INTRODUCTION TO TABULATA

MORPHOLOGY

The Tabulata are an extinct, almost entirely Paleozoic order of corals characterized by their exclusively colonial mode of growth and by secretion of a calcareous exoskeleton of slender tubes crossed by many fragile transverse partitions called tabulae. Relative prominence of these tabulae and inconspicuousness of radial longitudinal skeletal elements (septa, spines, and squamulae) are features that suggested the name of the group.

Mechanical and photographic techniques used in the preparation of Tabulata for study are the same as those described for the Rugosa on page *F*64 of this work. The biometric techniques of statistical analysis and numerical taxonomy are mentioned in the section on Classification.

Morphological terms applied to tabulate corals are printed in boldface type in the introductory text that follows. Most are included in a glossary of morphological terms used in describing both Rugosa and Tabulata (see page *F*32). The following morphological terms are used exclusively for Tabulata.

alveolitoid. Type of reclined corallite having vaulted upper wall and nearly plane lower one parallel to surface of adherence of corallum, as in *Alveolites*.

canal. See mural tunnel.

cateniform. Corallum with corallites united laterally as palisades that appear chainlike in cross section, the palisades commonly forming a network.

coenenchymal increase. Type of increase in which offsets arise from coenenchyme, as in Heliolitina and Halysitina.

COENENCHYME (coenosclerenchyme). Common skeletal tissue uniting offsets.

cribriform wall. Irregularly perforate wall.

encrusting. Thin corallum adhering to a surface and following its irregularities.

MURAL PORE. Circular or oval small hole in wall between adjacent corallites, as in *Favosites*.

mural tunnel (canal). Elongate space extending through thick common wall from mural pore.

pore-plate. Thin diaphragm closing a mural pore.

reclined. Corallite growing and opening obliquely with respect to surface of corallum.

septal spine (spine). Spinelike trabecula projecting free from wall or septal comb, one of a longitudinal series.

squamula. Small plate projecting subhorizontally in eavelike manner from wall of corallite toward axis.

terminal calice. A surface calice that differs structurally from the earlier, vacated calices of deeper levels of the corallum.

FORM OF CORALLUM

The form of the complete, compound skeleton (**corallum,** pl., **coralla**) varies widely, depending mainly on the manner of increase and the arrangement and shape of the exoskeletons (**corallites**) built by the constituent individual polyps of the colony. The polyps are assumed to have been of one kind, with no differentiation of function.

The possibility that more than one kind of polyp was present in the tabulatan colony was first suggested by Nicholson (1875a, p. 248) for *Heliolites.* Following Moseley's descriptions (1877; 1881) and views of the development of the monomorphic alcyonarian *Heliopora,* Nicholson (1879, p. 242) considered two kinds of polyp to be present in this genus, and extended the conception to *Halysites* (1879, p. 230), in which Etheridge (1904, p. 19) thought three kinds were present; fairly wide acceptance of these ideas followed, but Bourne (1895), after detailed studies on *Heliopora,* concluded that its smaller tubuli are not modified zooids but are part of a complex system of coenosarcal solenia, while Lindström (1899, p. 8-18) effectively argued for the coenenchymal nature of the intertabularial skeleton in Heliolitina. Gradually a consensus emerged, expressed by Jones and Hill (1940, p. 192), that dimorphism in Heliolitina could not be accepted. Durden (1966, p. 49), in an abstract, denied that polymorphism was present in the halysitids, and their interstitial tubuli are herein considered coenenchymal, as they were by Lindström (1873a, p. 17). In some Favositina large corallites appear, surrounded by small corallites, and Moseley (1881, p. 124) suggested that these might have been secreted by autozooids and siphonozooids, respectively. Jones (1936b, p. 4) investigated this condition and found that it was governed by the rate of increase of the corallum

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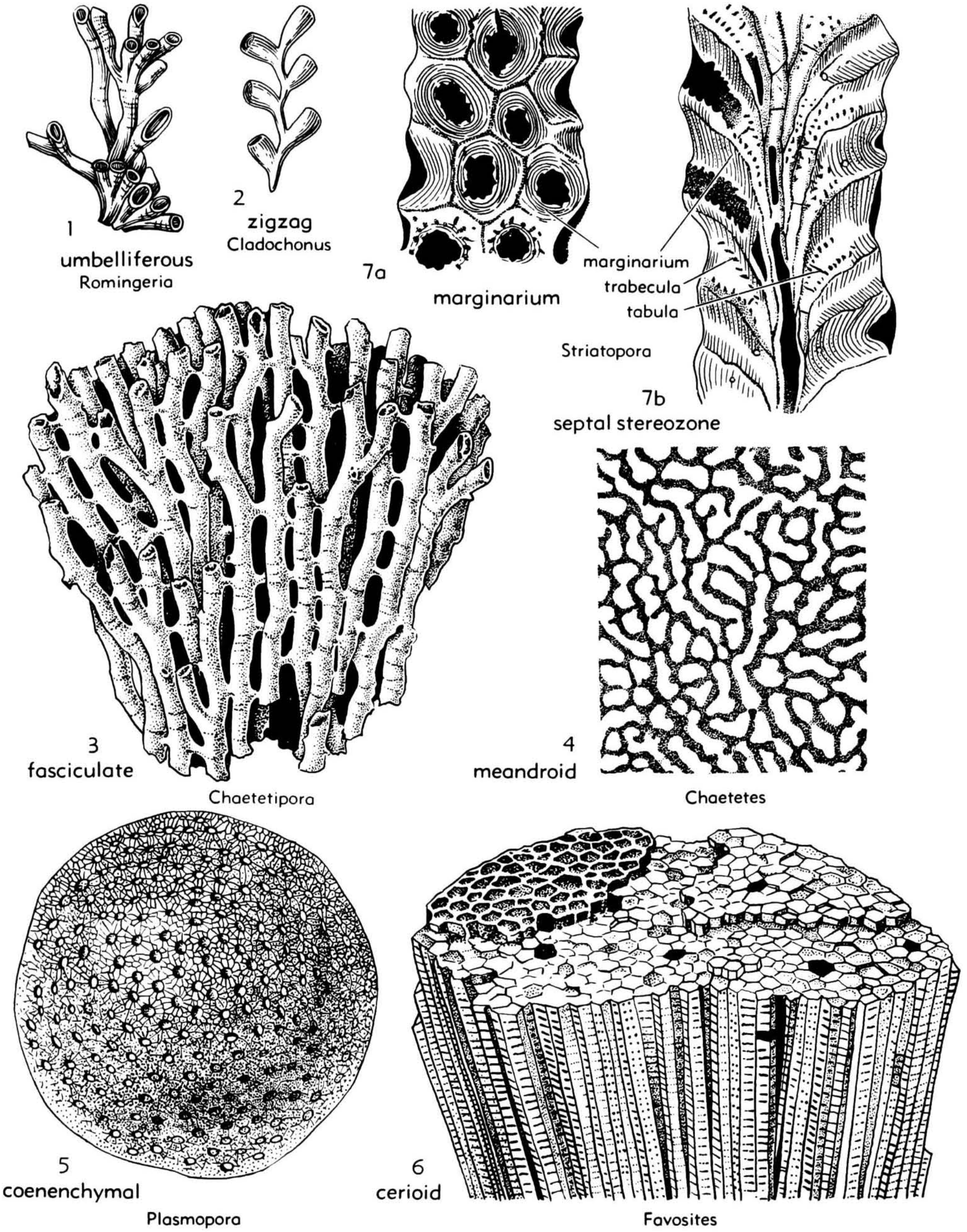

FIG. 284. Tabulate coral morphology; types of coralla (after Hill & Stumm, 1956).——*1.* Umbelliferous; *Romingeria umbellifera* (BILLINGS), M.Dev., Ont.; side of corallum, ×1.——*2.* Zigzag; *Cladochonus brevicollis* McCOY, L.Carb., Eng.; side of corallum, ×1.——*3.* Fasciculate; *Syringopora ramulosa* GOLDFUSS, L.Carb., Belg.; side of corallum, ×1.——*4.* Meandroid; *Chaetetipora septosa* (FLEMING), L.Carb., Wales; transv. sec., ×8.——*5.* Coenenchymal; *Plasmopora petalliformis* (LONSDALE), M.Sil., U.K.; surface of corallum, ×1.——*6.* Cerioid; *Favosites gothlandicus* LAMARCK, Sil., Gotl.; corallum broken along walls of prismatic corallites, ×1.——*7.* Marginaria in corallites of massive branching coralla; *Thamnoptychia ornata* (ROMINGER), M.Dev., N.Y.; *7a,* tang., *7b,* long. secs., both ×7.

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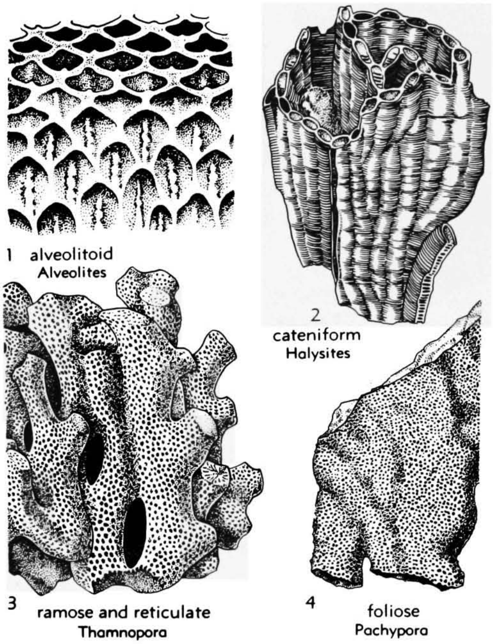

FIG. 285. Tabulate coral morphology; types of coralla (after Hill & Stumm, 1956).——*1.* Alveolitoid; *Alveolites suborbicularis* LAMARCK, M.Dev., Ger.; part of surface showing form of nearly recumbent (alveolitoid) corallites with large septal spine in middle of lower wall, ×0.7.——*2.* Cateniform; *Haylysites labyrinthicus* (GOLDFUSS), Sil., Netherlands; corallum, ×0.7.——*3.* Ramose and reticulate; *Thamnopora reticulata* (DE BLAINVILLE), M.Dev., Ger.; surface of corallum, ×1.——*4.* Foliose; *Pachypora lamellicornis* LINDSTRÖM, Sil., Gotl.; surface, ×0.7.

and the rate of growth of the offset. SOKOLOV (1955, p. 136) gave a similar explanation for *Oculipora.* Similarly, regularities in location and rate of production of offsets have been described by OLIVER (1966, p. 449) in the branching *Striatopora flexuosa* HALL, but the results of such regularities can scarcely be described as dimorphic. OLIVER (1975b) considered dimorphism to be present in his two new genera *Lecfedites* and *Bractea.* In both, corallites are of two sizes, large and cylindrical with projecting calical wall, and small and prismatic; squamulae are developed only in the large corallites in *Lecfedites,* but in *Bractea* they are found in the smaller corallites also.

The corallites of Tabulata are slender in comparison with those of other Zoantharia, their diameter ranging from approximately 0.2 to 20.0 mm. Maximum diameter of coralla ranges from a few millimeters to two meters or more.

Coralla in which the corallites are not separated by space are **massive** (Fig. 284, *4-6*); those in which corallites are straight or curved cylinders that are not laterally contiguous are termed **fasciculate** (fruticose, shrubby) (Fig. 284,*1-3*). The corallum, whether massive or fasciculate, may be a laminar expansion, thin to almost filmy, or thicker and turf- or sodlike; such coralla result from concentration of the production of offsets (new corallites) in basal and peripheral parts of coralla. The corallum may be domed or hemispherical as a result of the more or less regular production of offsets throughout the corallum, or it may be nodulose, tuberoid, or irregular from the irregular production of offsets. A massive corallum may be slenderly or coarsely branching, the branches being cylindrical (**ramose,** Fig. 285,*3*) or flattened (**foliose,** Fig. 285,*4*), and either separate or joining to form a network (**anastomosing,** Fig. 285,*3*); branches form when production of offsets is localized and continued forward from particular points.

Massive coralla in which the corallites are contiguous and prismatic and have their axes normal to the surface are **cerioid** (Fig. 284,*6*); these characterize the Favositina. If the axes are inclined to the surface so that the upper side of the corallite is vaulted, the corallum is **alveolitoid** (Fig. 285,*1*), as in the Alveolitina; proximally these have a sheet of thin-walled corallites with axes parallel to substrate; **meandroid** coralla arise when new walls dividing offset from parent fail to develop fully (Fig. 284,*4*) as in some Chaetetina. Massive coralla with individual tabularia separated by common skeletal tissue are **coenenchymal** (or more pedantically, coenosclerenchymal, Fig. 284,*5*) as in Heliolitina. Massive coralla that are also branching and in which the corallites each develop distally a marginarium of thickened skeletal tissue distinguish the Pachyporicae (Fig. 284,*7a,b*) and some Alveolitina.

In massive coralla all except the calical surface is enclosed in epitheca with transverse growth wrinklings that may appear continuous or discontinuous between neigh-

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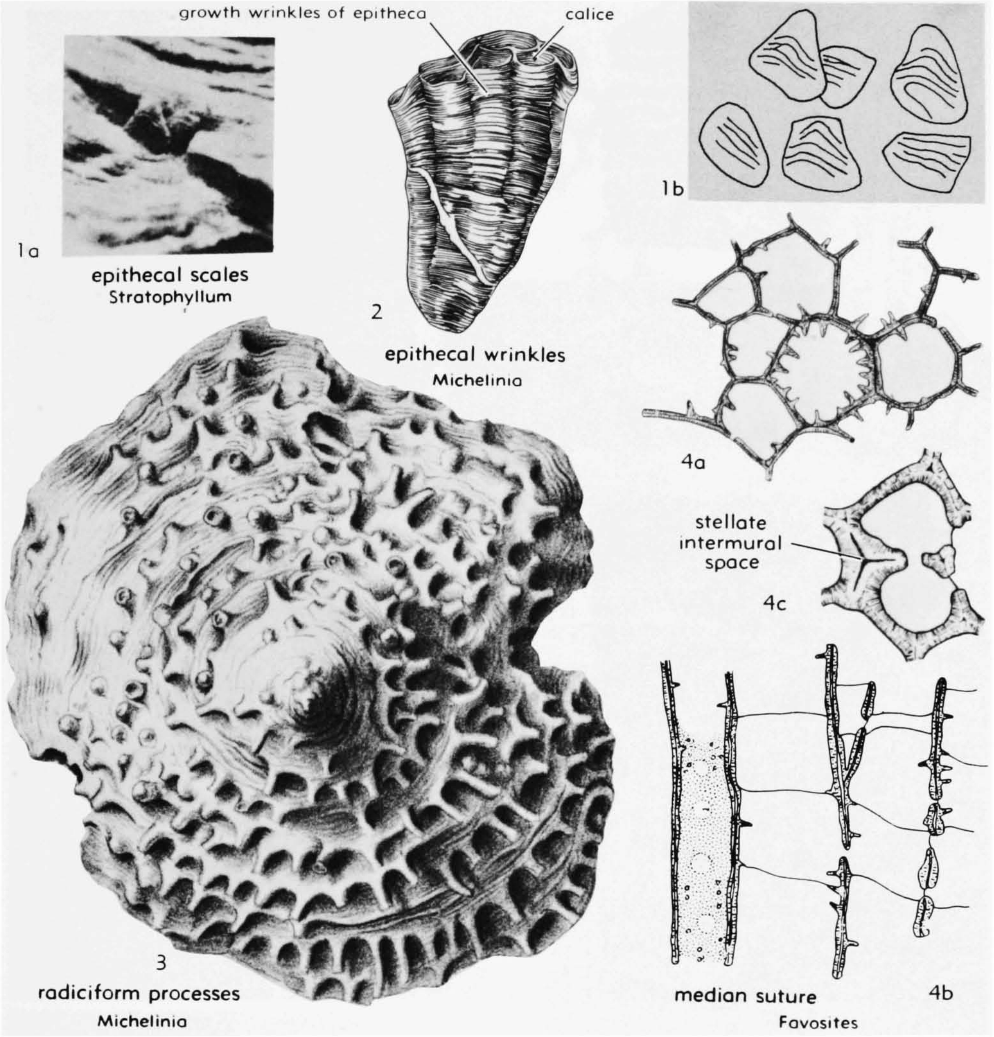

Fig. 286. Tabulate coral morphology; epithecal features.——*1.* Epithecal scales; *Stratophyllum tenue* Smyth, L.Carb., Belg.; *1a,* part of epitheca showing two scales, ×12, *1b,* scales showing pattern or ridges, ×20 (Smyth, 1933).——*2.* Epithecal wrinkles continuous in places from corallite to corallite, also calices; *Michelinia tenuisepta* (Phillips), L.Carb., Eng.; side of corallum, ×1 (Hill & Stumm, 1956).——*3.* Radiciform processes; *Michelinia favosa* (Goldfuss), L.Carb., Belg.; ×1 (de Koninck, 1872).——*4.* Median suture (dark line) in wall; *Favosites* sp., Dev., USSR; *4a,* transv. sec., *4b,* long. sec., both ×4 (Dubatolov, 1969); *4c, "F." grandiporus* Etheridge, transv. sec. showing "well-developed stellate intermural space" (herein interpreted as secondary alteration of median suture), ×20 (Philip, 1960).

boring corallites (Fig. 286,*2*). Schouppé and Oekentorp (1974, p. 88) interpret it as the sum of the outer layers of the outer walls of all the contiguous peripheral corallites.

