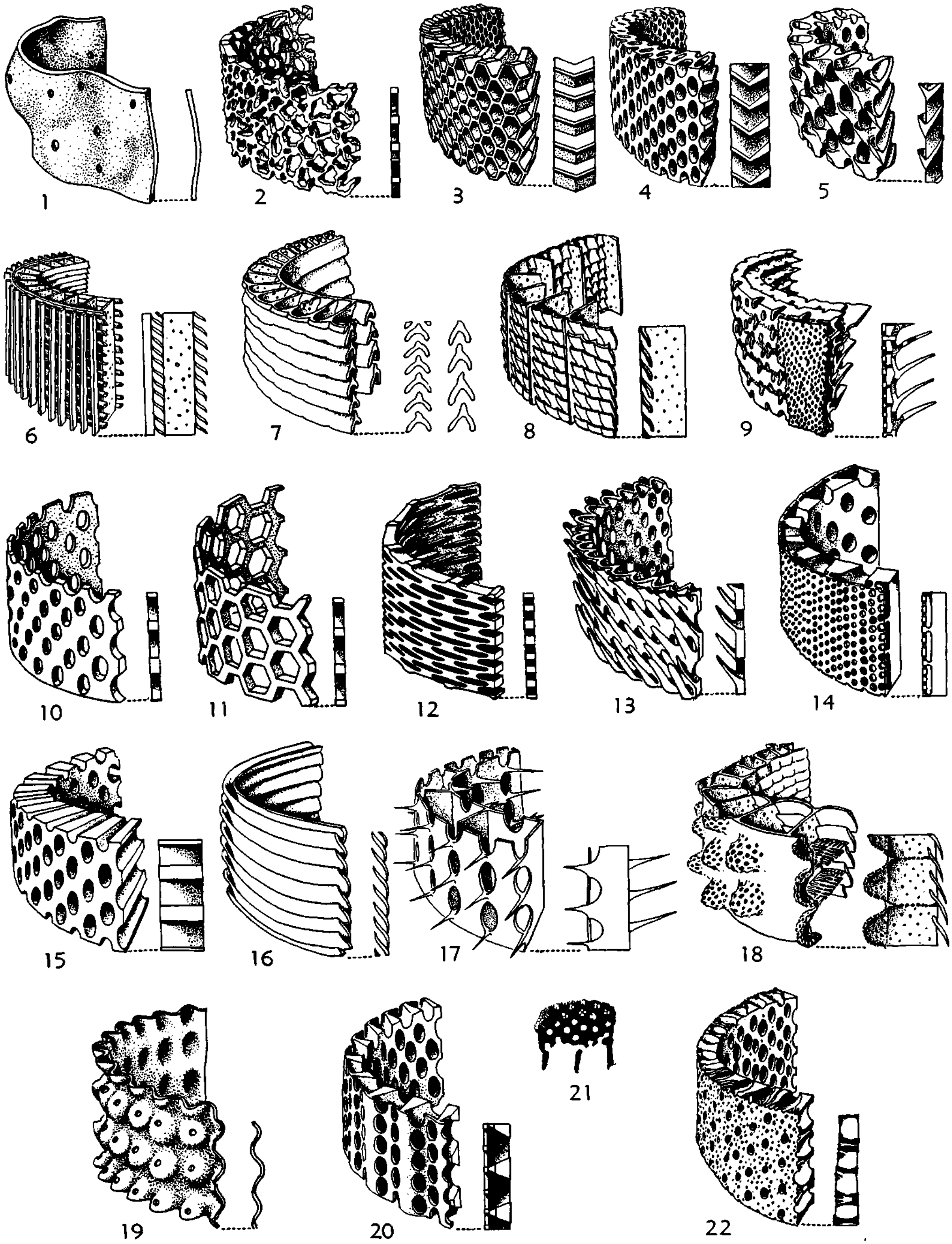


Fig. 7. Outer wall structures, diagrammatic.

1. Thin perforate wall with scattered small pores in *Bicyathus* sp. (mod. Debrenne, 1964).

2. Thin retiform wall with irregular pores (mod. Debrenne, 1964).

3. Thick wall with hexagonal geniculate pore-tubes, in *Coscinocyathus* (mod. Debrenne, 1964).

4. Thick wall with cylindrical geniculate pore-finer than those of the coarse framework it sheaths (Fig. 7,*21*). It may be a network growing tangentially from the thinned outer edges of the coarse framework (Fig. 7,*20*), or it may be suspended from short rods extending outward from the framework (Fig. 7,*14*). In some Irregulares with much imperforate dissepimental tissue, an imperforate pellis or pellicle is considered by DEBRENNE (1964) to be present (Fig. 10). A clathrate wall consists of a fine grill of tenuous longitudinal plates applied to a series of thin annuli (Fig. 7,*8*); the grill of longitudinal laths may develop without the second system of transverse plates.

The outer wall of some Archaeocyatha is formed by conjunction of the downturned peripheral edges of the tabulae and an external microporous sheath may cover it (Fig. 7,*9*). An outer wall may be formed in some by lamellar thickening of the peripheral ends of the septa (e.g., *Anthomorpha*). In older forms of *Protopharetra* and *Dictyocyathus* the wall is not independent of the intervallar elements but is formed by them. Some Irregulares have an aporose external wall (*Archaeopharetra*), which may show growth lineation as in the epitheca of a coral.

INTERVALLUM

GENERAL FEATURES

The space between the outer and inner skeletal walls in Archaeocyatha is the intervallum. It becomes defined when the inner wall appears; in the Regulares this is commonly at a cup diameter between 0.13 and 0.2 mm., and in the Irregulares at a slightly greater cup diameter—0.5 to 0.7 mm. In a few species width of the intervallum is proportional to width of the central cavity, expressed as intervallum coefficient = width of intervallum/width of central cavity. In other species the width of the intervallum varies little once the adult characters are stabilized.

The two walls are commonly connected

FIG. 7. *(Continued from facing page.)*

canals (mod. Debrenne, 1964).

5. Thick wall with cylindrical, oblique pore-canals whose outer lower lips are extended as bracts, thus forming geniculate pore-tubes in *Porocyathus* (mod. Debrenne, 1964).

6. Clathrate wall, composed of longitudinal laths applied to oblique annuli that are in turn applied to outer edges of septa, in *Botomocyathus zelenovi* ZHURAVLEVA (Hill, n).

7. Wall of opposed peaks forming wide inverted V's at the outer edges of neighboring septa in *Annulocyathus pulcher* VOLOGDIN (Hill, n).

8. Wall of slightly resupinate louvers in three longitudinal series connecting outer edges of neighboring septa (Hill, n).

9. Wall formed from downturned edges of tabulae and with external microporous sheath (mod. Debrenne, 1964).

10. Simply perforate thin wall, circular pores in alternating rows in *Ajacicyathus* (mod. Debrenne, 1964).

11. Retiform thin wall with hexagonal pores, shown in *Erismacoscinus* (mod. Debrenne, 1964).

12. Thin wall with alternating chinky or slit-like pores (mod. Debrenne, 1964).

13. Perforate thin wall with an obtuse bract springing obliquely from the outer lower lip of each pore, the rows of pores alternating (mod. Debrenne, 1964).

14. Thick wall with conical pore-canals, covered by microporous sheath (mod. Debrenne, 1964).

15. Thick wall with horizontal pore-canals (mod. Debrenne, 1964).

16. Annulate wall formed by a series of resupinate horizontal shelves applied to outer edges of septa (mod. Debrenne, 1964).

17. Perforate thin wall with acutely pointed bract springing horizontally from the lower rim of each pore, the rows of pores concordant, shown in *Robustocyathus spinosus* ZHURAVLEVA (Hill, n).