Some Palaeacidae have superficial **epithecal scales** (Fig. 286,*1a,b*). *Michelinia* may have **radiciform processes** consisting of rootlike epithecate outgrowths (Fig. 286,*3*).

Fasciculate coralla in which the corallites are connected by tubuli (Fig. 284,*3*) characterize the Syringoporicae. In the Thecostegitidae, Chonostegitidae, some Roemeriidae, and some Sarcinulida, the corallites may be connected at intervals by horizontal laminar expansions (Fig. 287,*1*) with or without

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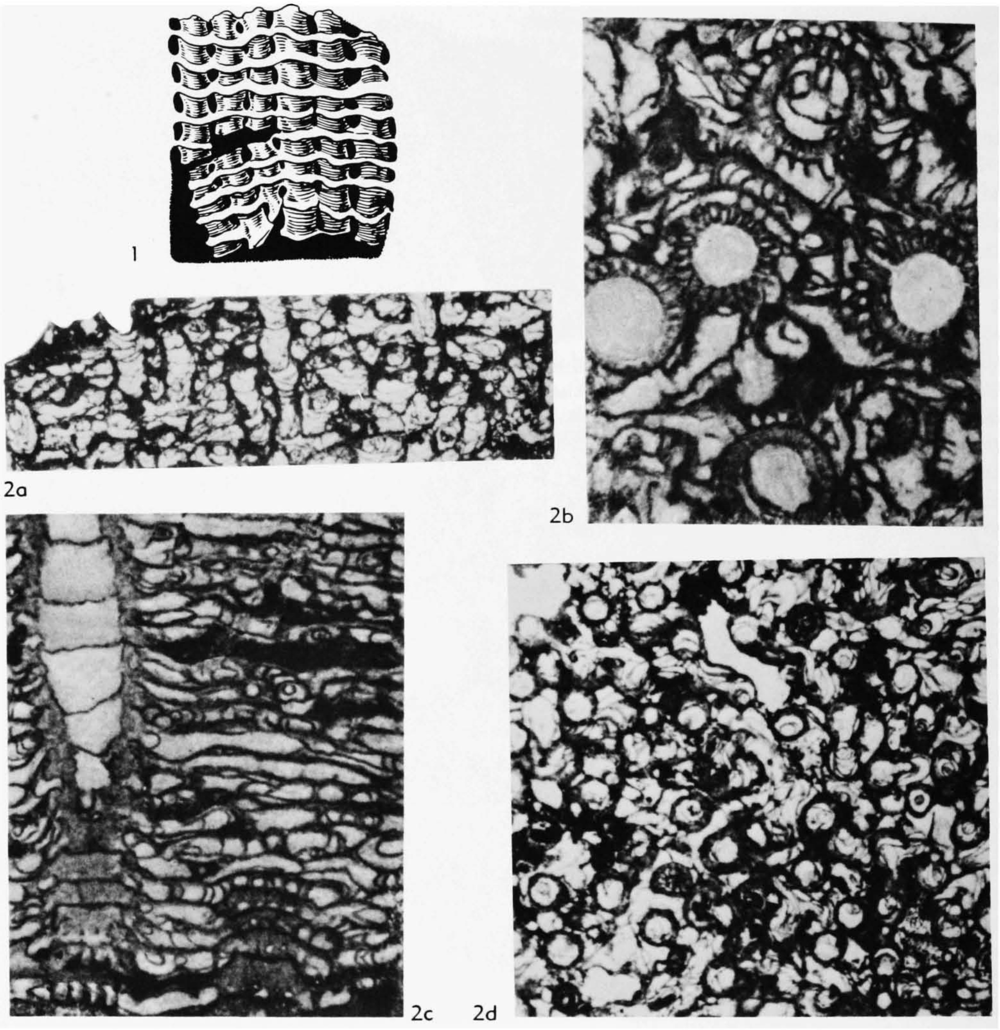

Fig. 287. Tabulate coral morphology; fasciculate coralla.——*1.* Coralla connected by horizontal lamellar expansions; *Chonostegites clappi* Milne-Edwards and Haime, M.Dev., Ohio; side of weathered corallum showing regularly spaced, flat, coenenchymal extensions connecting the cylindrical corallites, ×1 (Hill & Stumm, 1956).——*2.* Coralla connected by lamellar expansions with halos of tubuli; *2a,d, Thecostegites bouchardi* (Michelin), U.Dev., Frasn., France, Fergues, near Boulogne, *a,* long. sec., *d,* transv. sec., both ×4 (Hill & Jell, 1970a); *2b,c, Sarcinula luhai* Sokolov, U.Ord., Est., *b,* transv. sec., *c,* long. sec., both ×4 (Sokolov, 1955).

associated haloes of tubuli (Fig. 287,*2a-d*).

Cateniform coralla have their corallites united laterally in palisades generally one corallite thick, the palisades forming a network (Fig. 285,*2*). These characterize the Halysitina; in other groups they are uncommon and less regular.

The Auloporicae and the proximal parts of many Syringoporicae are **reptant** (procumbent, prostrate, Fig. 288,*3*) and formed

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Fig. 288. Tabulate coral morphology; types of coralla and increase.——*1.* Intracalicular peripheral increase; *1a-d, Favosites alpenensis bellensis* Swann, M.Dev., Mich., cross secs., ×25 (Swann, 1947); *1e-i, Paleofavosites* sp., U.Sil., USSR, serial cross secs., ×10 (Sharkova, 1971).——*2.* "Intermural" in-

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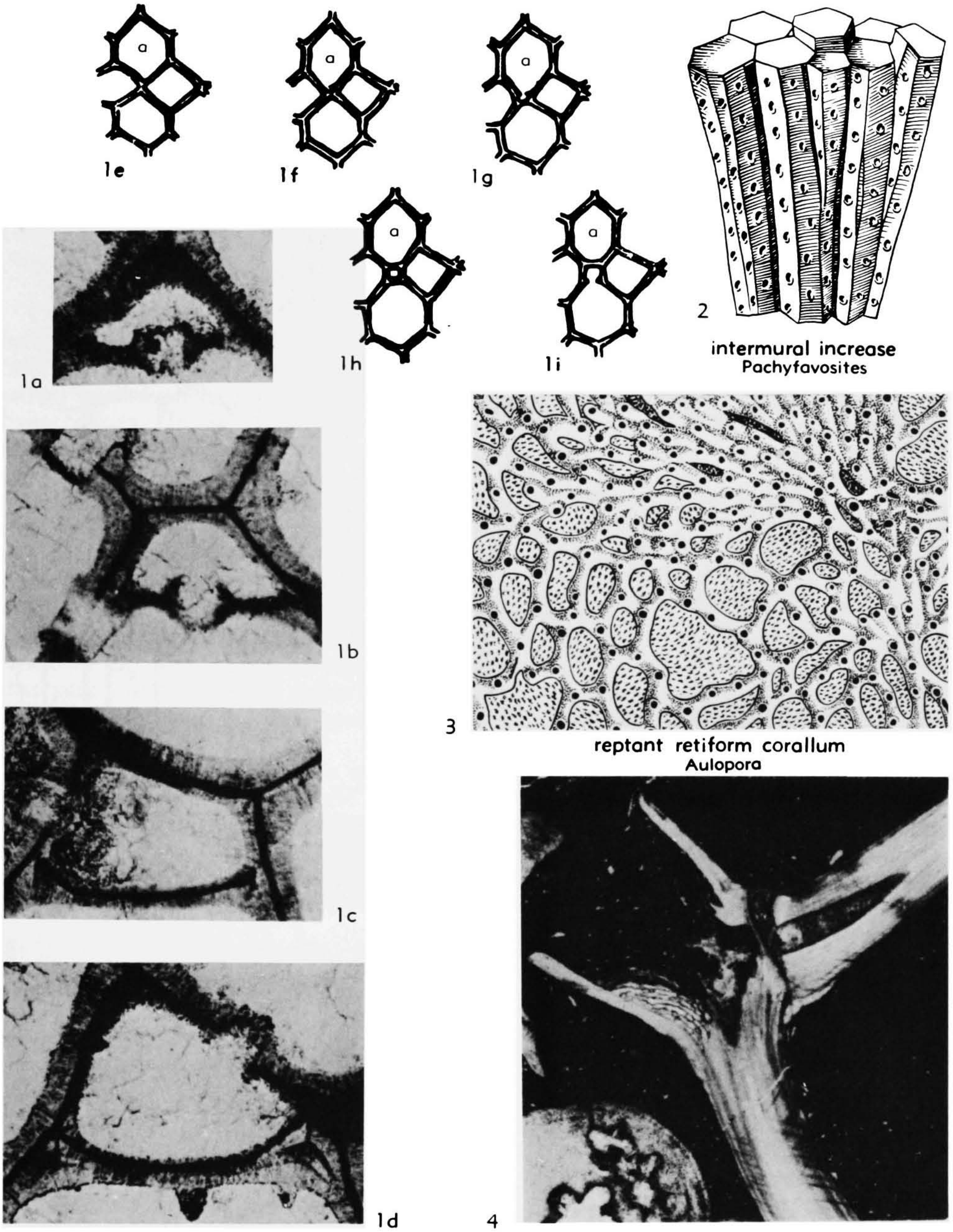

intracalicular peripheral increase
Favosites Paleofavosites

intermural increase
Pachyfavosites

reptant retiform corallum
Aulopora

lateral increase
Cladochonus

FIG. 288. *(Explanation continued from facing page.)*

crease; *Pachyfavosites polymorphus* (GOLDFUSS), M.Dev., Ger.; part of corallum broken along walls of prismatic tubes, showing prominent mural pores, enl. (Hill & Stumm, 1956).——*3.* Reptant retiform corallum; *Aulopora ?repens* MILNE-EDWARDS and HAIME, M.Dev., Ger.; upper surface of corallum showing circular calices of branching corallites (reptant on another coral), ×1 (Hill & Stumm, 1956).——*4.* Lateral increase; *Cladochonus crassus* (MCCOY), L.Carb., Eire; long. sec. of branch showing offset fractured along diaphragm, ×11 (Hill & Smyth, 1938).

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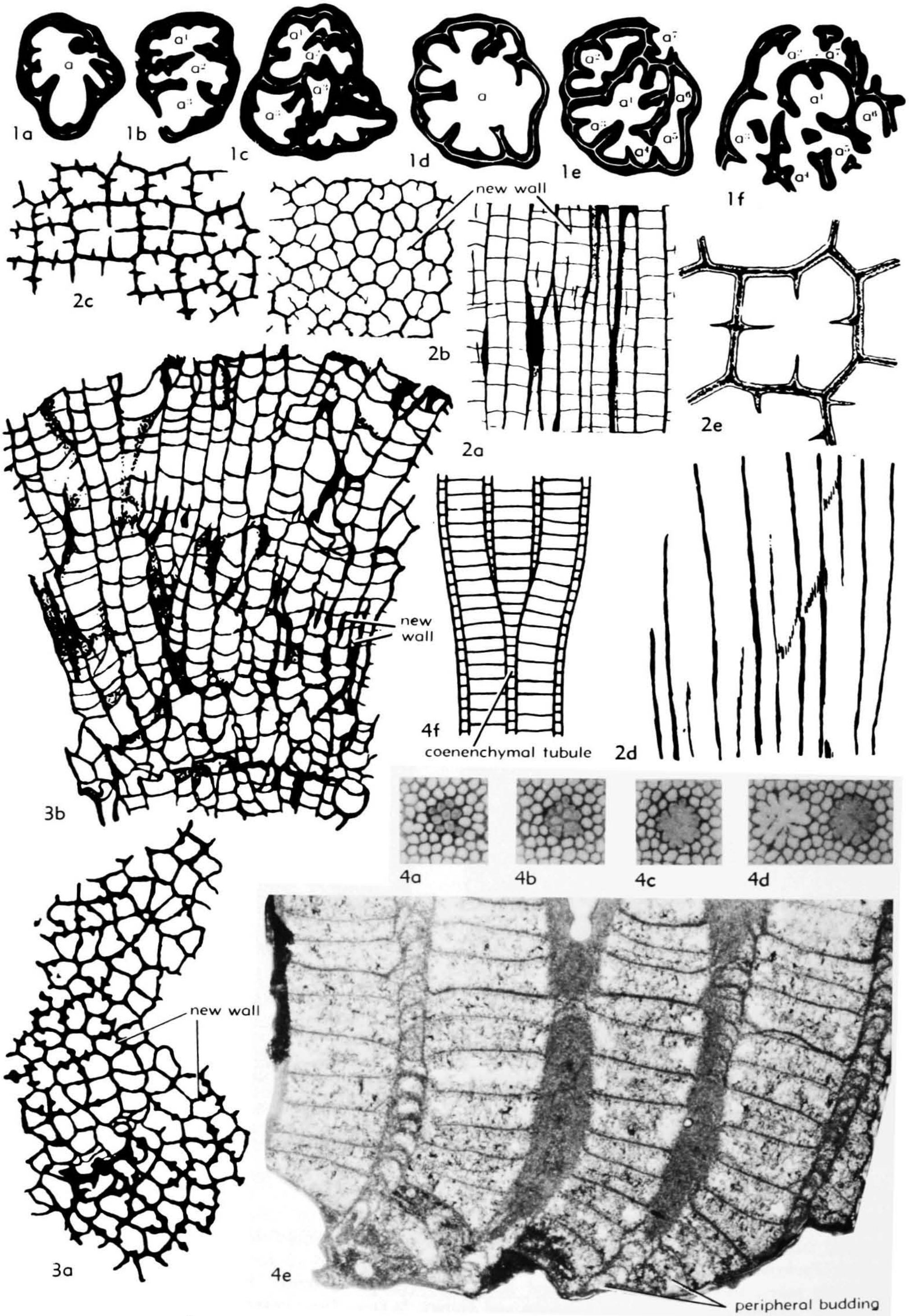

FIG. 289. Tabulate coral morphology; increase.——*1.* Axial increase in *1a-c,* Alveolitidae, *Scoliopora,* ×30; *1d-f,* Agetolitidae, *Somphopora,* ×25 (Sharkova, 1971).——*2.* Axial intracalicular increase;

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of separate or anastomosing chains of conical or cornute corallites that lie parallel to and in many cases are adherent by their basal surface to substrate. Either erect corallites, or slender branches, may arise from the reptant chains, singly or in whorls (**verticillate, umbelliferous,** Fig. 284,*1*); arrangement of corallites in the slender branches may be **zigzag** (Fig. 284,*2*) or **racemose** (like grapes on a stalk), or not regular.

INCREASE

The compound coralla of Tabulata are believed, by analogy with the compound Scleractinia, to result from asexual (vegetative) reproduction of the polyps of the living colony. In Scleractinia such reproduction is achieved by the budding of new polyps (buds, daughter polyps) from the mother polyp, either within or outside the ring of tentacles (intratentacular or extratentacular budding). For the new corallites formed in the compound coralla of extinct orders, the purely descriptive term **offsets** is used without genetic significance. Speculation on the kinds of asexual reproduction that gave rise to the new polyps secreting the offsets can thus be kept separate from factual observation.

Until recently few researches have been undertaken specifically on increase in Tabulata, but recent studies have caused considerable questioning of our traditional conceptions (OLIVER, 1966, 1968; WEBBY & SEMENIUK, 1969; SHARKOVA, 1971; MIRONOVA, 1974b; SCHOUPPÉ & OEKENTORP, 1974). The definitions and descriptions that follow are those appropriate to our present knowledge, but will assuredly be modified as results of studies using modern fine-scale serial sectioning techniques become available.

In fasciculate coralla the common form of increase is **lateral** (Fig. 284,*3*); the offset is found on one side of a corallite and joint epitheca appears to enclose continuously both corallite and offset; the diameter of the offset at its point of origin is seldom more than half that of the corallite and commonly is much smaller. The rate of expansion and the direction of growth of the offsets affect the form of the corallum. The **lumen** (space enclosed by the wall, in Tabulata the **tabularium**) of the offset may be continuous with that of the corallite, or there may be a diaphragm (porous in some) separating the two (Fig. 288,*4*). Lateral increase is dominant in Auloporicae and Syringoporicae; in the former HAMADA (1973, p. 28) described uniserial, unilateral, bilateral, and annular types as basic, with intermediates possible. STASINSKA (1974, p. 266) described lateral offsets in some Auloporida as originating on the calical surface of the wall, i.e., as peripheral intracalicular offsets; perhaps lateral increase is really only an extreme type of peripheral intracalicular increase.