18. Thin wall with tumuli each with several small pores (mod. Debrenne, 1964).

19. Thin wall with tumuli each with small, circular pore (mod. Debrenne, 1964).

20. Thick wall with conical pore-canals, covered with coarsely porous sheath (Hill, n).

21. Obliquely tangential thin section of a wall with a finely porous sheath developed externally, shown in *Ladaecyathus* (Hill, n).

22. Thick wall with large and small pore-canals, the latter opening from the surface through the wall segments into the large pores, shown in *Cryptoporocyathus junicanensis* ZHURAVLEVA (Hill, n).

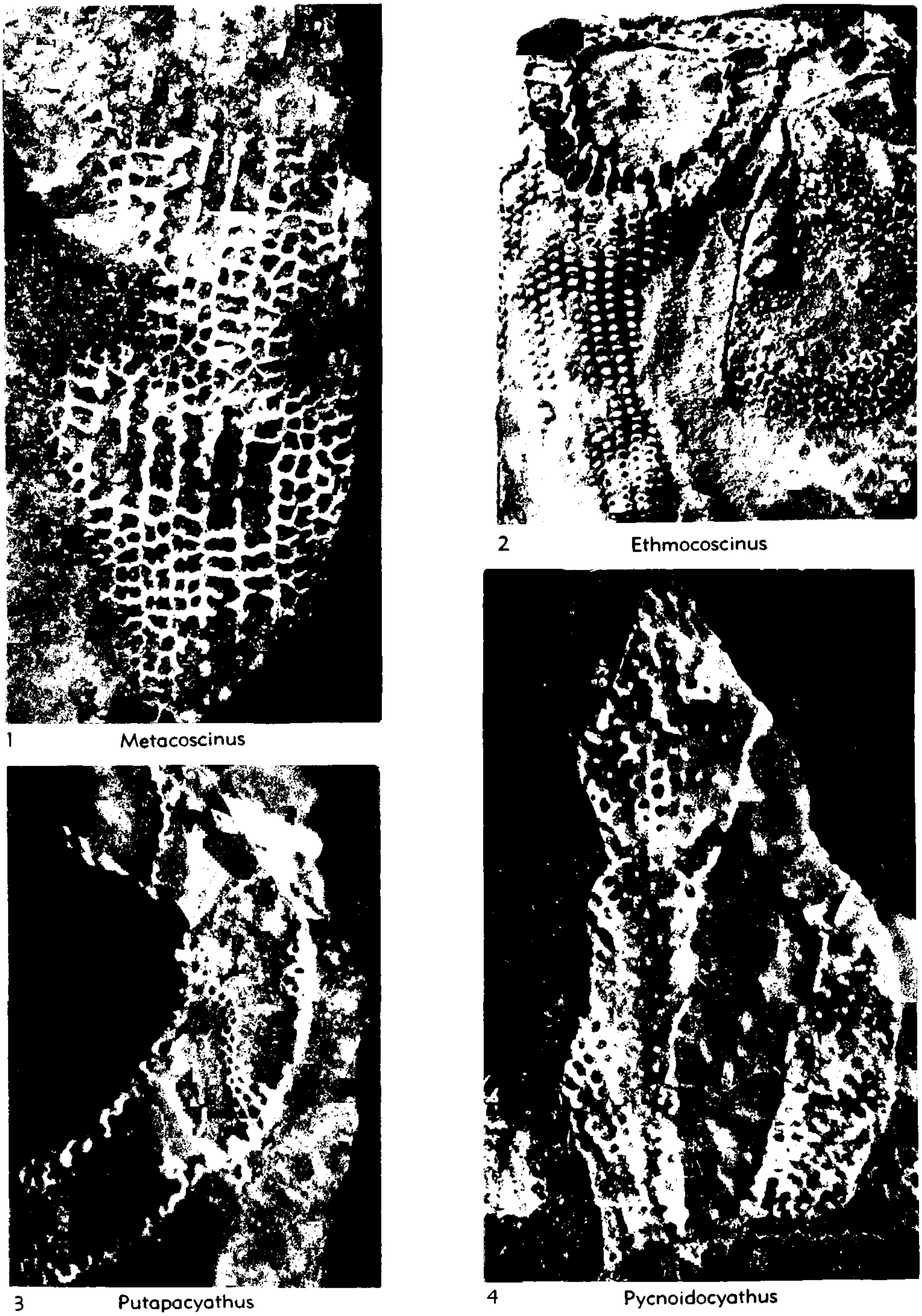


FIG. 8. Etched silicified specimens from the Ajax Limestone, South Australia.——*1.* Outer wall and outer edges of septa of *Metacoscinus reteseptatus* BEDFORD & BEDFORD, ×6 (Debrenne, 1969a).——*2.* Outer

and the intervallar space divided into interradial loculi by various types of radial skeletal elements—septa, pillars, rods, or tubules. **Septa** are more or less regular plates that divide the intervallar space into interseptal loculi, and interseptal segments of the walls may be referred to as **intersepts.**

The radial coefficient RK (number of radial elements/diameter of cup) is a useful magnitude, if for a given species the width of the interradial space is constant. In many species, however, this width increases slightly with growth of the cup. The size of pores and distance apart of the longitudinal rows of pores in the outer wall increase perceptibly with increase in diameter of the cup, so that the expression Rk defined as number of longitudinal rows of pores per intersept/diameter of cup is also useful in the description of species.

The intervallum is divided transversely except in the relatively small suborder Ajacicyathina and in the order Syringocnemidida. Transverse skeletal elements are tabulae (porous or pectinate) and imperforate dissepiments. Normally only the dissepiments may extend into the central cavity. The height of the intertabular loculi is seldom constant in a species.

SEPTA

In the two-walled Regulares, except in the suborder Dokidocyathina (with radial skeletal elements formed by radial rods arranged in horizontal planes), and the Putapacyathida (with the walls connected only by tabulae), the walls are connected by unwaved normally porous radial longitudinal plates or septa (Fig. 11,*1-11*). In the Regulares the pores are simple, rounded, or oval and arranged in longitudinal rows. In the Coscinocyathina these rows diverge from the middle of the septum toward the inner and the outer walls, and range in number up to 20; the pores are also arranged in transverse lines that curve perpendicularly to the rows they cross, with curvature the same as that of the tabulae

FIG. 9. Development of new longitudinal series of pores in intersept of outer wall shown by *Ajacicyathus sunnaginicus* ZHURAVLEVA, ×100 (Zhuravleva, 1960b).

(Fig. 11,*5*). New longitudinal rows appear near the axis of divergence of the rows. In the Nochoroicyathina the rows are in horizontal lines parallel to the tabulae. Normally the size of the pores is fairly constant in any one species, but some species have a few large pores in the older parts of the septum, and more and smaller pores higher up (Fig. 11,*2,3*). The pores of septa have

FIG. 10. Pellis of *Capsulocyathus subcallosus* ZHURAVLEVA, ×1.7 (Zhuravleva, *et al.*, 1964).

FIG. 8. *(Continued from facing page.)*

wall of *Ethmocoscinus papillipora* (BEDFORD & BEDFORD), with tumuli, each with single pore, ×4 (Hill, 1965).——*3*. Partial transverse section of *Putapacyathus regularis* BEDFORD & BEDFORD, showing walls and part of tabula, ×8 (Hill, 1965).——*4*. Longitudinal section of *Pycnoidocyathus decipiens* BEDFORD & BEDFORD, showing walls and septa, ×6 (Hill, 1965).