Increase in the cerioid coralla of the Favositida has commonly been described as intermural (or intercalicular or interstitial), but has been considered, and even defined, as lateral increase affected by the conjunction of corallites so that the offset is forced to originate in the median suture between two corallites (Fig. 288,*2*). However, this is not yet confirmed by modern work. It is perhaps more likely that 'intermural' increase is peripheral intracalicular increase in which the offset arises at the extreme edge of the calice.

Peripheral intracalicular increase has been described in Devonian Favositidae by SWANN (1947; Fig. 288,*1a-d*); a new dividing wall encloses an initially very small peripheral part of the calicular platform of a corallite, commonly in the angle where two sides meet, or on a very short side, and may grow distally so that an offset is formed, the corallite continuing with

FIG. 289. *(Explanation continued from facing page.)*

2a,b, bipartite in Chaetetina, *Chaetetes giganteus* SOKOLOV, *a,* long., *b,* transv. secs., both ×4 (Sokolov, 1955); *2c-e,* quadripartite in *Tetradium fibratum* SAFFORD; *c,d,* corallum, transv., long. secs., ×4, *e,* corallite, transv. sec., ×12 (Bassler, 1950).——*3.* Unequal adaxial bipartite increase in Cryptolichenariidae; *Cryptolichenaria miranda* SOKOLOV; *3a,* transv., *3b,* long. secs., both ×10 (Sokolov, 1955).——*4.* Coenenchymal increase; *4a-d,* in Heliolitidae, *Heliolites interstinctus* LINNÉ, Sil., Gotl., serial cross secs., ×6 (Lindström, 1899); *4e,* in Halysitina, *Cystihalysites* sp., Sil., Gotl., peripheral production of coenenchymal dissepiments, ×7 (Hill, n; photograph courtesy B. D. Webby); *4f,* in Halysitina, *Halysites,* diagram., ×1 (Webby & Semeniuk, 1969).

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scarcely decreased diameter; mural pores may be developed in the new wall almost at its point of origin. Whether the new wall is laid down as a single partition as in peripheral calicular increase in Rugosa, as appears likely from SWANN's figures, remains to be established. SHARKOVA (1971, p. 59) stated that, in Ludlovian *Paleofavosites* and *Favosites,* intracalicular increase is effected peripherally, in the corners of corallites, by two laminae that extend, one from each of the opposite sides of the corner or short side, and join to form a dividing wall between corallite and offset (Fig. 288, *1e-i*).

Axial (adaxial, septal, longitudinal) **intracalicular increase** occurs in Chaetetida (Fig. 289,*2a,b*) and Tetradiida (Fig. 289,*2c-e*), in some Alveolitina and in the coenenchymal tubuli of Heliolitina. In bipartite axial increase, common in Chaetetida, a radial longitudinal lamina grows adaxially from the wall of a corallite to join at the axis with one from the opposite wall. Each of the two subequal corallites so formed are called offsets. Quadripartite axial increase is characteristic of the Tetradiida. Increase that has been described as unequal bipartite axial increase occurs in Cryptolichenariidae (Fig. 289,*3*), wherein dividing laminae grow out from either side of the angle between two walls, and in this form, which appears almost identical with peripheral intracalicular increase, only the smaller corallite is appropriately called an offset. In Alveolitina axial calicular increase is effected by the adaxial growth and union of opposite or neighboring coarse septal combs, up to three offsets being produced simultaneously, replacing the corallite (Fig. 289,*1*).

Coenenchymal increase occurs in Heliolitina (LINDSTRÖM, 1899, p. 19) and in Halysitina. Offsets may arise from coenenchymal tubuli by expansion in diameter and insertion of septal spines (Fig. 289,*4f*), or by gradual replacement of several tubuli to give a tabularium of normal diameter (Fig. 289,*4a-d*); other offsets may arise from coenenchymal dissepiments (Fig. 289,*4e*).

The adjective basal, like the adjective peripheral, should not be used without qualification to denote whether the increase being described is related to position in the corallum as a whole or in the calice of a single corallite.

MIRONOVA (1974b, p. 106) considered that three types of vegetative increase characterize the subclass Tabulata. The commonest is division, typical of Tetradiida, where the offsets are equal, but also typical of Favositida, in which it is very unequal. Lateral increase is typical of Auloporida, and coenosarcal (=coenenchymal) increase of Sarcinulida and Halysitida *(s.s.),* which MIRONOVA combined with Heliolitida in a subclass Heliolitoidea.

Speculations on the nature of the living tabulatan colony include those of PREOBRAZHENSKIY (1974b, p. 89) and BONDARENKO (1971a, p. 22). PREOBRAZHENSKIY considered that there were four types of tabulatan organism: individual (solitary, e.g., *Monotubella*), temporarily colonial *(Fletcheriella),* periodically colonial *(Syringopora),* and truly colonial (e.g., *Cladochonus,* with polyps somatically connected throughout the life of the colony). BONDARENKO suggested that the light and dark (or clear and dense) zones noted in many heliolitinan coralla are to be related to periods of alternating asexual and sexual reproduction in the living colony.

WELLS (1971, p. 748) in assessing what a colony is in anthozoan corals considered that the Rugosa increased asexually exclusively (except for rare abnormalities) by extratentacular budding followed by separation of the corallites as individuals. Extratentacular budding results in complete homeomorphic individuals, organically or structurally united as corms or colonies. Intratentacular budding in Scleractinia gives a compound individual, not a colony. WELLS did not discuss Tabulata specifically.

Perhaps one might speculate that in Tabulata, lateral, 'intermural,' peripheral calicular, and coenenchymal increase are found in coralla formed from colonies where asexual reproduction was by extratentacular budding, and that equal or subequal axial calicular increase (except in coenenchyme) was ultimately related to intratentacular budding.

CORALLITES

Each corallite is a slender tube of $CaCO_3$. Cross section varies from genus to genus and species to species, and even within spe-

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cies; it ranges from round to oval to elliptical; rounded-polygonal to polygonal (with from 3 to 12 sides, commonly 5- to 6-sided); or it may be alveolitoid, ranging from compressed-polygonal to semilunate to crescentic to chinklike. Corallites expand more or less rapidly in diameter and may be erect throughout their length or may curve more or less sharply over part or all of their length.

CALICE

The distal surface of each corallite is the **calice** (Fig. 286,*2*). It is commonly wider than deep, with a narrow border, steeply sloping sides, and flat or concave base. In corallites with thick walls (wide peripheral stereozones) the border may be wide and but slightly sloping; the border may show septal spines or septal ridges. In corallites that open obliquely, the calice is not round or rounded-polygonal in outline, but is compressed, commonly transversely to a branch, but in some longitudinally; in transversely compressed calices of branches or foliae the lower (outer) lip may be projected beyond the common surface; in alveolitoid calices the upper lip is vaulted and the lower reflects the shape of the surface of adherence of the inclined lower wall (Fig. 285,*1*). In cerioid coralla the sutural area between neighboring calices may be raised and acute or rounded, or faint to indistinguishable (Fig. 290,*1*). VOYNOVSKIY-KRIGER (1970, p. 106) has distinguished as **terminal calices** those surface calices that differ structurally from the earlier and vacated calices of deeper levels of the corallum; for instance, constricted terminal calices of *Mastopora,* and terminal calices with everted margins as in *Aulohelia.*

EPITHECA

In all fasciculate and probably in most cerioid coralla, each corallite is enclosed laterally in a sheath **(epitheca)** of $CaCO_3$. The epitheca is commonly without the longitudinal interseptal ridges and septal furrows that are seen in the Rugosa, but they are visible in some (Fig. 290,*4*), and transverse growth ridges or wrinkles are common. In thin section the epitheca is denser ('darker' by transmitted light) than the rest of the wall. The sutural area between neighboring corallites in most cerioid coralla is believed to contain the epithecas

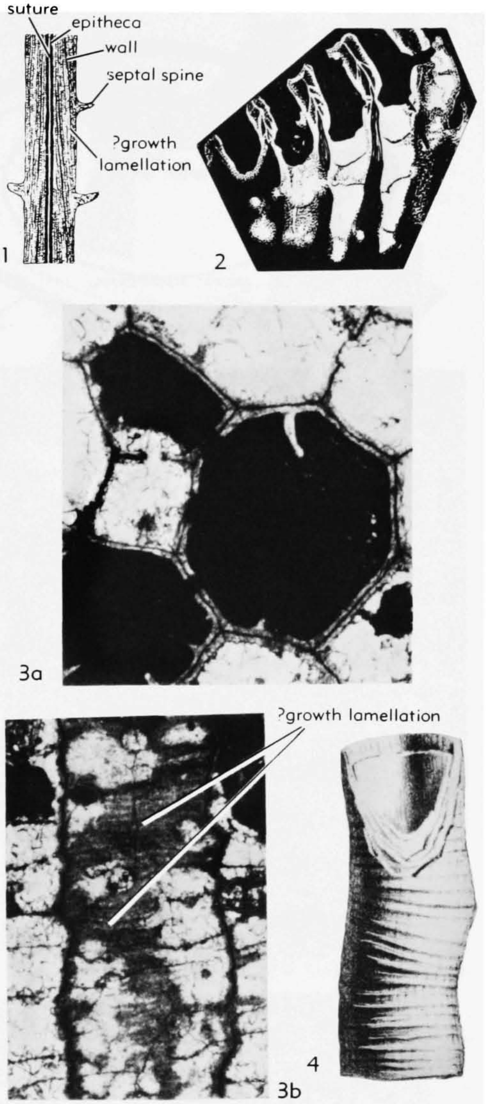

FIG. 290. Tabulate coral morphology; epitheca of corallites.——*1*. Sutural area of favositid, diagram. (Sokolov, 1955).——*2*. 'Median suture' in cerioid corallum; *Thamnopora cervicornis* (DE BLAINVILLE), M.Dev., Givet., Eu.; long. sec., ×4 (Hill & Stumm, 1956).——*3*. Epitheca between corallites of cerioid corallum; *Favosites gothlandicus* LAMARCK, U.Sil., Podolia; *3a,* transv., *3b,* long. secs., both ×13 (Tesakov, 1971b).——*4*. Epitheca in fasciculate corallite with traces of longitudinal (?septal) grooves; *Syringopora abdita* DE VERNEUIL, Dev., France; ext. view, enl. (Milne-Edwards & Haime, 1851).

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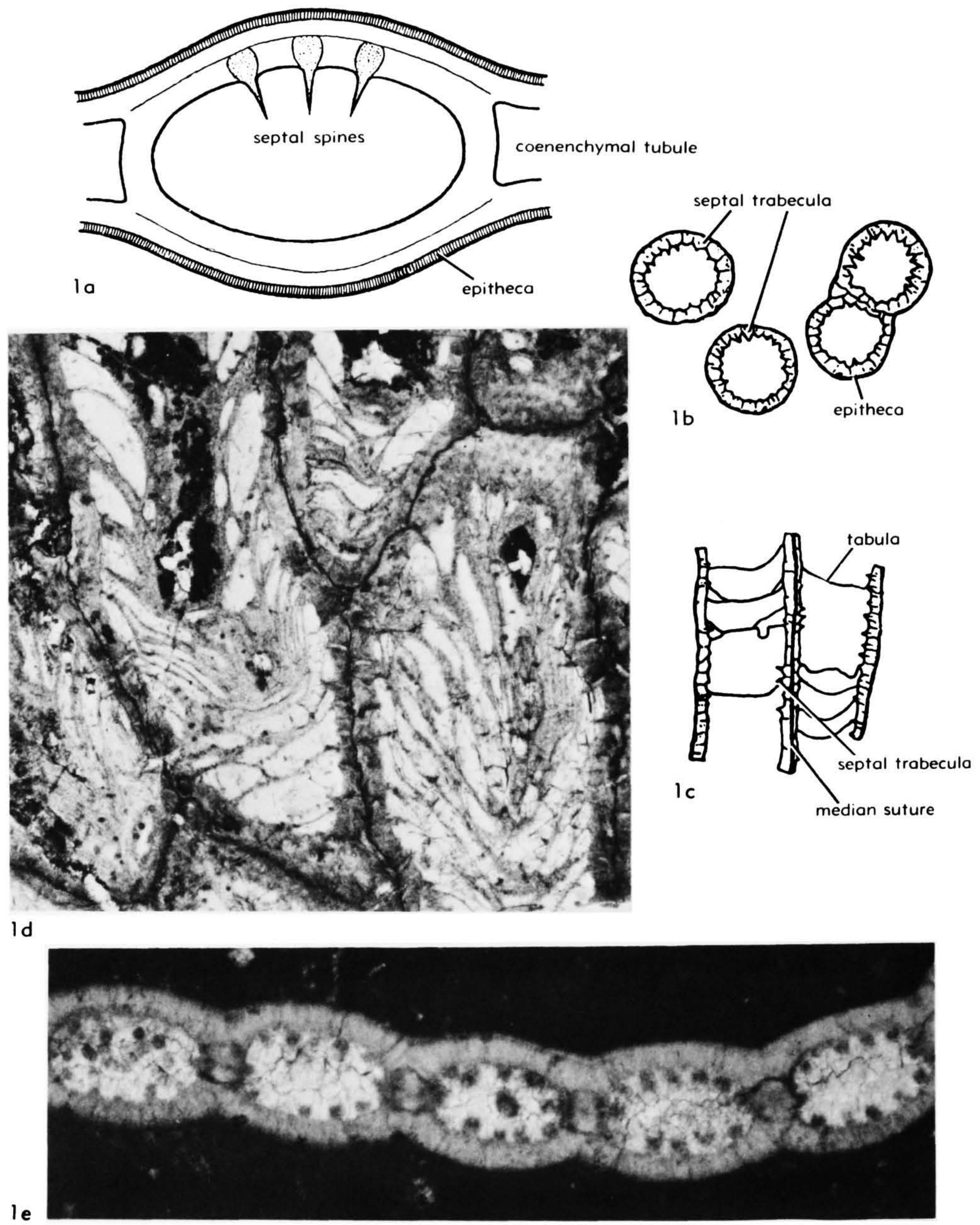

FIG. 291. Tabulate coral morphology; wall (peripheral stereozone).——*1a.* Example of bases of septal combs which appear not to reach epitheca but appear to be separated from it by ?independent wall; *Halysites australis* ETHERIDGE, M.Sil., U.K.; transv. sec., enl., diagram. (Hamada, 1957a).——*1b,c.* Wall composed of laterally contiguous, thick septal trabeculae; *Eofletcheria orvikui* (SOKOLOV), M.Ord., Est.; *1b,* transv. sec., *1c,* long. sec., both ×5 (Sokolov, 1955).——*1d.* Wall composed of clear septal spines (holacanths) enclosed in secondarily lamellar sclerenchyme; *Roemeripora progenitor* (CHAPMAN), L.Dev., Vict.; oblique sec., ×4 (Hill & Jell, 1970a).——*1e.* Wall composed of septal bases and ?independent wall segments; *Catenipora workmanae* FLOWER, U.Ord., Texas; transv. sec., ×12 (Flower, 1961).

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of both corallites (Fig. 290,*2*; *3a,b*; see also Fig. 286,*4a-c*). Inside the epitheca the corallite consists of wall (peripheral stereozone), septal (radial, longitudinal) elements, and tabulae or tabellae (transverse elements). Schouppé and Oekentorp (1974, p. 92) use the term epitheca for the entire wall of the corallite, including the crustose sheet for which it is used herein, and which Schouppé and Oekentorp consider to be merely the primary layer of the wall, secreted first, its crystallites acting as a "seeding layer" for the main part of the wall. This is consistent with the structure of the epithecate wall described in Scleractinia by Barnes (1972, p. 334), who gives a clearer picture of the relationship to the soft parts.

WALL AND MURAL PORES

The **wall** in the tabulatan corallite is a peripheral stereozone which may be narrow, moderately wide, or wide, and is normally sheathed externally by epitheca. Owing to diagenesis, its original constitution is commonly obscured. It is composite, being composed at least in part of the bases of septal elements, the fibers of which, or the axes or midplanes of which, in some well-preserved material, may be traced to their junctions with the epitheca (Fig. 291,*1d*); in some genera the septal elements may be so dilated that their bases are contiguous laterally and alone form the wall (Fig. 291,*1b,c*); in others there appear to be narrow interseptal segments that connect neighboring septal elements and may perhaps be interpreted as independent wall (Fig. 291,*1e*); in yet others, the bases of septal spines appear not to reach the epitheca but to be separated from it perhaps by an independent wall (Fig. 291,*1a*); possibly this last appearance is secondary and due to diagenesis.

In some Chaetetida the common wall between neighboring corallites consists of a single series of laterally conjunct longitudinal trabeculae composed of clinogonally radial fibers (Fig. 292,*1a-d*); in such walls no epitheca, indeed, no suture is visible. However, in other Chaetetidae a suture is plainly to be seen (Fig. 292,*2a,b*). In *Trabeculites* Flower, 1961, parts of the common wall in some corallites also appear to consist of a single series of longitudinal monacanths; in other parts a median suture is visible, with low septal ridges alternating in position in contiguous corallites. It is possible that longitudinal trabeculae form segments of common wall in some Thecidae.

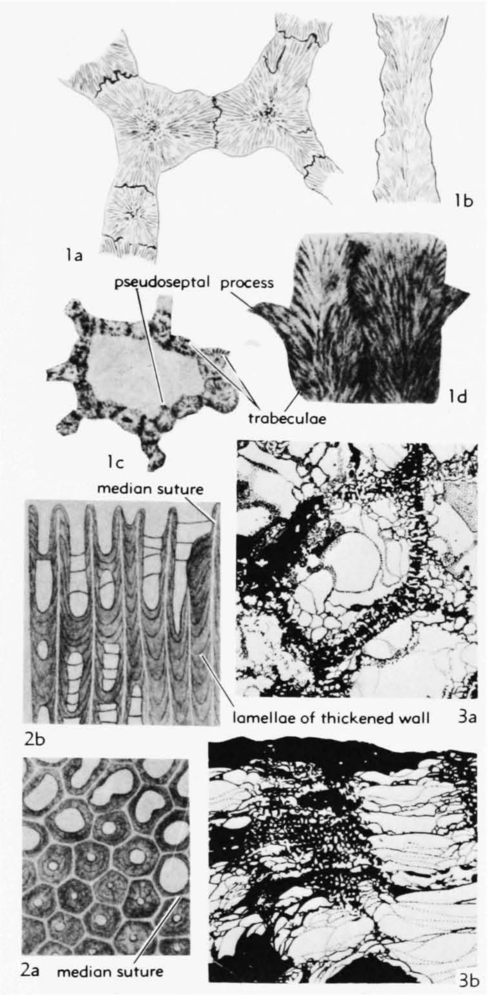

Fig. 292. Tabulate coral morphology; wall.——*1.* Contiguous trabeculae; *1a,b,* a single series of contiguous trabeculae; *Chaetetes cylindraceus,* L. Carb., Moscow Basin; *1a,* transv. sec., ×125, *1b,* long. sec., ×50 (Lafuste & Fischer, 1971); *1c,d, Chaetetes* sp., L.Carb., Moscow Basin, enl. (Sokolov, 1955, after Struve, 1898).——*2.* Chaetetid wall with median 'suture'; *Pachytheca irregularis* Yanet, M.Dev., N.Urals; *2a,* transv., *2b,* long. secs., both ×16 (Yanet, 1965).——*3.* Spongy (cribriform) walls; *Yavorskia antiqua* (McCoy), L.Carb., Ire.; *3a,* transv. sec., *3b,* long. sec., showing perforate walls and irregular tabulae, enl. (Smyth, 1929).

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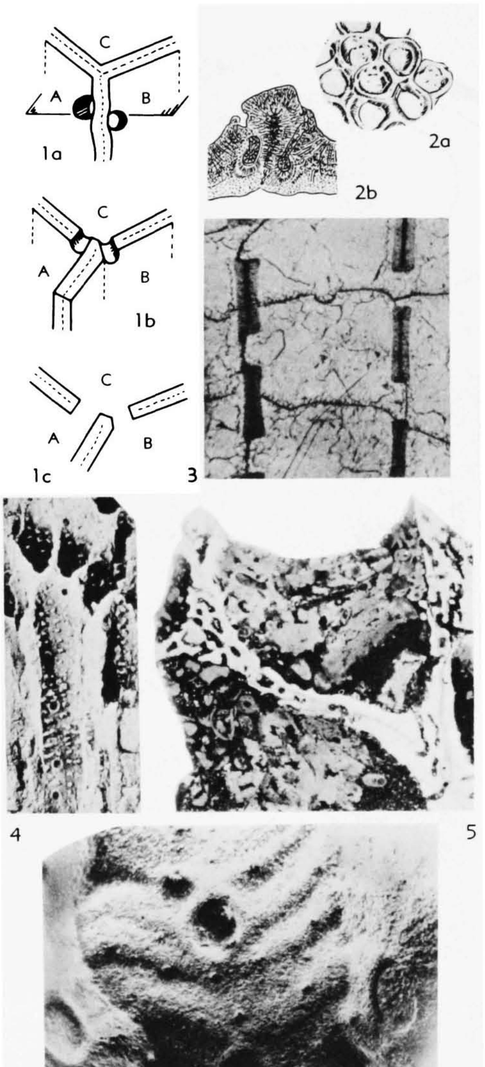

FIG. 293. Tabulate coral morphology; mural pores. ——*1.* Alternating angle pores giving false impression that tabularia of three corallites are placed in communication; *1a-c,* diagram. (Oekentorp & Schouppé, 1969).——*2.* Peripheral canal; *Vaughania cleistoporoides* GARWOOD, L.Carb., Eng.; *2a,* surface, ×0.8, *2b,* long. sec., ×7.5 (Hill & Stumm, 1956). ——*3.* Pore-plate; *Favosites alpenensis killiansensis* SWANN, M.Dev., Mich.; long. sec., ×15.0 (Swann, 1947).——*4.* Raised rim of pore, also squamulae and septal spines; *Favosites romingeri romingeri* SWANN, M.Dev., Mich.; ×3.6 (Swann, 1947).——*5.* Irregular mural pores; *Palaeacis axinoides* SMYTH; long. sec., ×6.6 (Smyth, 1929).——*6.* Midface mural pores at concavity in growth ridges; *Favosites gothlandicus* LAMARCK; viewed from inside corallite, ×30.0 (Oekentorp & Sorauf, 1970).

Spongy **(cribriform)** walls are found in some Favositina (Fig. 292,*3a,b*) and regularly arranged mural pores or pore tunnels in others.

The tabularia of neighboring corallites in cerioid coralla may be connected by perforations in the common walls. Such **mural pores** are commonly round or oval (Fig. 293,*6*) seen from inside the corallite, but in some (*Palaeacis,* Fig. 293,*5*) may be irregular. They are also commonly arranged in longitudinal rows, one to five in a corallite face, those of neighboring rows being opposite or alternate; they may be spatially related to the centers of the faces, or to the edges at the angles between faces. In *Paleofavosites* they alternate in position from one side of an angle to the other (Fig. 293,*1a-c*) and the edge appears wavy. Pores may or may not have a raised rim or collar (Fig. 293,*4*) and in some, squamulae (see septal elements) may project from the upper or the lower rim. Many are closed by a filmy longitudinal **pore-plate,** which may lie in the midplane of the wall or may have its edges on the rim of the pore (Fig. 293,*3*). SCHOUPPÉ and OEKENTORP (1974, p. 161) consider the diameter of the pores to be constant within a species, measured at the median suture; and (1974, p. 81) that pores were formed at the upper edge of the walls, remaining stationary while the walls grow up and around them, and that they were subsequently sealed by pore-plates. When the wall widens to a thick peripheral stereozone, the pore is lengthened into a **mural tunnel** (canal). In some, these tunnels are excavated farther by parasites or commensals. In *Vaughania* GARWOOD, a peripheral canal (Fig. 293, *2a,b*) is reported to encircle the wall just below the calice.

The **connecting tubuli** of Syringoporicae may be analogous to the mural pores of Favositida. SCHOUPPÉ and OEKENTORP (1974, p. 87) interpret the pores of Favositida as due to upward growth of the wall around short soft-body connecting tubules

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that temporarily connected two neighboring gastrovascular cavities for the transmission of nutrients and stimuli. They suggest that the tubules formed by the fusion of short protrusions from the column walls and subsequent resorption.

SEPTAL ELEMENTS

The septal elements of a corallite are radially and longitudinally arranged in the outer parts of the tabularium; they are commonly short (extending but little toward the axis from the periphery), and, being equal, are presumably of one order; nevertheless, in some Theciidae, some Agetolitidae, and some Cyrtophyllidae they may alternate in length, longer and shorter. In many they are 12 in number, and, indeed, 12 is characteristic of Heliolitina and Halysitina; in other suborders the number is commonly variable. Studies are still required to establish whether there is an order of insertion, or whether the symmetry of the Tabulata is radiobilateral rather than radial. Interseptal loculi of different outline and size, like the fossulae due to pinnate septal insertion in Rugosa, are not noted in Tabulata, in which it is commonly assumed that there is no regularity in septal insertion.

The commonest septal element in Tabulata, and, indeed, the type considered characteristic of the order, is the more or less regular longitudinal row of **septal spines,** each of which is assumed in this *Treatise* originally to have been a monacanthine trabecula. The base of the spine is within the peripheral stereozone and commonly originates against the epitheca, doubtfully against the inner surface of a thin segment of independent wall as suggested by HAMADA (1973; Fig. 294,*1*) for Halysitidae. The spines are directed adaxially and typically upward, but in some forms horizontally or, rarely, downward (Fig. 294,*2*).

In some genera the bases of the spines of a longitudinal row are connected by a low septal ridge (Fig. 294,*1*) forming a **septal comb.**

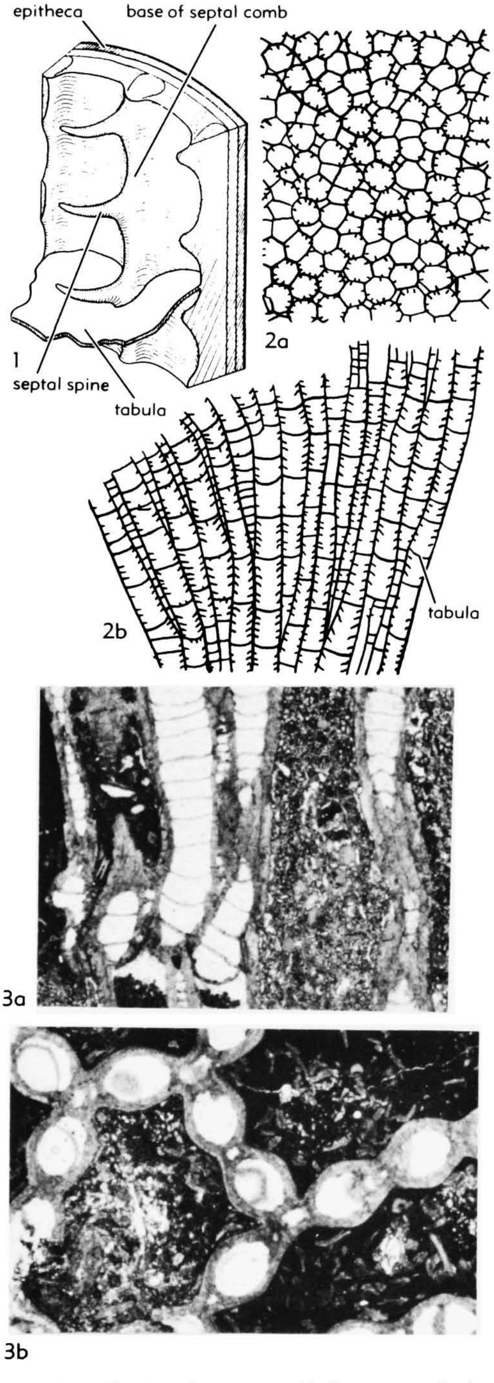

FIG. 294. Tabulate coral morphology; septal spines and tabulae.——*1*. Septal comb; *Halysites*; diagram. (Hamada, 1957a).——*2*. Downwardly directed spines; *Proheliolites norvegicus* BONDARENKO, U.Ord.-L.Sil., Eu.; *2a,* transv., *2b,* long. secs., both ×4.3 (Hill & Stumm, 1956).——*3*. Bases of septal combs; *Halysites ?catenularius* (LINNÉ), Wenlock., U.K.; *3a,* long., *3b,* transv. secs., both ×6.7 (Hill, n).

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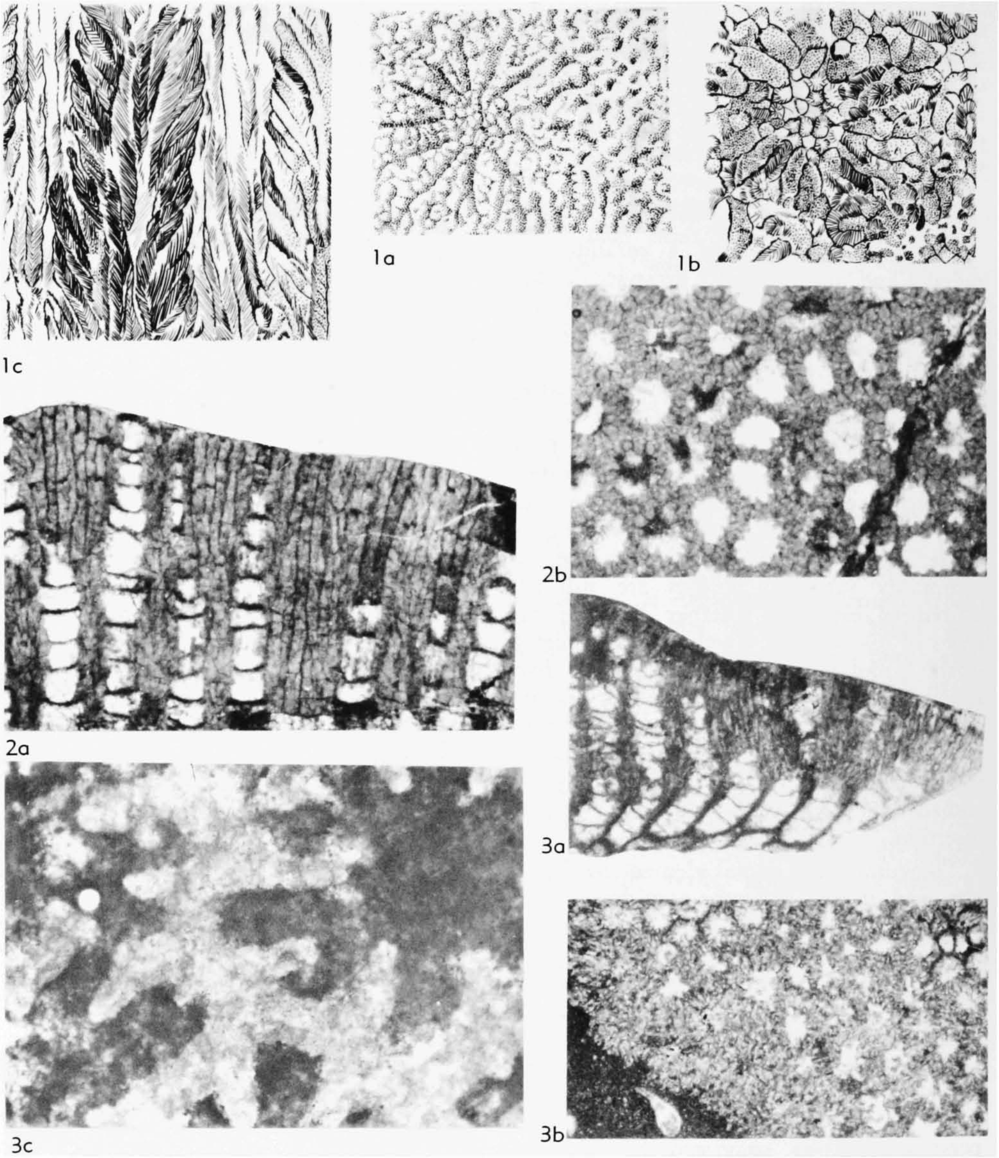

FIG. 295. Tabulate coral morphology; septal elements.——*1.* Trabeculate septa; *Coccoseris ungerni* EICHWALD, U.Ord., Est.; *1a,* part of distal surface, *1b,* transv. sec., *1c,* long. sec., all ×10 (Hill & Stumm, 1956).——*2.* Monacanthine trabeculae contiguous to form septum; *Lyopora favosa* McCOY, Ord., Girvan., Scot.; *2a,* long., *2b,* transv. secs., both ×7 (Hill, n; photographs courtesy J. S. Jell).——*3.* Secondarily altered monacanthate septa of *Thecia* sp.; *3a,b, Thecia expatiata* (LONSDALE), M.Sil., Eng., *3a,* long., *3b,* transv. secs., both ×7 (Hill, n; photographs courtesy J. S. Jell); *3c, T. swinderniana* (GOLDFUSS), erratic from Sil., Neth., center of corallite showing effects of diagenesis, ×67 (Hill, n; photograph courtesy K. Oekentorp).

Less common in Tabulata is the **septum,** composed of monacanthine trabeculae conjunct except at their axial ends, which give dentate distal and axial edges to the septum; the trabeculae are generally in single series, the axis of each in the midplane of the septum, but in some (Fig. 295,*1a-c*) the axes may diverge from the midplane.