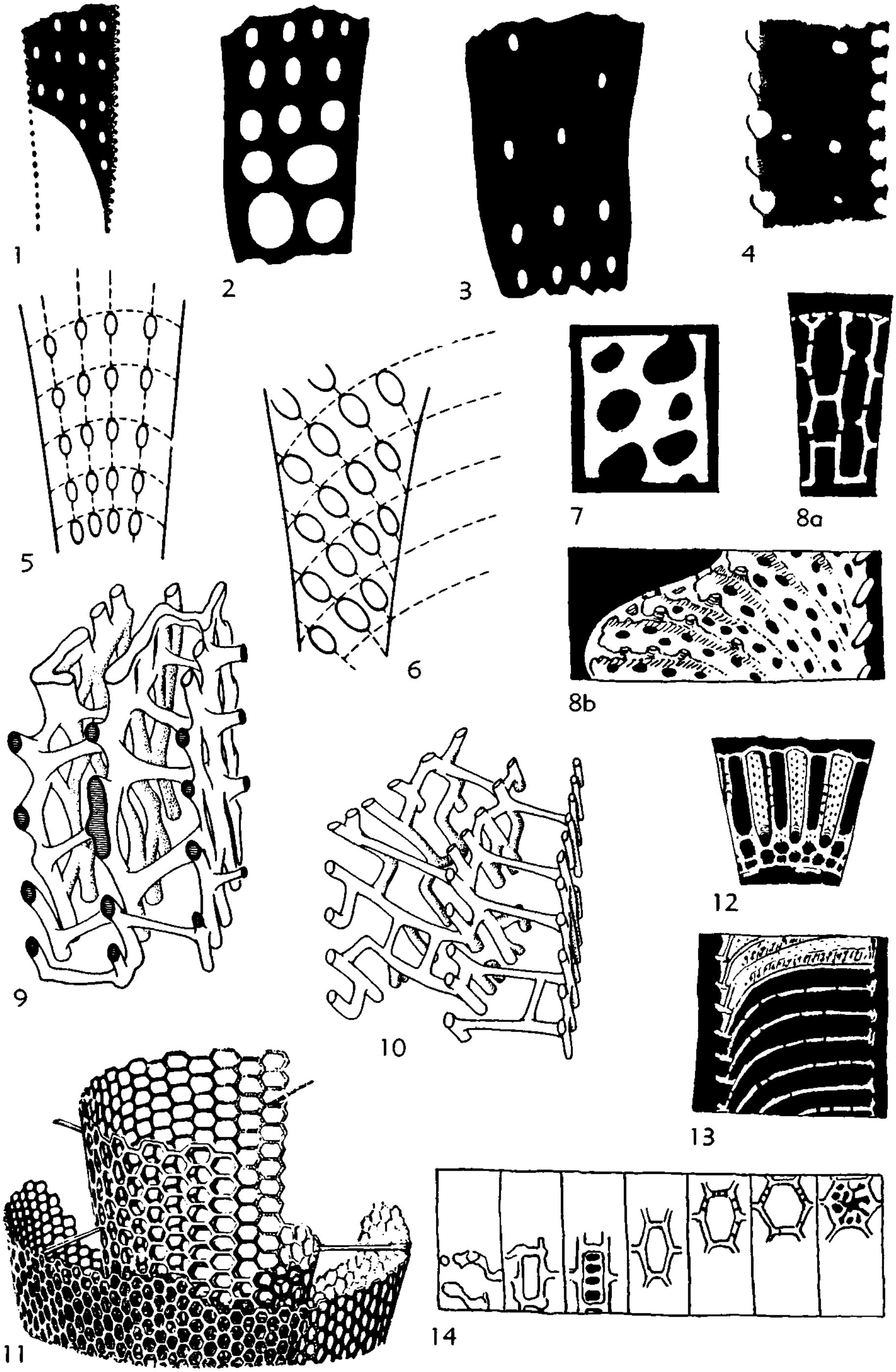


FIG. 11. Intervallar structures: septa and tubuli.

1. Growth of a new septum in *Ajacicyathus* sp., lateral view, outer wall to right, ×15 (Zhuravleva, 1960b).

2. Decreasing size of pores with growth of septum no screening devices or projections from their rims. Where the pores are large and close the septum becomes retiform, but commonly width of septal tissue between the pores is subequal to the diameter of the pores. In a few species the septa are porous only at their junction with one or both walls, where wall pores may be excavated in them to form stirrup pores (Fig. 11,*4*). Septal thickness commonly is characteristic for a species, but a few species have septa thicker in the middle of the intervallum, whereas in others the septa thicken at their junction with the walls. Especially in retiform septa one can analyze the septal tissue into longitudinal pillars and radial bars.

In the Anthomorphidae the septa are described as aporose plates showing a median dark zone surrounded on each side by clear, nonlaminated carbonate.

In the two-walled Irregulares the septa commonly are neither straight nor flat-sided, but appear irregularly waved or may be composed of irregularly sized and curving segments (taeniae); the name taeniae has also been used as a general term for septa of the Irregulares, but in view of the variety in methods of construction of the radial longitudinal plates in the class, the still more general term "septa," used for the radial longitudinal plates of Regulares, is preferred here, supplemented by phrases descriptive of the particular construction.

The commonly unequal to ragged pores of the irregularian septa in many genera are arranged in longitudinal rows curving slightly upward and outward from the inner wall (Fig. 11,*6*), and in transverse rows parallel to the curvature of tabulae; in some of these the septa may be waved in similar longitudinal curves, with crest of the waves occurring between the longitudinal rows. Where the crests of neighboring septa are opposite to one another and connected by synapticulae, a *Syringocnema*-like tubular boxwork is obtained.

In many Irregulares the radial elements are irregularly retiform due to their large unequal pores (Fig. 11,*7*); they then appear to consist of cylindrical or laterally flattened unequal pillars directed upward and outward from the inner to the outer wall, united in the radial plane by irregular rods (Fig. 11,*8*). This suggests that possibly the irregularian septum is built up from the rodlike skeletal elements of the early family Dictyocyathidae. In the young stages of this family no particular orientation of the rods is evident (Fig. 11,*9*,*10*), but in adult stages of some the radial skeletal elements consist of radial rows of longitudinal pillars that may be directed upward and outward from the inner wall with connection to one another in the radial plane by rods and to those of neighboring radial rows by synapticulae (Fig. 11,*11*). A very coarsely porous septum may thus be formed. Septal pores are unscreened and have no outgrowths from their rims.

Radial longitudinal pillars as such are

FIG. 11. *(Continued from facing page.)*

in *Ajacicyathus sunnaginicus* ZHURAVLEVA; lateral view of septum, ×30 (Zhuravleva, 1960b).
3. Decrease in number of pore-rows with growth of septum in *Erbocyathus heterovallum* (VOLOGDIN); lateral view of septum, ×30 (Zhuravleva, 1960b).
4. Septum with stirrup pores at outer (to left) and inner wall of *Tumulocyathellus unicumus* ZHURAVLEVA; lateral view, ×30 (Zhuravleva, 1960b).
5. Pore arrangement common in Regulares Coscinocyathina in diverging longitudinal rows and curving transverse rows (Zhuravleva, 1960b).
6. Pore arrangement common in Irregulares, in longitudinal rows curving upward and outward from inner to outer wall (Zhuravleva, 1960b).
7. Pores of different diameter and form in septum of Irregulares (Repina, *et al.*, 1964).
8. Pores of septum of *Pycnoidocyathus synapticulosus* TAYLOR; *8a*, part of transv. sec.; *8b*, lateral view of septum; ×3 (R. Bedford & W. R. Bedford, 1936).
9. Septa of *Volvacyathus* (Debrenne, 1964).
10. Rods and bars of *Dictyocyathus (Dictyocyathus)*, outer wall to left (Debrenne, 1964).
11. Radial rods between inner and outer walls of *Dokidocyathus regularis* ZHURAVLEVA, ×7.5 (Zhuravleva, 1960b).
12-14. Hexagonal tubuli of *Syringocnema favus* TAYLOR (R. Bedford & W. R. Bedford, 1936).——*12*. In transverse fracture of cup, ×3.——*13*. In longitudinal fracture of cup, ×3.——*14*. Serial sections of single hexagonal tubulus from inner to outer wall, ×6.