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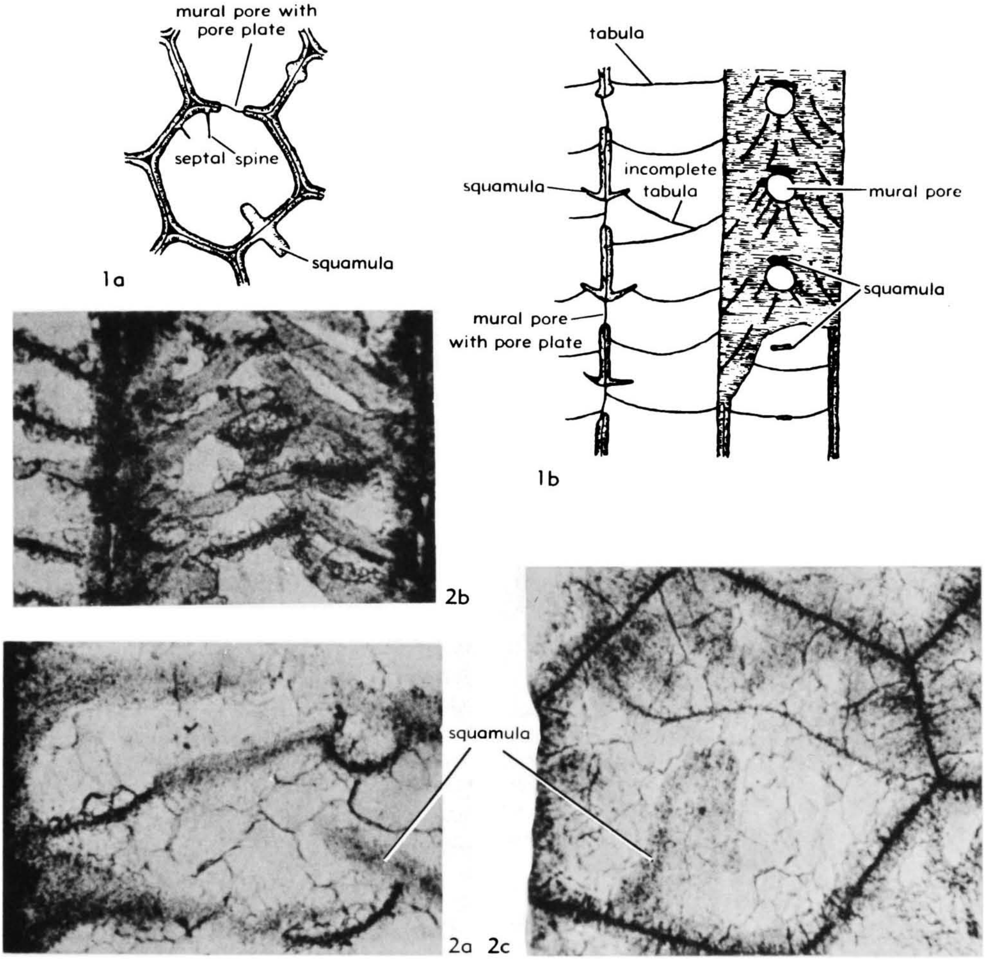

FIG. 296. Tabulate coral morphology; septal elements.——*1.* Squamulae; *Squameofavosites; 1a,b, S. squamuliferus* (ETHERIDGE), forma *bryani* (JONES), transv., long. secs., diagram., ×20 (Philip, 1960). ——*2.* Squamulae; *Emmonsia emmonsii* (ROMINGER), M.Dev.; *2a,* Ohio, transv. sec., ×50; *2b,* N.Y., long. sec., ×25; *2c,* Ohio, transv. sec., ×25 (Swann, 1947).

The fibers of these trabeculae, when retained, are clinogonal at least near the axis, but may curve to become orthogonal at the periphery. Such trabeculae are commonly nearly longitudinal at their bases, but curve adaxially distally. This type of septum is well developed in the Theciidae, the Coccoseridicae, and the Parastriatoporidae. In the first two it is commonly altered by diagenesis to a characteristically mottled secondary texture (Fig. 295,*2,3*).

Squamulae are tongue-shaped or spoonlike projections from the wall of many late Silurian and early Devonian Favositida (Fig. 296,*1,2*). They have wide and, in some, thickened bases, and may have curved upper surfaces such that transverse sections of the corallite may show two subparallel lines representing the cut downturned or upturned sides; they are commonly associated with mural pores, when they are developed either as shelf- or eaves- or hoodlike extensions from the upper rim of the pore, or as scooplike extensions from the lower rim; or they may be independent of pores. They are mostly developed in longitudinal rows, and in contiguous corallites are mostly base to base; generally they are directed

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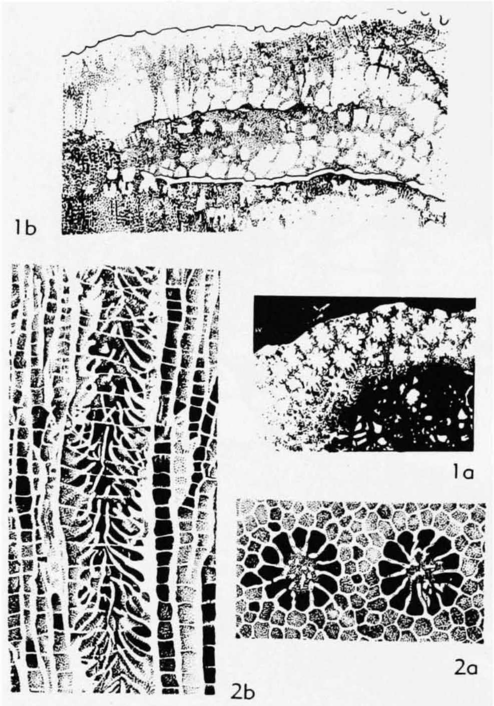

FIG. 297. Tabulate coral morphology; axial structures (Hill & Stumm, 1956).——*1.* Trabeculae based on tabulae; *Billingsaria parva* (Billings), M.Ord., N.Am.; *1a,* transv., *1b,* long. secs., both ×4.——*2.* Upturned ends of long septal trabeculae; *Heliolites barrandei* Penecke, U.Sil.-L.Dev., Eu.; *2a,* transv., *2b,* long. secs., both ×12.

horizontally toward the axis of the corallite, but may be inclined upward.

AXIAL STRUCTURES

Axial structures are exceptional in Tabulata and, where formed, consist merely either of vertical separate trabeculae or spines based on tabulae (Fig. 297,*1*) or of the upturned axial ends of very long septal trabeculae (Fig. 297,*2*).

TABULAE, TABELLAE, AND DISSEPIMENTS

Of the horizontal skeletal elements, **tabulae** extend completely across the corallite and are attached by their edges to the inner surface of the wall. In Tabulata, the entire lumen of the corallite, thus, is the tabularium. Tabulae may be flat, or uparched (convex), or sagging (concave), or they may have shallow peripheral depressions, none of which can be identified as a fossular depression such as may be found in rugosan tabulae. **Tabellae** are smaller, convex plates, which do not extend completely across the tabularium but whose edges may lie either on the wall or on one another or on tabulae; in some they may be developed only or mainly at the periphery of the tabularium, when they are steeply inclined (Fig. 298,*1*). **Dissepiments** are the small plates that are developed as part of the coenenchyme and outside the tabularium; some are similar in size and convexity to tabellae, others are scarcely curved, or horizontal, or inclined.

In the Tabulata the transverse skeletal elements are commonly very thin; when thickened, they show growth lamellae and fibers at right angles to these in the least altered material (see Fig. 304,*1*). In *Favosipora clausa* (Lindström) the tabula forming the floor of a calice shows concentric lineation and a central convexity (Stasinska, 1967, p. 101); this can be interpreted as indicating centripetal growth like that described for the "primary layer" of the scleractinian dissepiment by Wells (1969, p. 20) and Sorauf (1970, p. 12). The undersurfaces of tabulae in *Favosites favosus* (Goldfuss) show this centripetal lineation, but their upper surfaces are smooth (Sorauf, 1974, p. 553).

COENENCHYME

Coenenchyme (coenosclerenchyme, cf. coenosarc, the common soft tissue) is the common skeletal tissue between neighboring tabularia in Tabulata, in which there is no line of demarcation between what is proper to one corallite and what is proper to any others. It is characteristic of the Heliolitina and of many Halysitina and is also found in some Sarcinulida and some Syringoporicae.

In the Heliolitina the coenenchyme may be dissepimentate, with trabeculae that may be separate and discontinuous (Fig. 299, *1a-c*), or united laterally to form continuous or discontinuous walls of longitudinal tubuli (Fig. 297,*2*). In the Halysitina it is similar but is confined to the lateral junctions of the corallites in a chain, or to junctions of chains, and it is absent in some (Fig. 289,*4e*).

In the Sarcinulida (Fig. 299,*2a,b*) and

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some Syringoporicae (Fig. 287,*1,2*) it may comprise horizontal connecting platforms with which may be associated connecting tubuli or canals.

Spatially the tabulatan coenenchyme is like the dissepimentaria of plocoid Rugosa (those massive Rugosa in which the common epithecate wall between neighboring corallites is not developed); dissepimentaria in the Rugosa also surround tabularia, but are developed only when minor septa are present either as plates or septal crests. However, no minor septa are known in Tabulata, so homology cannot be claimed. One may, nevertheless, speculate that both the coenenchyme of Tabulata and the dissepimentaria of plocoid Rugosa were formed beneath coenosarc such as is present in plocoid Scleractinia, placing the gastrovascular cavities of neighboring polyps in communication.

MICROSTRUCTURE

PRIMARY MICROSTRUCTURE

In this *Treatise* it is assumed, on the basis of comparative studies by optical and electron microscopes of scleractinian, rugosan, and tabulatan skeletons, that if interseptal segments of wall exist beneath the epitheca, they are constructed like those parts of the dissepiments of Scleractinia above the basal layer ('dark line') of the dissepiment. That is, it is assumed that when first formed they consisted of successive growth lamellae of crystallites of $CaCO_3$ deposited by composite, planar (one-sided), spherulitic crystallization from a gel secreted by the unfolded basal ectoderm of the polyp. The crystallites as seen in Scleractinia by means of the scanning electron microscope are oriented perpendicular to the secreting ectodermal surface and are grouped in **microtufts,** in each of which they converge proximally, the proximal points of all the microtufts at the base of the tabula being closely spaced (Fig. 300,*1*). Crystallization is approximately equal at all these points (Bryan & Hill, 1941; Kato, 1963, 1968b; Sorauf, 1970, 1971; Oekentorp, 1972; Jell & Hill, 1974; Schouppé & Oekentorp, 1974; Hill, herein, section on biocrystallization). Through the optical microscope, groups of microtufts, continuing in the same average direction from one growth lamella to another, appear as single **fibers,** the fibers being grouped in tufts or fascicles (sclerodermites) (Fig. 301,*1,2*). Growth lamellae crossing these fibers may be indi-

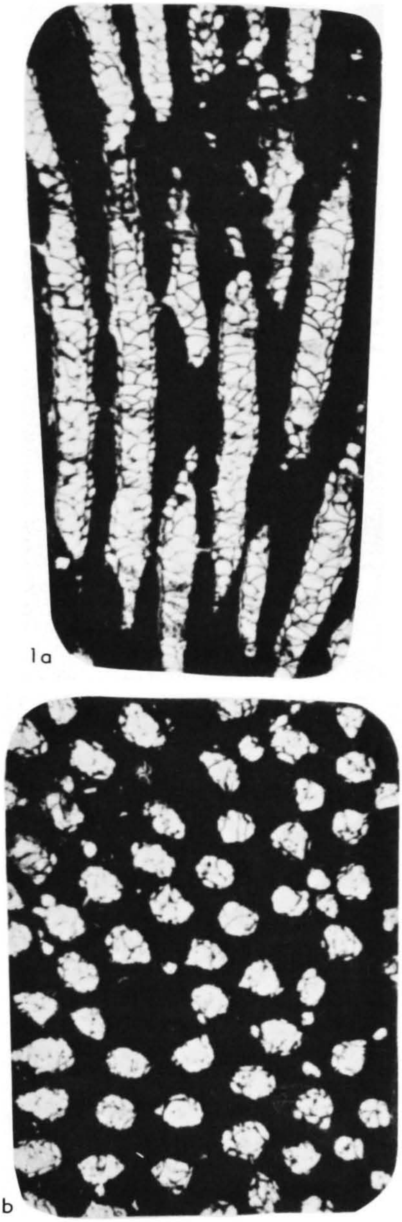

Fig. 298. Tabulate coral morphology; tabellae.——*1.* Peripheral tabellae and large tabellae replacing tabulae; *Hayasakaia elegantula* Yabe and Hayasaka, Perm., China; *1a,* long., *1b,* transv. secs., both ×4 (Huang, 1932).

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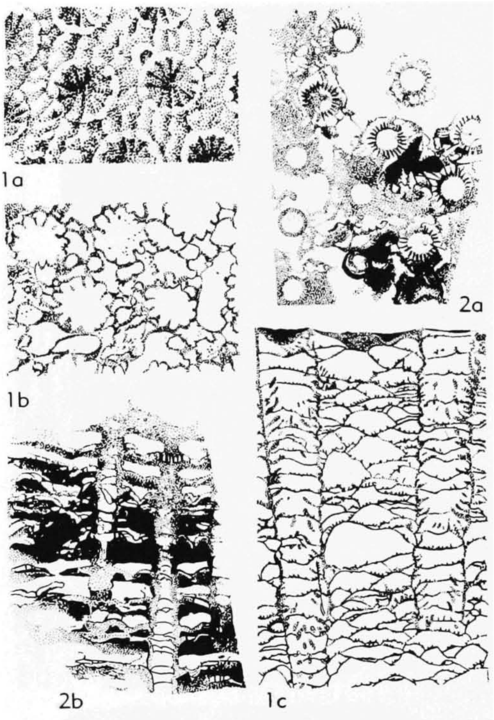

FIG. 299. Tabulate coral morphology; coenenchyme. ——*1. Propora tubulata* (LONSDALE), Sil., Eu.; *1a*, part of surface, *1b*, transv. sec., *1c*, long. sec., all ×4 (Hill & Stumm, 1956).——*2. Sarcinula organum* (LINNÉ), M.Ord.-L.Sil., N.Eu.; *2a*, transv., *2b*, long. secs., both ×1 (Sokolov, 1955).

cated by slight tonal changes or by slight breaks in the continuity of fibers at the upper and lower surfaces of the lamellae.

Similarly, it is assumed that those components of the wall that are septal spines (trabeculae, as in most Favositina, Halysitina, Heliolitina, Auloporicae, and Syringoporicae), septal combs (in which the trabeculae of a single longitudinal row are united at their peripheral bases, as in Sarcinulida and some Heliolitina), and septa (in which the trabeculae are contiguous throughout their length as in some Theciidae and in Parastriatoporidae) are built of similar successive growth lamellae, but differ in that the composite spherulitic crystallization is localized and very active at a series of points radially arranged with respect to the axis of the corallite (and located in invaginations in basal ectoderm). The apparent centers of radial growth of crystallites move progressively upward on axes aligned from their original positions. A **trabecula** (spine) represents the accumulated deposition from such a point of calcification (Fig. 302,*1*). Within each trabecula the crystallites are directed perpendicularly to the surface of the growth lamellae that pass through the trabecula, and presumably, therefore, to the outer surface of the ectoderm in the invagination. The growth lamellae of a septum may thin laterally and become continuous with those of a tabula.

In assuming that the septal spines of Tabulata are fine trabeculae, each originally with an axis of calcification, this *Treatise* differs from SCHOUPPÉ and OEKENTORP (1974, p. 167), who, having found no trace of such axes of calcification in their thin sections, consider that the fibers in a spine are based not at the axis of the spine but at its base. I also have no convincing evidence of the presence of axes of crystallization in fine spines such as those of *Favosites, Halysites,* or *Syringopora.* In the coarse spines of the sarcinulidans *Lyopora* and *Thecia,* axes of calcification do appear to be present (FIG. 295,*2,3*), as also in the heliolitinan *Coccoseris ungerni* EICHWALD (Fig. 295,*1*). The similarity in appearance between the holacanths immersed in secondarily lamellar sclerenchyme in the walls of the favositidan *Pleurodictyum,* many Syringoporicae, and Halysitina, and the holacanths of trabecular origin in the rugosan Tryplasmatidae, is considered presumptive evidence that finer spines also had axes of calcification. The presence of holacanths in the wall tissue of some parts of some corallites in the favositidan *Parastriatopora* and the absence of all traces of them in other parts indicates suppression during diagenesis.

Squamulae in some instances show traces of a median 'dark' plane or ?axis (Fig. 296, *2a-c*). SCHOUPPÉ and OEKENTORP (1974, p. 169) consider them to be simply prolongations of fibers based on the inner surface of the epithecal layer of the wall. Perhaps, however, they are of trabecular origin like the peripheral crossbar plates of the contemporary rugosan Digonophyllidae.

Only rarely is it found that fibers and growth lamellae of tabulatan walls are distinguishable with the optical microscope.