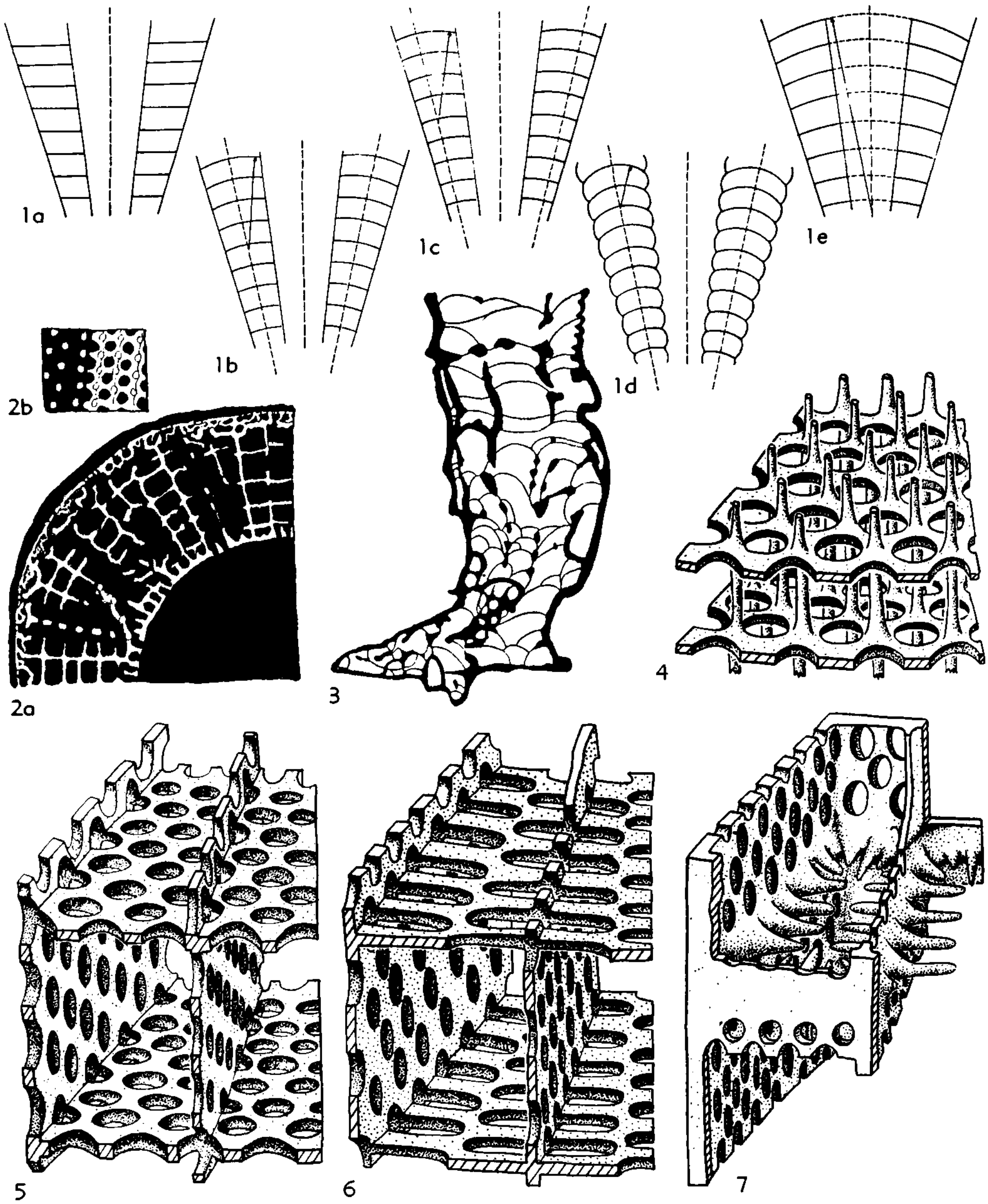


FIG. 12. Intervallar structures: synapticulae, tabulae, and dissepiments.——*1.* Different curvature of tabulae, shown diagrammatically in longitudinal section of the cup; *1a,* horizontal as in *Nochoroicyathus* and rarely in Coscinocyathina; *1b,c,d,* curved with axis of curvature within the intervallum, as in Coscinocyathina and Putapacyathida; *1e,* curved with axis of curvature in central cavity as in Archaeosyconina (Debrenne, 1964).——*2.* Synapticulae connecting septa in *Metafungia reticulata* BEDFORD & BEDFORD; *2a,* part of transv. sec. of cup; *2b,* oblique tang. sec. of septum, ×2.7 (R. Bedford & W. R. Bedford, 1934).——*3.* Dissepiments shown in long. sec. of *Bicyathus bateniensis* (VOLOGDIN) (Vologdin, 1959).——*4.* Harrow-like tabulae in *Hupecyathus* sp. (Debrenne, 1964).——*5.* Tabulae and septa with rounded pores in *Coscinocyathus* sp. (Debrenne, 1964).——*6.* Tabulae with slit-like pores in *Retecoscinus* sp. (Debrenne, 1964).——*7.* Pectinate tabulae in Nochoroicyathina (Debrenne, 1964).

present in the intervallar framework of the Archaeosyconidae. They curve upward and outward from inner to outer wall and perpendicularly to the tabulae, and may be homologous with the "pillars" of septal tissue between the longitudinal rows of pores in septa.

TUBULI

In the order Syringocnemidida the intervallum is filled with prismatic, porous-walled tubuli alternating in position in superposed rows; commonly the later young stages have randomly disposed rods and bars in the intervallum, the tubuli appear only after the inner wall is developed (Fig. 11,*12-14*). The tubuli are directed upward and outward from the inner wall, steeply upward at first, but then flattening to meet the outer wall almost at right angles.

TABULAE

Tabulae are the perforate horizontal skeletal elements that connect inner and outer walls surrounding the central cavity (Fig. 12,*1*,*4-7*). In the Regulares they may be convex upward, quite flat, or absent; where they are convex the crest of the curvature lies midway between inner and outer wall (Fig. 12,*1a-e*); commonly the tabulae of neighboring interseptal loculi are on the same level. Tabulae are commonly porous, with round or oval pores (Fig. 12,*5*); in *Retecoscinus* the pores are slit- or chink-like (Fig. 12,*6*). Tabulae become retiform when the diameter of the pores is greater than the width of skeletal material between the pores; the pores are never protected by spinules or rims. In one suborder with flat tabulae, the Nochoroicyathina, the tabulae are pectinate (Fig. 12,*7*); in each loculus the tabula consists of two opposed rows of cylindrical spines, that is, each tabula is formed of two combs, with teeth not quite meeting in the radial midline of the intervallum; these spines themselves may carry smaller spinules. Pectinate tabulae are of sporadic development. In the Irregulares only curved porous tabulae are known, but the curvature is centered within the central cavity. Synapticulae may be so positioned as to form a floor like a tabula (Fig. 12,*2*). In the Archaeosyconidae each tabula extends as a complete plate right around the cup, and the radial longitudinal pillars may be discontinuous above it (Fig. 12,*4*).

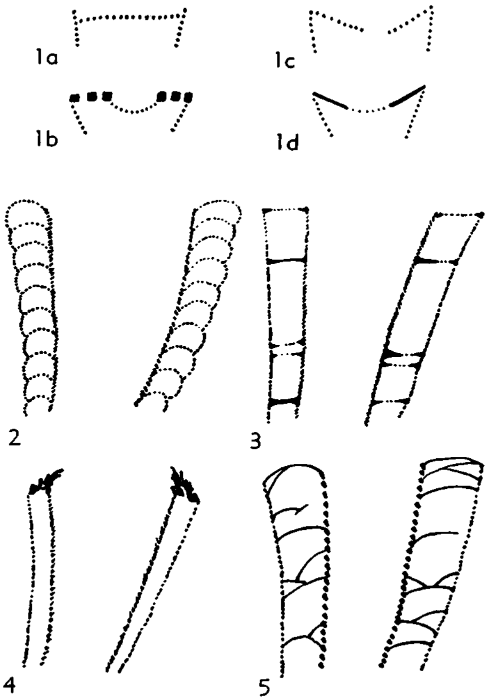


FIG. 13. Distal surface of cup (all from Zhuravleva, 1960b).——*1*. Pelta in single-walled cups, diagrammatic long. secs; *1a*, flat, porous pelta without central orifice in *Archaeolynthus polaris* (VOLOGDIN); *1b*, flat pelta with central orifice screened by porous membrane, in *Archaeolynthus uralocyathoides* ZHURAVLEVA; *1c*, curved porous pelta with central orifice, in *Archaeolynthus sibiricus* (TOLL); *1d*, curved aporose pelta with central orifice screened by porous membrane, in *Archaeolynthus uralocyathoides* ZHURAVLEVA.——*2*. Coscinocyathine with curved tabulae.——*3*. Nochoroicyathine with pectinate tabulae.——*4*. Ajacicyathine with hirsute cap.——*5*. Dictyocyathine, with dissepiments.

DISSEPIMENTS

These imperforate thin plates are nearly always convex as seen from above and may be either horizontally based, or inclined toward either the outer or the inner wall (Fig. 12,*3*). They cross interradial spaces in the intervallum and also may be found in the central cavity. They appear to have formed later than the septa against which they abut and are always thinner than the septa; only

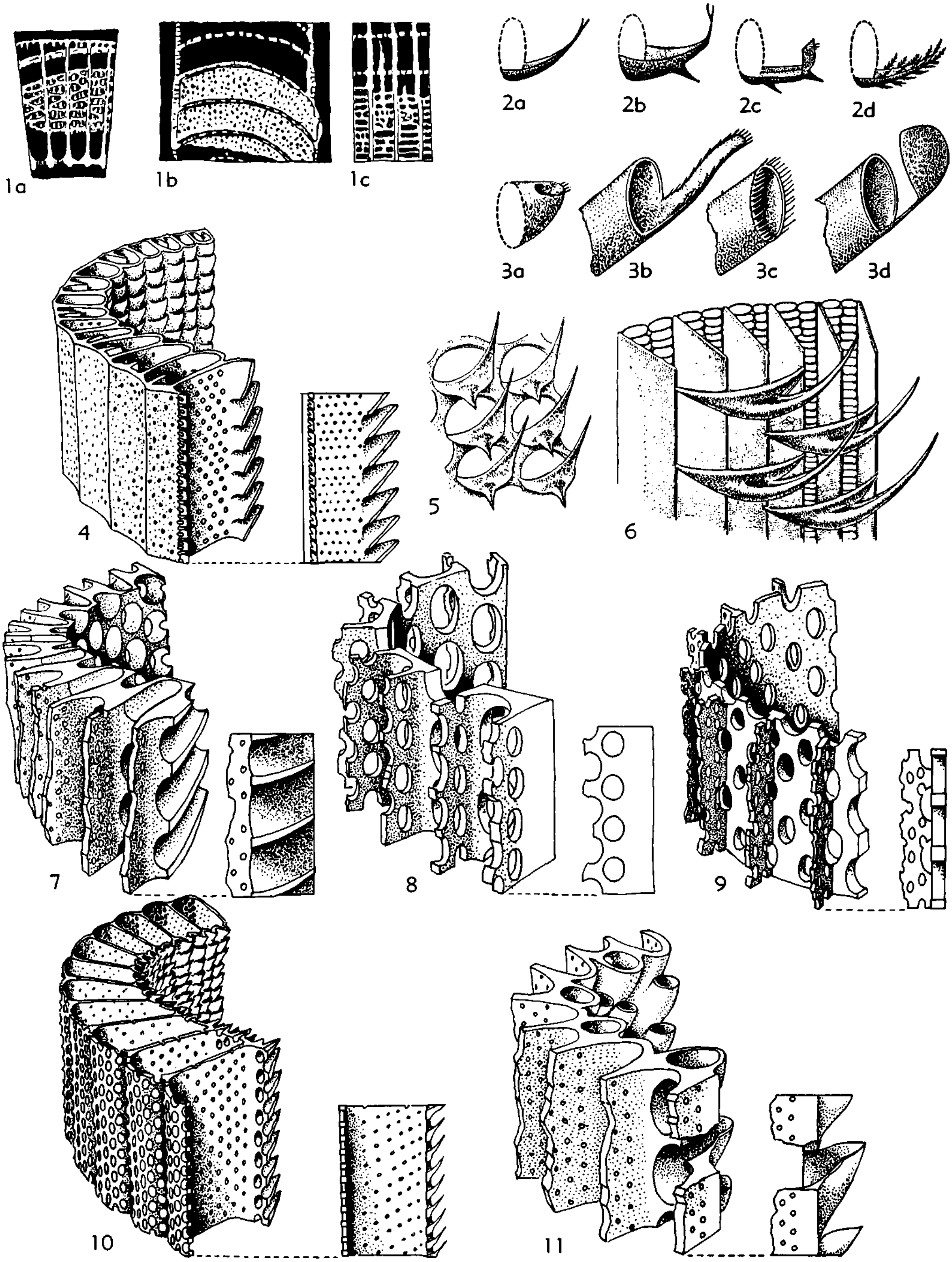


FIG. 14. Inner wall of Archaeocyatha.

1. Wall with rectangular pores and lintels, *Pycnoidocoscinus pycnoideum* BEDFORD & BEDFORD; *1a,* part of transv. sec.; *1b,* part of radial long. sec.; *1c,* tang. sec. inner wall, all ×2.7 (R. Bedford & W. R. Bedford, 1936).

2. Four types of spines projecting from the lower in rare cases are layers of secondary thickening seen on their upper surfaces. Very small dissepiments may be concentrated at the periphery of the intervallum in Irregulares, and may take over the binding function of the wall when the thin wall of such species is not preserved. Dissepiments are always the first skeletal elements formed in the apical cavity of Irregulares and are characteristic of this class. They may occur in the intervallum of some Regulares.

UPPER SURFACE OF CUP

It seems probable that individuals of tabulate Archaeocyatha ended their development and existence with the formation of the top tabula, whether porous or pectinate (Fig. 13,*2-3*). In the dissepimented *Loculicyathus* the upper surface is formed by dissepiments (Fig. 13,*5*). In at least one nontabulate species, the intervallum may be closed above by the union of the outer and inner walls in a cap from which spinules project (Fig. 13,*4*). In some single-walled Archaeocyatha a pelta is developed over the cavity, in some by the wall arching or bending over (Fig. 13,*1*).