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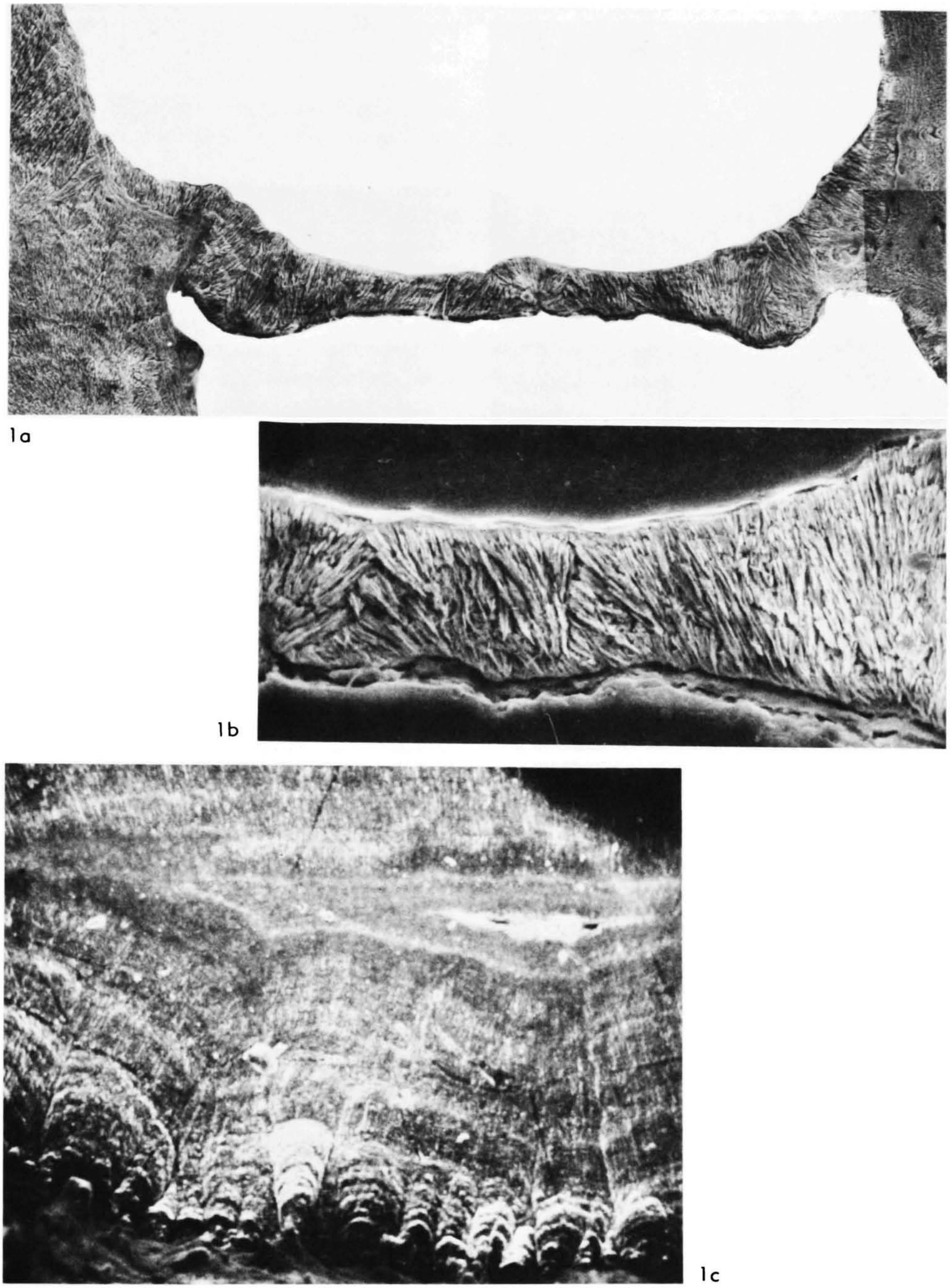

Fig. 300. Tabulate coral morphology; ultramicrostructure of recent Scleractinia (Hill, n; SEM photographs courtesy J. S. Jell).——*1.* Dissepiment; *Favites virens* (Dana), Holo., Great Barrier Reef; *1a,b,* microtufts seen in etched long. sec. and based on centripetally grown primary (basal) layer, ×160, ×630; *1c,* undersurface of basal layer of crystallites grown centripetally, ×200.

Mostly, diagenetic processes have obscured them.

Dubatolov (1971, p. 30, text-fig. 16) has given interpretative diagrams of microstruc-

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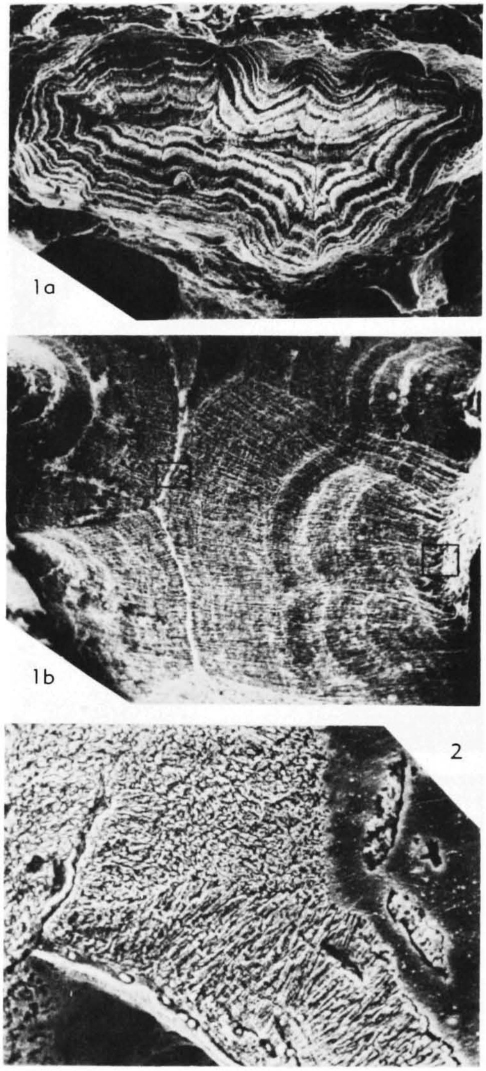

FIG. 301. Tabulate coral morphology; microstructure of scleractinian dissepiment (Sorauf, 1970).——*1. Cladocora caespitosa* (LINNÉ), Holo., shoreline, Rovinj, Istrea, Yugo.; *1a,b,* underside of dissepiment between two septa, showing growth lines, ×68, ×136.——*2. Manicina areolata* (LINNÉ), Holo., Fla., SE. of Big Pine Key; junction of dissepiment with wall, ×200.

tural types seen in the tabulatan wall through the optical microscope, and of these, the following, reproduced herein as Figure 303, appear to retain at least traces of primary structure: Figure 303,*1,* radially fibrous with traces of growth lamellae; Figure 303,*2,* radially fibrous with distinct growth lamellae; Figure 303,*3,4,* radially fibrous and cryptoradially fibrous without trace of growth lamellae, Figure 303,*2-4* being orthogonally fibrous to the epitheca; and Figure 303,*5,* clinogonally fibrous with faint traces of growth lamellae. DUBATOLOV termed all these *"fibralnyy tip"* (fibrous type). If, as this *Treatise* assumes, axes of calcification were originally present in the septal spines, they have been obscured during diagenesis. Figure 303,*6* shows a wall composed of clinogonally fibrous septal trabeculae **(monacanths)** as in *Echyropora,* which wall, however, DUBATOLOV called paratrabeculate, following TONG-DZUY (1966a, p. 24).

Seen through the optical microscope, tabulatan tabulae seldom show any distinction between a basal layer and an overlying succession of growth lamellae, unless the plates are thicker than average and well preserved, when the lamellae are seen to consist of fibers arranged perpendicular to the curvature of the plate, like those of Scleractinia (Fig. 300,*1a-c*). It is assumed in this *Treatise* that the growth lamellae were deposited by planar, composite, spherulitic crystallization from a gel secreted by unfolded parts of the basal ectoderm of the polyp. They are affected by diagenesis in the same way as the growth lamellae of walls or septa, and develop similar secondary microfabrics, including secondary lamellar structure.

SECONDARY MICROSTRUCTURE

In the Scleractinia the original crystallites are of aragonite, with their c-axes parallel to their length, and are topped by pyramidal faces. The mineral now present in tabulatan skeletons is calcite, with the c-axis, where it has been reported, parallel to the length of the fibers. It is not known whether the original mineral in the tabulatan skeleton was aragonite; it seems possible, as OEKENTORP (1972) has indicated, that it was, and that it has subsequently been transformed to calcite, in a few cases with retention of the fine morphological architecture, but in nearly all with greater or lesser changes to secondary structures.

The microtextures of skeletons of Tabulata seem to have been particularly susceptible to alteration during diagenesis; it is

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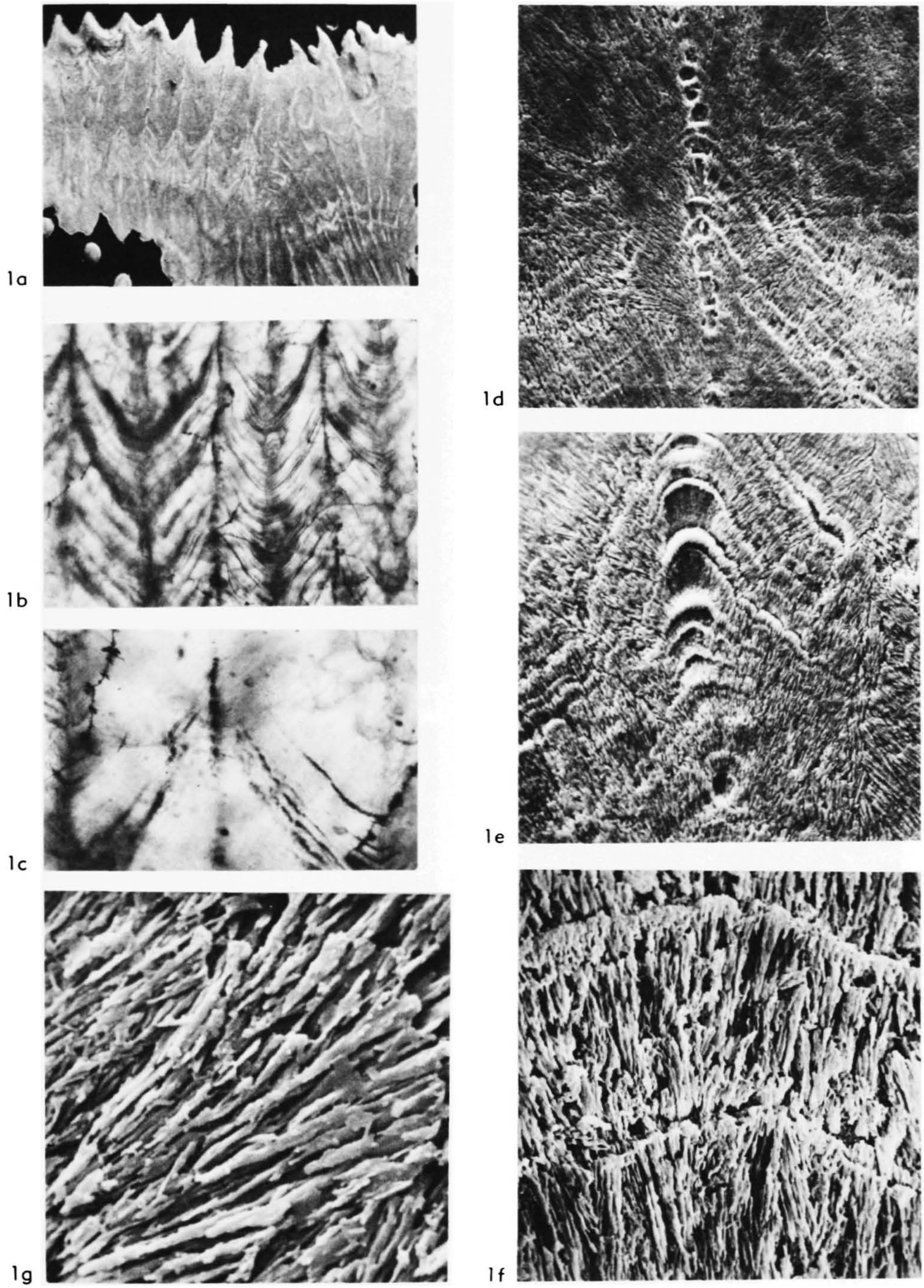

FIG. 302. Tabulate coral morphology; ultramicrostructure of recent Scleractinia (Hill, n; SEM photographs courtesy J. S. Jell).——*1.* Growth lamellae falling from growing points and axes of trabeculae in septum; *Fungia scutaria* LAMARCK, Holo., Great Barrier Reef; med. long. secs., *1a,* ×13; *1b,* ×47; *1c,* ×121; *1d-g,* SEM showing microtufts of crystallites of aragonite, *1d,* ×400; *1e,* ×500; *1f,* ×1,470; *1g,* ×4,350.

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even hard to find specimens that are only slightly altered. Discussion of secondary structures may be found in Kato (1968b) and Oekentorp (1972, 1974b), following earlier work on such structures in Rugosa by Hill and Butler (1936) and particularly by Kato (1963).

Among the processes which may cause alteration or suppression of the original so that secondary microstructures are developed are:

1) Replacement of the skeletal mineral by dolomite or by noncarbonate mineral. In *Pachyfavosites polymorphus* (Goldfuss) in the Eifelian of the Eifel, replacement by dolomite first affects the median sutural region of the wall, and may then encroach along radial fibers into the rest of the wall (Fig. 304,*3a-d*). Replacement by silica or other noncarbonate mineral commonly destroys the original microstructure.

2) Recrystallization of the original mineral. If it be assumed that the original mineral was aragonite as in Scleractinia, recrystallization may be an inversion to calcite; a fine granular mosaic may first be formed, through which in some places original microstructural features (boundaries between plates, between fibers, or between growth lamellae) may still be retained; where few such traces are retained, the microstructure may be described as cryptofibrous or cryptolamellar; further recrystallization may result in a coarse calcite mosaic in which all traces of the original microstructure are lost.

If it be assumed that the original mineral was calcite, the recrystallization is from the original fibrolamellar fabric to a fine, and later a coarse, granular calcite mosaic.

Diagenesis of skeletal carbonates is far from being fully understood. For a summary of published work see Folk (1965) and Land (1967).

3) Deformation due to pressure. This may occur during mechanical stress, such as diastrophism; the plates of the skeleton may be grossly deformed, and cleavage lamellae may be developed in the wall fabric. Small, crudely rhombic cleavage or

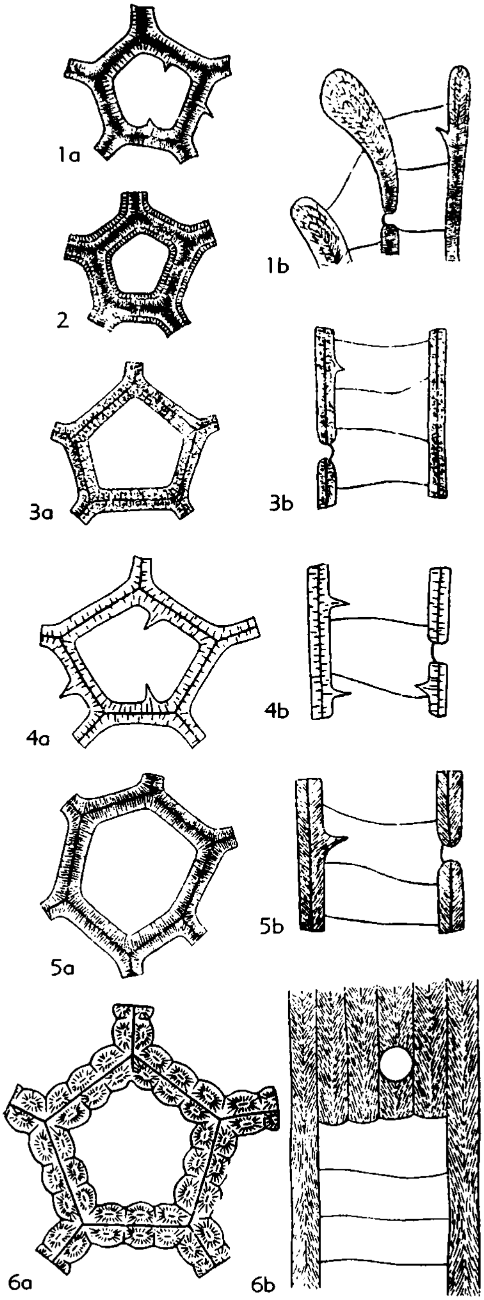

Fig. 303. Tabulate coral morphology; wall with traces of primary structures; *a,* transv. secs., *b,* long. secs. (diagram., Dubatolov, 1971).——*1.* Radially fibrous with traces of growth lamellae.——*2.* Radially fibrous with marked growth lamellae.——*3.* Radially fibrous without trace of growth lamellae.——*4.* Cryptoradially fibrous without trace of growth lamellae.——*5.* Pinnately (clinogonally) fibrous.——*6.* Wall composed of clinogonally fibrous septal trabeculae (monacanths).

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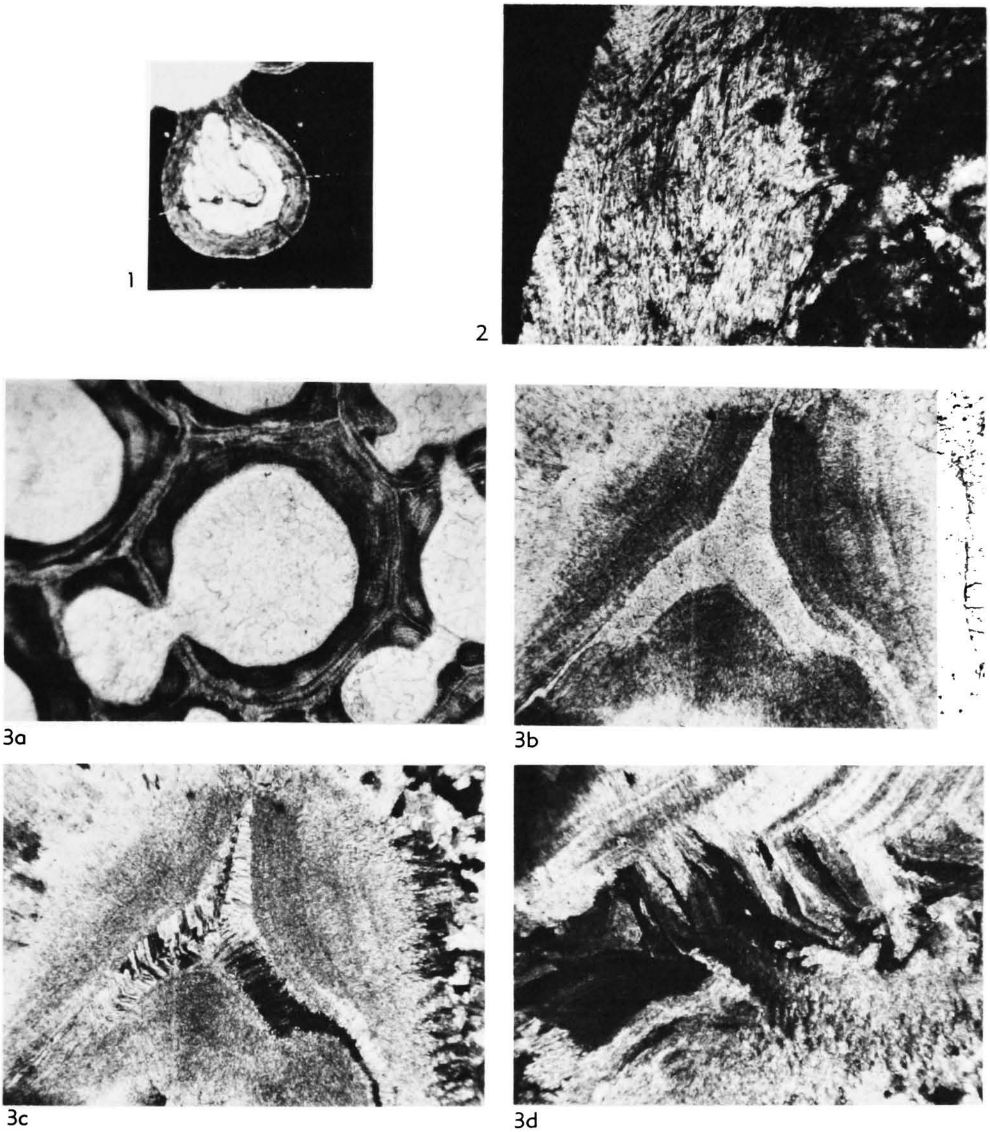

FIG. 304. Tabulate coral morphology; secondary wall structures.——*1.* Secondary lamellar structure, tabulae thickened, showing 'dark' basal layer and light thickening tissue; *Syringopora* sp., U.Dev., W. Australia; ×7 (Hill, n).——*2.* Zigzag (secondarily lamellar) structure; *Syringopora* sp., U.Dev.-M.Dev., Spain; ×80 (Oekentorp, 1972).——*3. Pachyfavosites polymorphus* (GOLDFUSS), M.Dev., Ger.; *3a,* showing the recrystallized median sutural region, light-colored in transmitted light, ×27; *3b-d,* the same affected by dolomitization, *3c,d,* show grain enlargement though original fibrolamellar structure is more or less retained, all ×80 (Oekentorp, 1972).

shearing cracks may develop in a corallite wall during preparation of a thin section.

Also, during diagenesis, pressure due to volume change, for instance during inversion from aragonite to calcite, may occur. OEKENTORP (1972, p. 55-62; 1974c, p. 321) has suggested such diagenetic pressures as causes of secondarily lamellar structure found in the walls of many Syringoporicae, Auloporicae, Halysitina and *Pleurodictyum,*

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in which the septal spines or their axial parts appear as clear calcite thorns (holacanths) surrounded by lamellae that are commonly at an angle to the original growth lamellae (Fig. 304,*1*). It was this type of secondary structure that Hill (1936, pl. 29, fig. 39) confused with original growth lamellation and called lamellar sclerenchyme. It is better described as **secondary lamellation.** Oekentorp (1972, p. 55) calls it pseudolamellar, but this term also is ambiguous, for the structure is still lamellar, even if it is secondarily so. Oekentorp offers a similar explanation for **zigzag structure,** seen, for instance, in the wall of some *Syringopora* (Fig. 304,*2*).

The term microlamellar has been applied by Lafuste (1962, p. 105) to the microstructure of the wall in *Favosites gothlandicus* (Lamarck). This is commonly a fine granular calcite mosaic in which an imperfect concentric platy structure is developed (Fig. 305,*5*) parallel to the median suture line. This was called "voloknistyy" by Chudinova (1959, p. 31) and pseudolamellar by Oekentorp (1972, p. 65). Lafuste considered it primary, but I agree with Oekentorp that it is secondary.

Of Dubatolov's (1971, p. 30, text-fig. 16) interpretative diagrams of microstructural types seen in Tabulata, the following are herein considered secondary: secondary lamellar structure as in Syringoporicae, Auloporicae, and some Halysitina (Fig. 305,*1*); secondary concentric structure, fine in *Favosites* (Fig. 305,*2,5*), coarser in *Pachypora* (Fig. 305,*3,6*); secondary plicate lamellation as in *Plicatomurus* (Fig. 305,*4*). Dubatolov termed all these "lamellyatnyy (plastinchatyy) tip" [lamellar (platy) type].

The normally thin tabulae may be augmented during diagenesis by secondary

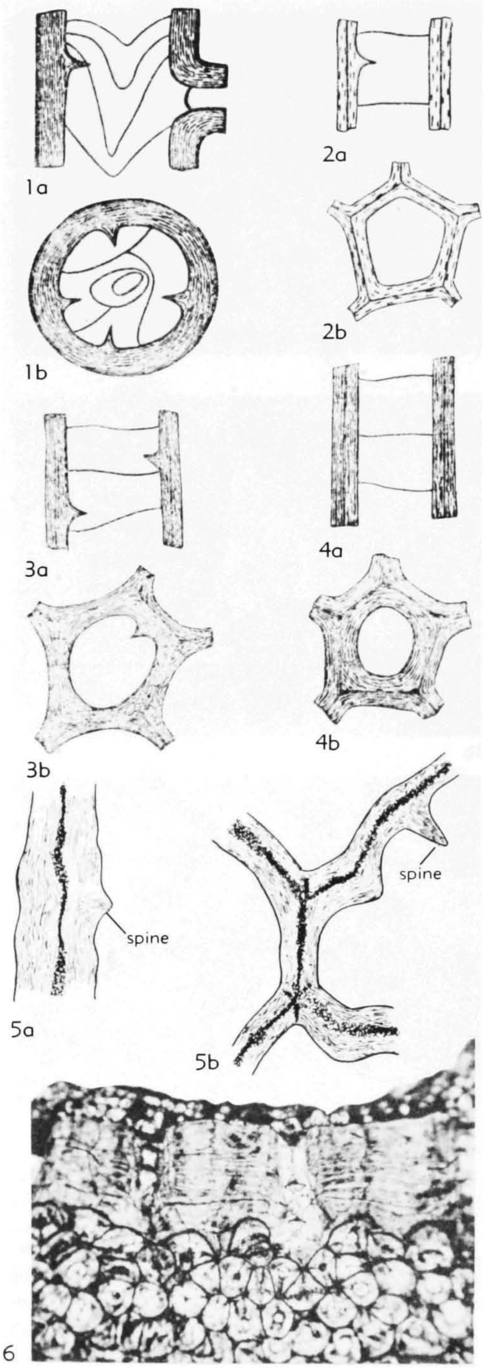

Fig. 305. Tabulate coral morphology; secondary wall structures.——*1.* Secondary lamellar structure as seen in *Syringopora; 1a,* long. sec., *1b,* transv. sec., diagram., ×1.0 (Dubatolov, 1971).——*2.* Secondary concentric structure, fine as in *Striatopora, Cladopora; 2a,* long. sec., *2b,* transv. sec., diagram., ×1.0 (Dubatolov, 1971).——*3.* Secondary concentric structure, coarse as in *Pachypora, Michelinia; 3a,* long. sec., *3b,* transv. sec., diagram., ×1.0 (Dubatolov, 1971).——*4.* Secondary plicate lamellar structure as in *Plicatomurus; 4a,* long. sec., *4b,* transv. sec., diagram., ×1.0 (Dubatolov, 1971).——*5.* Secondary concentric structure, fine; *Favosites gotlandicus* Lamarck, Sil., Gotl.; *5a,* ×1.3; *5b,* ×0.5 (Lafuste, 1962).——*6.* Secondary concentric structure, coarse; *Pachypora lamellicornis* Lindström, Sil., Gotl.; transv. sec. of folia, ×10.0 (Lecompte, 1936).

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growth, from both upper and lower surfaces, of very fine needles whose distal ends project unequally into the lumen and do not form a level surface like a natural skeletal surface; nor do they show the characteristic yellowish tone of the biofibers; coarser secondary crystals are usually easy to distinguish from the coral fibers. These secondary deposits, like the growth lamellae, are subject to recrystallization to a fine or coarse granular mosaic.

Secondary structures of coral skeletal tissue (sclerenchyme) are variable in the degree to which they replace the original structure in different parts of one corallite, the one corallum, in the one species and the one genus, and in one stratum formed at one time. Nevertheless, our present knowledge suggests that certain genera are predisposed to particular types of secondary structure; this could perhaps be due to some specific character of their original sclerenchyme, such as the spacing of the crystallites, or the molecules of trace elements that they contain, or perhaps to the amount and kind of organic material trapped between the crystallites. Much research is required for a full understanding.

SPECULATIONS ON THE ORIGIN OF TABULAE

In a perceptive review, Wells (1969, p. 22) discussed the origin of the dense basal layer ('dark line') of dissepiments in Zoantharia, and concluded that it grew centripetally from the margins (either wall or septa or both). As Manton (1932, p. 165) described it, "A tabula [in the recent scleractinian *Pocillopora bulbosa*] arises as a thin ring of smooth calcite [*sic*] about 0.1 mm or less in thickness, projecting directly inwards from the walls of the calix. Further growth enlarges the flat projection and reduces the central pore leading to the basal part of the calyx. Finally the pore is closed and a horizontal tabula is completed (Pl. 1, fig. 2)." As Wells observed, after closure is complete, subsequent thickening in most cases obscures the centripetal increments. In this centripetally deposited basal layer (to which, maybe, the normally tenuous tabulae of the Tabulata correspond) the crystallites are deposited with their long axes rudely arranged in the plane of the 300,*1c*). In any subsequent growth-layering that thickens this sheet, the fibers (groups of microtufts as seen under the electron microscope) are perpendicular to the upper surfaces of the growth lamellae (Fig. 300, *1a,b*). Sorauf (1974, p. 553) thought that the concentric lines on the undersurface of the tabulae of Silurian *Favosites* are daily growth lines and that they might be due to the presence of symbiotic algae (zooxanthellae) in the polypal flesh, with a resultant diurnal differentiation of crystallite growth (rapid and luxuriant during sunlight hours, slower and more orderly during hours of darkness).

In Wells' view, the spaces beneath tabulae or dissepiments are produced by hydraulic lifting of the secreting surface as a result of the accumulation of fluid, or possibly of gas, which increases pressure in the potential space between a dissepiment and the skeletotrophic tissues ("Wedekind's theory"). The shape of the upper surface of the void is then outlined by centripetally growing corallites, and on this thin sheet (basal dark line) the lighter longitudinally radiating crystallites are deposited. This explanation is perhaps to be preferred to one supposing discontinuous tractive uplift of the polyp (due to the more rapid growth of the septa), followed by deposition of a sheet of skeletal material sealing off the voids (Hill, 1936) or to one supposing upward traction effected by polyp "muscles" (Carlgren, 1949, pl. 3, fig. 9, 10), though Wise (1970) has noted marks on the sides of septa in some Scleractinia, which he identified as locations of attachment of "desmocytes."

A quite different method for the formation of tabulae and dissepiments has recently been advocated for Tabulata with porous walls by Weyer (1972b, p. 715). He argues that the views of von Koch (1896, p. 261) and Matthai (1914, p. 10) are correct; that is, that centripetal growth of a tabula in a ring-fold of soft tissue extending from the column wall, or from the soft tissue lining an interseptal loculus, cuts off a basal part of the gastrovascular cavity of the polyp; the cut-off part then atrophies below the new skeletal plate. In this method, which receives some support from Sorauf's (1970)

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scanning electron microscope investigations, transversely advancing calcareous sheet (Fig. uplift of part or the whole of the polyp would not occur. Specially designed investigations on living Scleractinia should solve this problem.

DEVELOPMENT

ONTOGENY

In the ontogeny, or development of an individual, various stages may be recognized: embryonic, nepionic, neanic (adolescent), ephebic (adult), and gerontic (old age); and in the exoskeleton of individual Rugosa, for instance, sequential changes in the skeletal morphology have been so named.

Tabulata being compound exoskeletons of many corallites, their ontogeny must be considered in two ways: the ontogeny of the **founding corallite (protocorallite)** and the ontogeny of the **hysterocorallites (offsets)**. The development of the colony as a whole (astogeny) is then discussed.

Protocorallites are difficult to identify in large compound coralla with small corallites, and there appear to be no records of studies of the protocorallites of Chaetetida, Tetradiida, Sarcinulida, Pachyporicae, Alveolitina, Halysitina, or Syringoporicae. In those species of Favositina, Heliolitina, and Auloporicae in which the protocorallite has been studied, it is an inverted cone, slender or wide, more or less curved, adherent or not, and commonly with an oblique calice; it is epithecate and shows growth lines and, in some, longitudinal (?septal) furrows. I have found no descriptions of the arrangement of these furrows, and do not know whether they are pinnate, as in Rugosa, or not. In large-celled Micheliniidae, septal granules arranged in radial rows appear early, but apparently not in the tip of the protocorallites (Beecher, 1891a, p. 207; 1891b, p. 215). In *Heliolites interstinctus,* Lindström (1899, p. 45) noted that septa first appeared on the adherent side of the protocorallite, and that coenenchyme first appeared subsequently, also on the adherent side. In many Auloporicae (Stumm, 1947), the protocorallite is recognizable, but does not appear to have been studied ontogenetically in thin section.

Jull (1965, p. 206) has indicated that in compound Rugosa, overlapping and perhaps skipping of stages occurs in the ontogeny of hysterocorallites; it might be expected that tabulatan offsets would be similarly affected. But, because of their small size, and the shortness and spinose constitution of their septa, it could be very difficult to ascertain any order of septal insertion. However, Schindewolf (1959, p. 309) reported that the offsets of *Pleurodictyum problematicum,* which are large, showed a pinnate arrangement of the septa, like that in the cardinal quadrants of rugosans; and that *Petridictyum petrii,* also with large offsets, showed two cycles of septa, longer and shorter, successively inserted. Plusquellec (1965, p. 44) agreed that cycles of septa could be distinguished in *Petridictyum,* but found no evidence of pinnate insertion in *Pleurodictyum*; although in some species, which he attributed doubtfully to that genus, two cycles were present in some, if not all, coralla. This line of investigation deserves intensive study, using modern serial sectioning techniques, for the light it could throw on a possible relationship between Tabulata and Rugosa.