INNER WALL

Endless variety, far greater than in the outer wall, is found in construction of the inner wall, but, in nearly all species, openings of the inner wall are larger than those of the outer wall (Fig. 14-16).

The inner wall is commonly a simply porous sheath developed at inner ends of the septa; if thin, it has round or hexagonal pores (Fig. 14,*8*), but if thick, horizontal, inclined, or elbowed pore-canals (Fig. 14,*7*; 15,*6*). In some walls pores, then called stirrup-pores, are excavated from the axial edges of the septa (Fig. 14,*9*). Another simple wall is one formed by growth of horizontal lintels between the septa or longitudinal ribs so that rectangular pores, which may have rounded corners, occur (Fig. 14,*1*).

In slightly more complex walls horizontal or inclined or resupinate scales or louvres grow into the central cavity from these lintels (Fig. 14,*4,10*); if the septa or longitudinal ribs also are produced into the central cavity, pore-tubes that are oblong or hexagonally prismatic spaces may be formed. Such pore-tubes may be geniculate upward or downward (Fig. 15,*6*), or be resupinate. In *Porocyathus* slats extend upward and inward to the intervallum opposite those that extend upward and inward to the axial cavity so that geniculate pore-tubes are formed.

Tuberculate and tumulose inner walls have perforate tubercles or tumuli springing from the rims of the pores (Fig. 14,*3*).

A spinose inner wall has spiny processes springing from beneath each pore, axially with an excavate upper surface, and curving upward and inward to the central cavity (Fig. 14,*2,5*; 15,*7*). In *Leptosocyathus* the bases of the spinose processes each extend across three interseptal loculi (Fig. 14,*6*). In others the spines may be interconnected by lateral and dorsal and ventral spinules (*Clathricyathus robustus*) (Fig. 15,*8*). In a bracted inner wall the lower lip of the pore is produced inward and upward into the central cavity, in some resupinately, and when the sides of neighboring bracts join, pore-tubes are formed (Fig. 14,*11*).

FIG. 14. *(Continued from facing page.)*

rims of pores; *2a-d,* diagram. (Zhuravleva, 1960b).

3. Tumulose and tubulose wall pores with protective hairs and screens; *3a-d,* diagram. (Zhuravleva, 1960b).

4. Wall of curved louvres, diagram., in *Beltanacyathus ionicus* BEDFORD & BEDFORD (Hill, n).

5. Spinose inner wall of *Archaeofungia suvorovae* ZHURAVLEVA, the spines partially screening the pores (Zhuravleva, 1960b).

6. Scaly inner wall in *Leptosocyathus polyseptus* (LATIN), with each spinose scale extending in front of three intersepts (Zhuravleva, 1960b).

7. Thick wall with straight pore-canals (Debrenne, 1964).

8. Simply porous, thin wall with round pores in one longitudinal row to an intersept (Hill, n).

9. Wall with stirrup pores and two longitudinal rows of simple pores to an intersept (Hill, n).

10. Scaly inner wall, scales laterally contiguous, forming incomplete annuli, in *Cadniacyathus asperatus* BEDFORD & BEDFORD (Hill, n).

11. Wall of pore-tubes projecting into inner cavity (Hill, n).

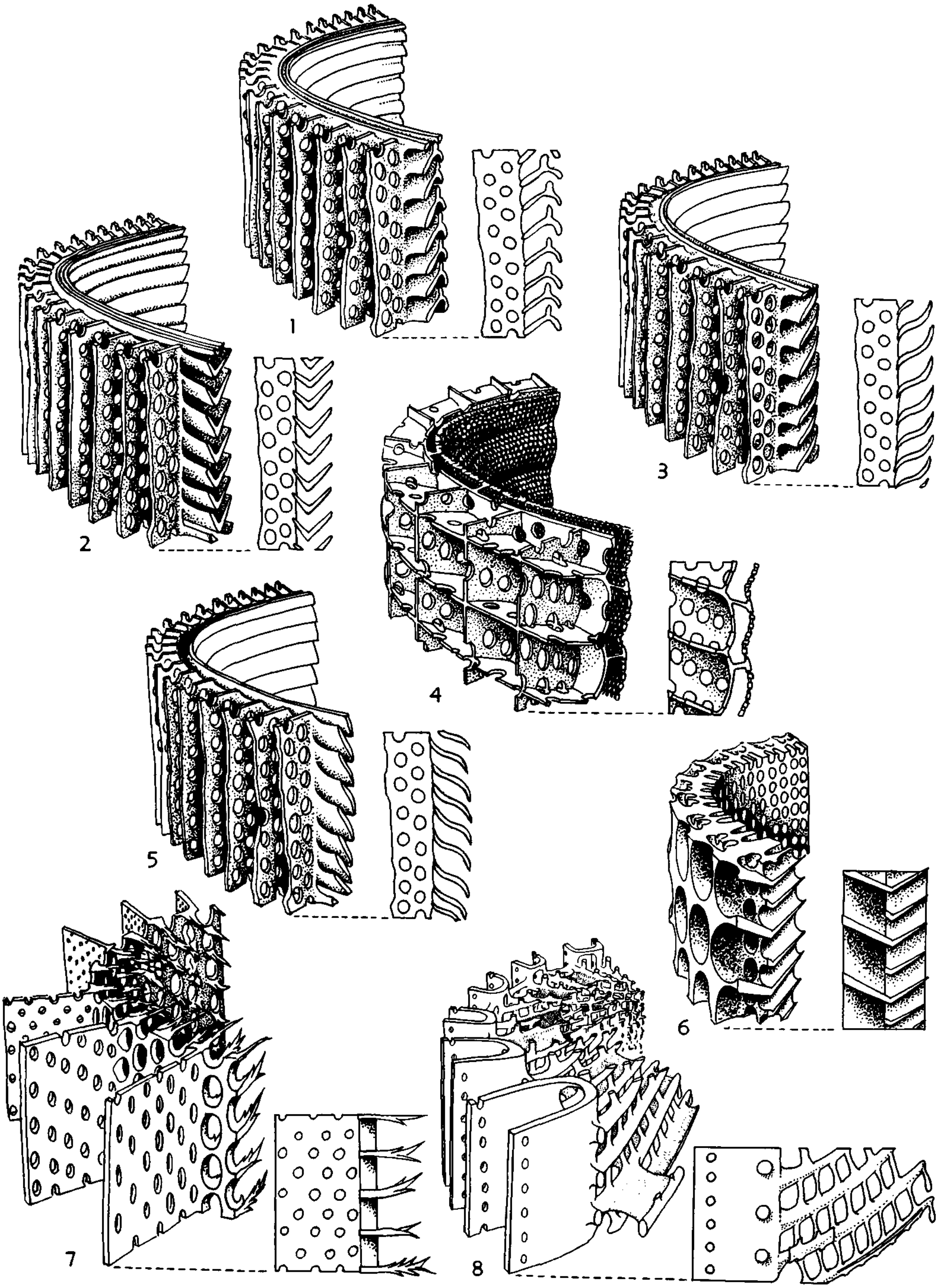


FIG. 15. Inner wall (continued) (Hill, n; all except 6 modified from Debrenne, 1964).——*1*. Annulate wall, annuli of inverted Y section.——*2*. Annulate wall, annuli of V section.——*3*. Annulate wall, annuli of S section.——*4*. Inner wall formed of downturned inner edges of tabulae to which auxiliary screen is

Tubulose inner walls may be formed in many different ways additional to those mentioned above. Pore-tubes may be bent and in more than one series radially (*Formosocyathus*) (Fig. 16,*3*). The inner edge of a pore-tube may be fringed with spines or have resupinate processes extending from its lower sector, or have a perforate domed shield separated from it by an extension of one part of the edge (Fig. 14,*3*).

Septal pore-tubes are partly formed by a transverse (in *Ethmocyathus*) or inclined (in *Ethmophyllum*) opposed waving of the inner edges of the septa so that opposite crests join (Fig. 16,*2*). In *Ethmocyathus* the pore-tubes have hexagonal openings (Fig. 17).

Annulate inner walls are fairly common. In these walls, annulate shelves, which are flat or upright, or inverted U-, V-, or S-shaped in section, are applied to the axial edges of the septa (Fig. 15,*1-3,5*). They may be fringed with spinules (Fig. 16,*4*). In some species the shelves may project slightly into the intervallum between the septal ends.

An inner wall formed by the downturned edges of tabulae is known in *Calyptocyathus*. This has an additional fine screen suspended on short spines (Fig. 15,*4*). Similar additional very fine screens are found lining some inner walls, facing the central cavity (Fig. 16,*1*). These may be porous, supported by the axial edges of pore-tubes, or by projecting spines (Fig. 16,*4*) or they may consist of close, very thin threads (*Ethmocyathus*) applied to the axial edges of pore-tubes (Fig. 17).

CENTRAL CAVITY

The central cavity is the space inside the inner wall. As a rule it is free of skeletal elements, but these may occur in the lower parts of the cup (Fig. 18; see Fig. 75,*4*). Thus dissepiments are found in some and may be continuous with the dissepiments of the intervallum. Radial rods may occur with the dissepiments. The cavity may be filled with secondary thickening deposited parallel to the inner wall and this may be canaliculate. More rarely it may be filled with septate (and tabulate) outgrowths from the intervallum. In some forms the outgrowths may be tubulose, the tubuli being bent and having porous and secondarily thickened walls. In discoid cups the central cavity scarcely can be regarded as a cavity. In some sections of a cateniform colony opposite intervalla are in contact without any intervening cavity.

SOFT PARTS

No impressions of the soft parts of Archaeocyatha have been found in mud or fine sand. Some authors hold that accidentally calcified soft parts have been found (VOLOGDIN, 1931, 1948, 1957b, 1962b; MASLOV, 1960). These "calcifications," which they suggest occurred because of the absence of putrefactive microorganisms in the water, or because the dead bodies fossilized very rapidly in water that was rich in dissolved bicarbonates of calcium and magnesium, are of two kinds: 1) dense enveloping material sheathing both the septa and the outer and inner surfaces of the walls, and 2) material surrounding canal-like spaces within the central cavity, the canals being continuous with the pores of the inner wall (Fig. 6,*11,14*). VOLOGDIN (1962b) considered that in some instances true skeletal supporting plates exist at the angles between three such surrounded spaces.

ZHURAVLEVA (1959b, 1960b), however, pointed out that the sheathing tissue of the first type, which has something of the appearance of the intracameral deposits of nautiloids, is often banded in such a way as to indicate periodic accretion parallel to its surface. This seems a better explanation than the one of accidental calcification of soft parts. The question of the origin of the second type is more difficult and is bound up with the interpretation of the nature of the archaeocyathan individual. VOLOGDIN interpreted the tubulose structure as due to accidental calcification of a ramify-

FIG. 15. (*Continued from facing page.*)

applied by thin rods, in *Calyptocoscinus* sp.——*5*. Annulate wall, annuli of inverted S section.——*6*. Wall of branching, geniculate pore-tubes, in *Heckericyathus heckeri* (ZHURAVLEVA).——*7*. Spinose inner wall.——*8*. Spinose inner wall with spines connected by transverse and longitudinal spines.

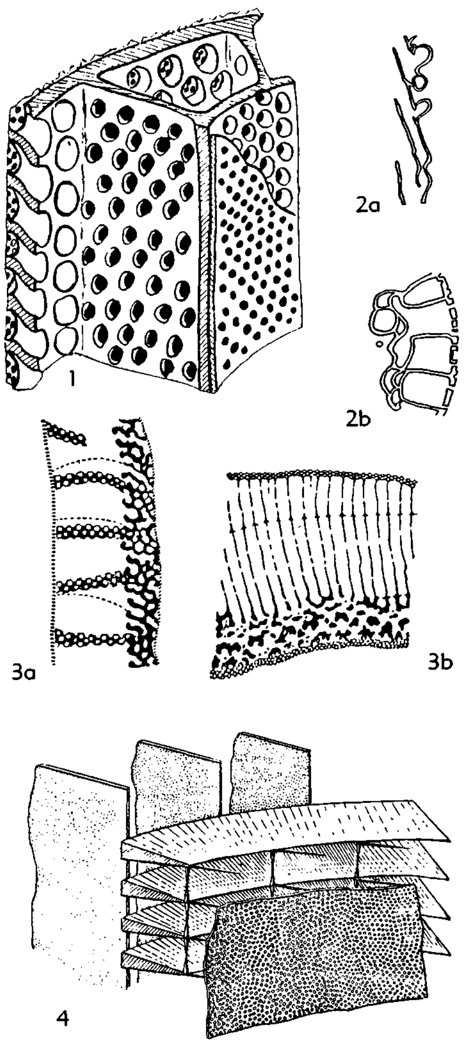


FIG. 16. Inner wall (continued).——*1*. Composite wall; simply porous, with auxiliary microporous screen (Repina, *et al.*, 1964).——*2*. Wall of ethmophylloid pore-tubes formed by the contiguity of waves of the inner edges of neighboring septa; *2a*, long. sec. of wall; *2b*, part of transv. sec. of cup, inner wall to left (Hill, 1965).——*3*. Formosocyathoid wall of tortuous pore-tubes and with a microporous auxiliary screen; *3a*, oblique radial long. sec. of part of cup, inner wall to right; *3b*, part of transv. sec., inner wall below (Vologdin, 1962d).——*4*. Annulate wall with microporous screen supported by radial spines, in *Compositocyathus* (Zhuravleva, 1960b).

ing digestive system; this would suppose an organization higher than that of sponges. ZHURAVLEVA regarded it as formed from an extrusion into the central cavity of soft tissue from the intervallum, this soft tissue then proceeding to secrete septal or dissepimental or tabular skeletal elements; and hers seems the better explanation. FONIN (1961) objected to both interpretations. He was unconvinced of the existence of an "internal digestive organ" in the central cavity, but could not accept that this was normally empty during the life of the individual. Another explanation offered for certain of the calcareous elements in the central cavity is that they were deposited by a second, single-walled archaeocyathan in symbiosis with the first (MASLOV, 1960).

The intervallum and not the central cavity is now generally considered to have been the site of the principal life processes. The pores of the walls are commonly considered to have enabled food-bearing currents to be drawn into the body. ZHURAVLEVA (1960b) and FONIN (1961) agreed that the currents flowed through the outer wall into the intervallum and then out through the central cavity via the inner wall. VOLOGDIN preferred the reverse direction. MASLOV (1961), basing his conclusion on his observation that either perforate or aporose pelta or opercula may develop at the growing end of the cup, considered that currents must have been able to flow either way through the pores of one-walled cups.

In ZHURAVLEVA's view, the skeleton of an archaeocyathan is an external, continuous sheet, formed in a similar way to that of the Protozoa. She considered the protoplasm to be continuous through pores in the septa but thought that the differing development of dissepiments, of skeletal thickening and sometimes of tabulae in neighboring interseptal loculi indicated a certain amount of independent vital activity from loculus to loculus. She thought this indicated that digestion took place not in a distinct layer of epithelial cells, as in coelenterates, but intracellularly, and also that special secretory organs were absent. Her view of the living matter of the archaeocyathan is thus that it consisted of uniform, undifferentiated cells (except for some sex cells), filling the intervallar loculi, the basic life processes taking place intracellularly, digestion and secretion being analogous to these in protozoans and sponges. This view seems to accord well with the facts. However, VOLOGDIN (1962b) thought, as a corollary to his views of "calcification" of the soft tissues, that the latter were cellular, having

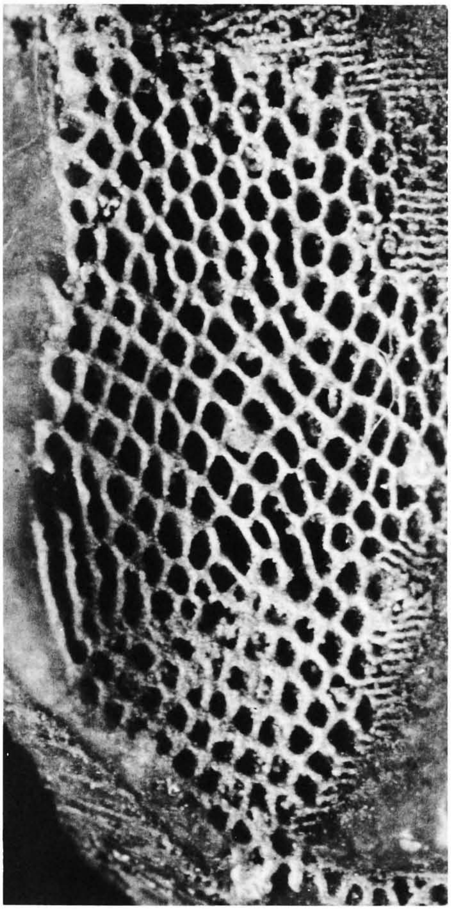


FIG. 17. Inner wall of *Ethmocyathus,* viewed from central cavity, showing inner ends of pore-tubes and part of screen of fine transverse laths (Hill, 1965).

FIG. 18. Central cavity shown in transv. sec. of *Asterocyathus salairicus* VOLOGDIN with inner wall to central cavity longitudinally deeply grooved at septal edges, ×?3.5 (Vologdin, 1962d).

functional and morphological differentiation, and that there was a system of capillary vessels connecting the various parts of the body in a single organism.

ZHURAVLEVA noted the presence of pores in both septa and tabulae, the continuity of the several skeletal elements and the fact that after injury to some loculi of the living cup, the archaeocyathan could heal the injuries and continue to build the cup. From these observations she concluded that the connection between the groups of cells in neighboring loculi was "incommensurably higher" than that between the cells even in such complex colonial unicellular organisms as the Volvocidae.

She concluded that the Archaeocyatha were the result of nature's first attempt to create a simple multicellular organism, and that with the beginning of a broad proliferation of the sponges, which were of similar ecology, the archaeocyathans were quickly extinguished. She considered the Archaeocyatha to be a multicellular phylum that arose independently from the unicellular organisms, with a degree of differentiation higher than that of the Protozoa, but lower than that of the Porifera.

ONTOGENY

The wide distribution of species and genera, and analogy with coelenterates and sponges, suggest that the Archaeocyatha had a planktonic larval stage that was without skeleton. However, certain small calcareous *problematica* from the Lower Cambrian of the USSR (Fig. 19) have been considered by VOLOGDIN (1932; 1957c) to represent larval or young stages of archaeocyathans and they were named by him "sphaerion," "fistula," and "dolium" stages, and to have been planktonic.

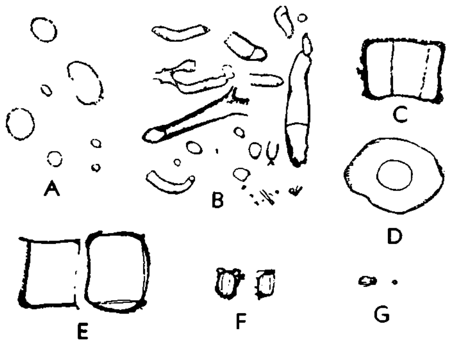


FIG. 19. Small calcareous problematica considered by VOLOGDIN (1931, 1932) to be larval and young stages of Archaeocyatha; *A*, "sphaerion"; *B*, "fistula"; *C-G*, "dolium"; all ×13.

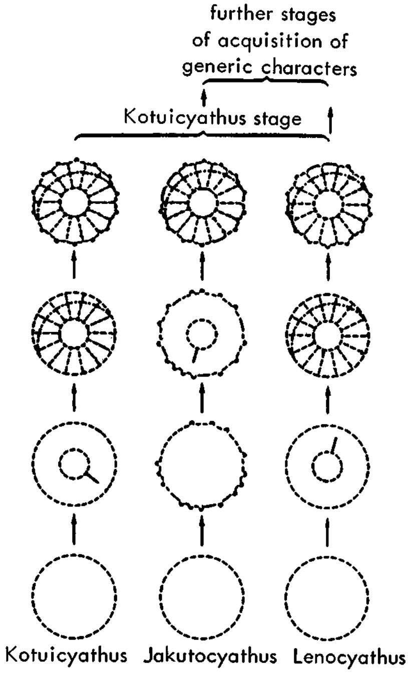


FIG. 21. Ontogenetic stages of development in genera of the family Lenocyathidae. Outer wall tumuli appear before inner wall, septa, and tabulae, in *Jakutocyathus (Jakutocyathus)* and after them in *Kotuyicyathus* and *Lenocyathus,* demonstrating heterochronous parallelism (after Rozanov, 1963).

The few studies of ontogeny based on longitudinal or serial transverse sections of individual archaeocyathan cups suggest that postlarval development began with the formation of an aporose curved sheet that became the tip of the cup as the archaeocyathan grew. The edge of this calcareous sheet grew upward and outward to form the outer wall of the conical cup (Fig. 20).

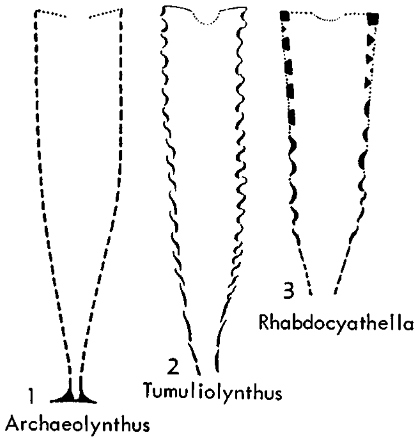


FIG. 20. Ontogenetic stages of development in one-walled cups (Zhuravleva, 1963b).——*1. Archaeolynthus,* showing wall with simple pores throughout.——*2. Tumuliolynthus,* showing adult wall with tumuli.——*3. "Rhabdocyathella,"* showing adult wall thick with external microporous sheath.

At a cup diameter of 0.15 to 0.2 mm., simple pores appear. In Irregulares, dissepiments next appear, followed in two-walled forms by disoriented rods, and then by the inner wall, simply porous at least at first, and by some tabulae; in later stages the disoriented rods may be replaced by septa, or, in the Syringocnemididae, by hexagonal tubuli, and either or both walls may become complex. In two-walled Regulares a simply porous inner wall appears with or slightly earlier than the first intervallar structures, which in some are rods, in others are septa; tabulae may then appear, and both walls may become complex, and the complexity may increase; in some, complication of the outer wall may begin before the appearance of the inner wall and septa (Fig. 21).

EVOLUTION

ONTOPHYLETIC SPECULATION

It has been suggested that current classification of the Archaeocyatha is a phyletic one, and that ontogenetic studies support this view. Thus, ZHURAVLEVA (1960b) con-