Such a study (Jull, 1976b) indicates that two orders of septa are not recognizable during ontogeny of the offsets of *Foerstephyllum halli* (Nicholson), nor is any order of septal insertion evident: septa either emerge singly and randomly around the offset, or more commonly in groups in a particular region; however, in *F. vacuum* (Foerste), which has even larger corallites than *F. halli,* septa possibly equivalent to the cardinal and alar septa of Rugosa were noted.

ASTOGENY

The development of a colony (astogeny) similarly may be divided into stages of initiation, immaturity, maturity, and possibly old age, and it may be possible to identify morphological changes in the exoskeletons of compound coralla that may reasonably be equated with such stages. Bondarenko (1971a, p. 22) has attempted such an approximation in the Proporicae. She deduced

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five stages: 1) the stage of the protocorallite; 2) the stage of formation of protocoenenchyme from the protocorallite, with horizontal growth dominant; 3) the stage of the immature corallum, with intensive production of offsets that are small and without order in arrangement; the skeletal tissue is 'light-colored' and dissepiments are relatively large; 4) the stage of maturity, with offsets regularly arranged and growing longitudinally; there is repeated alternation of growth zones of 'darker' or denser skeletal tissue with zones of light-colored tissue in which dissepiments are smaller and corallites are larger than in the immature stage; 5) the stage of old age, occurring over either the whole or parts of the corallum; the corallites retain their previous diameter, but the vertical skeletal elements are thickened and the dissepiments are flatter. Bondarenko (1975b, p. 26) equated the dark bands with sexual maturity and the emission of planulae, and the light bands and the immature stage with asexual reproduction by budding.

Zonality in Tabulata had previously been discussed, e.g., by Sokolov (1955, p. 42), Dubatolov (1959, p. 278), Tong-dzuy (1965, p. 44), and Preobrazhenskiy (1967b, p. 3). Each zone commonly extends throughout the corallum; zones of close spacing of tabulae and with thicker or relatively darker vertical skeletal elements alternate with zones of more widely spaced tabulae and thinner, lighter-colored walls and septa. Such zonality is commonly attributed to periodic seasonal variations of climate and is considered to be without taxonomic significance. Preobrazhenskiy concluded that it may be only indirectly due to seasonal change, in being an expression of cyclical rejuvenation, which itself was probably seasonal, the zones of thickened skeletal tissue indicating sexual maturity and those of thinner tissue, rejuvenescence. He interpreted the peripheral zone of thickening in branches (e.g., in *Parastriatopora*) as indicative of sexual maturity.

Ma (1956, p. 2) has interpreted this zonality in Scleractinia, Rugosa, and Tabu-

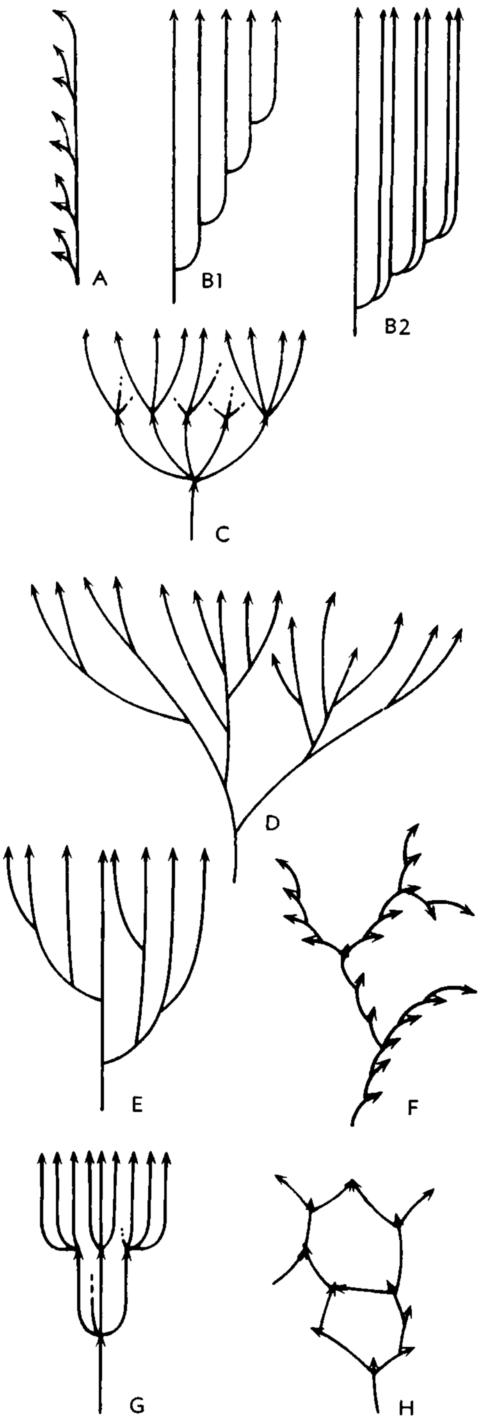

Fig. 306. Astogeny; pattern in Paleozoic coral colonies. Each line represents one corallite; arrow heads indicate position of calice and direction of growth (after Oliver, 1968). *A. Striatopora flexuosa. B.* Halysitina. *C, D, E.* Favositina. *F. ?Cystihalysites. G. Romingeria. H. Aulopora.*

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lata as annual, and has used the distance between the bases of consecutive 'dark' bands to measure annual skeletal growth. On the assumption that rate of skeletal growth decreases with water temperature, that is, with distance from the equator, he has constructed for each period world maps showing continents arranged in positions to fit these equators.

As OLIVER (1968, p. 18) has said, astogeny may also be described in terms of form, increase, pattern, and individual morphology, pattern being the spatial or sequential arrangement of corallites in a corallum. Form and mode of increase may be variable in many species and genera, and even within a single corallum; but other species or genera may have a characteristic form or a characteristic mode of increase or both. Pattern appears to be a more stable character than form, since differing forms may result from similar or identical patterns. However, pattern can also vary within species or genera, particularly where mode of increase is variable. OLIVER has given a useful diagram (Fig. 306), showing patterns in Paleozoic coralla.

KRASNOV and PREOBRAZHENSKIY (1972, p. 137) have discussed patterns formed by areal, axial, and consecutive arrangements of centers of increase, the first leading to convex or hemispherical forms, the second to cylindrical and branching forms, and the third to flat, encrusting, reptant, reticulate, or dichotomous or dendroid coralla.

It is clearly important that descriptive work should include an analysis of pattern within the corallum. A start has been made. Thus, BEECHER (1891a, p. 207; 1891b, p. 215), GIRTY (1895, p. 131), and SMYTH (1927, p. 426; 1929, p. 130) have studied species of Micheliniidae, Favositidae, and Vaughaniidae and Palaeacidae, respectively; OLIVER (1966, p. 448) investigated the pachyporican *Striatopora flexuosa,* SHARKOVA (1971, p. 56) the alveolitinans *Scoliopora* and *Alveolites,* BUEHLER (1955, p. 11), HAMADA (1959a, p. 276), and WEBBY and SEMENIUK (1969, p. 355) some Halysitina, and BEECHER (1903, pl. 5) the auloporican *Romingeria.*

REGENERATION

Tabulatan coralla, like those of Scleractinia and Rugosa, show evidence of reparative regeneration of soft parts after localized damage, by a return to normal skeletal secretion above the area where the skeleton showed damage or was prevented from forming. DUBATOLOV (1961, p. 75) has given a discussion of this phenomenon. In many cases the new skeleton is laid down in the same spatial mode that it would have had if no damage had occurred, although its plates may be somewhat thicker than normal; in others there may be, for a short distance, a disturbance in the normal architecture. Soft foreign bodies may be encapsulated, possibly by epitheca, or possibly by horizontal skeletal tissue. Many coralla show levels where skeletal formation was interrupted except for a small area where it proceeded normally; such negative areas were commonly rapidly covered by intensive basal horizontal increase from the undamaged region, whereupon normal longitudinal growth resumed; this is particularly characteristic for Alveolitidae; the areas of growth above or below the interruption may or may not correspond; whether the new skeletal tissue is epithecate below requires investigation. Periodic rejuvenescence has been mentioned in the section on astogeny.

SYMBIOSIS AND PARASITISM

There are many examples of association of tabulate corals with other organisms in which both associates continue their growth and skeletal formation. Stromatoporoid-tabulatan intergrowths are common, especially those involving *Syringopora* (MORI, 1970, p. 52). *Moyerolites* SOKOLOV, 1955, was subsequently shown to be an intergrowth of *Favosites* with a stromatoporoid (SOKOLOV & TESAKOV, 1963, p. 58); and *Trachypora circulipora* KAYSER was shown by LECOMPTE (1939, p. 148) to consist of a pachyporican and a stromatoporoid overgrowth. HILL (1960, p. 54) thought that *Trachypsammia* GERTH, 1921, may be an intergrowth between *Cladochonus* and an encrusting organism, possibly stromatoporoid.

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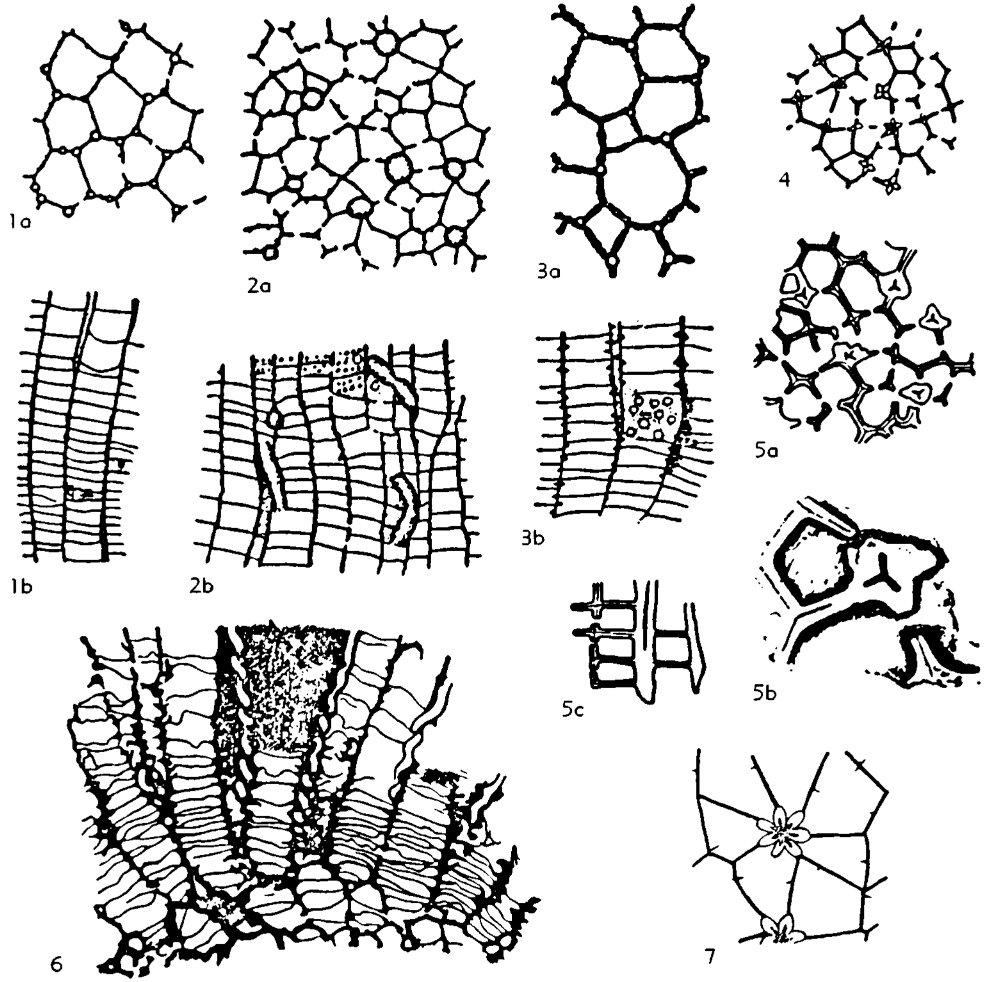

FIG. 307. Symbiosis and parasitism: symbiosis with favositids (after Oekentorp, 1969).——*1. Chaetosalpinx ferganensis* SOKOLOV; *1a,* transv. sec., *1b,* long. sec., both ×6.0.——*2. Camptosalpinx sibiriensis* SOKOLOV; *2a,* transv. sec., *2b,* long. sec., both ×4.5.——*3. Phragmosalpinx australiensis* SOKOLOV; *3a,* transv. sec., *3b,* long. sec., both ×4.5.——*4. Asterosalpinx asiaticus* SOKOLOV, transv. sec., ×4.0.——*5. Actinosalpinx uralensis* SOKOLOV; *5a,* transv. sec., ×10.0; *5b,* enl. transv. sec., ×16.0; *5c,* long. sec., ×10.0.——*6. Helicosalpinx asturiana* OEKENTORP, long. sec., ×6.0.——*7. Antherosalpinx yanetae* SOKOLOV, transv. sec., enl., diagram.

Commensalism with a polychaete worm, *Hicetes innexus* CLARKE, has been discussed (SCHINDEWOLF, 1959, pl. x) for *Pleurodictyum problematicum,* internal molds of which characteristically show the twisted U-shaped mud-filled tube of the worm in their proximal parts.

A common association in Tabulata, particularly in Favositina, is of fine tubes enclosed in the angles of the walls of *Favosites.* In his useful review of this group, OEKENTORP (1969, p. 177; Fig. 307) considered them to have been produced by commensal worms. *Chaetosalpinx* SOKOLOV, 1948, is straight, cylindrical, predominantly in the angles of the walls, and without distinct walls of its own, but it may have tabulae; *Helicosalpinx* OEKENTORP, 1969, is like *Chaetosalpinx* but spiral and is found in the thick walls of *Pachyfavosites* as well as in *Favosites, Alveolites,* and *Thamnopora.* (STEL, 1976, p. 726, found both these

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genera in *Thecia.*) *Phragmosalpinx* Sokolov, 1948, is of straight, cylindrical tubes, with thick walls of their own and occasional transverse plates, and is found in *Favosites*. *Asterosalpinx* Sokolov, 1948, with distinct walls, *Antherosalpinx* Sokolov, 1962b, also with distinct walls, and *Actinosalpinx* Sokolov, 1962b, without walls of its own, are all thick tubes of star-shaped section (*Asterosalpinx* 4-rayed, *Antherosalpinx* 4- to 8-rayed, *Actinosalpinx* 3-rayed), found in the angles of the walls of *Favosites*. The 3-rayed (and 4-rayed) forms have occasioned much discussion, still continuing, as to whether they are proper to the coral, symbionts with the coral, or postmortem or diagenetic structures. Thus, Swann (1947, p. 247) called them "intermural coenozone." Hill (1950, p. 147) thought some of them to be diagenetic and inorganic; Ross (1953, p. 40) called some of them intermural spaces formed in response to adverse environmental conditions. Sokolov (1948, p. 106; 1962b, p. 47) considered them commensals as did Oekentorp (1969). Possibly some of them are diagenetic, others commensal.

Lamellerima Kim, 1965b, was described as a longitudinal midwall slit in the faces of the corallites, and commonly arcuate in transverse section; not rarely it is oriented across and may cut the wall; he considered it commensal to Alveolitina. Better figures are required.

Another commensal, forming walled, empty tubes of somewhat greater diameter than the above, and not confined to the walls of the favositid but winding somewhat irregularly into two or three neighboring corallites, is *Camptosalpinx* Sokolov, 1948.

Oekentorp (1969, p. 201) described threadlike, forking tubes of smaller dimensions than all of the above in the lumina of *Favosites,* and regarded them as traces, probably of boring (etching) algae, which entered the corallites after the death of the polyps.

EVOLUTION

ORIGIN

The Order Tabulata had its beginnings in possible Precambrian and Cambrian ancestors. Speculation on the origin of the order is still very insecurely based. Composite molds (and casts in part), attributable to four classes of Cnidaria have been described mainly from the Ediacaran of South Australia and considered late Precambrian by Glaessner (but see Cloud, 1968, p. 37; Sokolov, 1972, p. 123). Glaessner (1971, p. 13) has suggested that the Hydrozoa Siphonophora, Hydrozoa Chondrophora, and the Conulata Conulariida all evolved from athecate Hydrozoa, and that Conulariida (Conchopeltidae) gave rise to Scyphozoa in pre-Ediacaran times. He considered that Anthozoa and athecate Hydrozoa had an earlier, common ancestry (Fig. 308). Glaessner and Wade (1966, p. 613) considered the Ediacaran *Rangea, Pteridinium,* and *Charnia* to be Anthozoa Octocorallia; but Pflug (1972, p. 56) suggested that they should be placed in his new phylum Petalonamae Pflug, 1970, and Glaessner in Part A of this *Treatise* treats them as problematical Coelenterata. Thus, no acceptable Precambrian Anthozoa are known at present.

Korde (1963, p. 20; 1971, p. 45) has included some Lower and Middle Cambrian central Asiatic conical and cylindrical fossils with characters suggestive of both scyphozoans and Rugosa in a new cnidarian class Hydroconozoa. These fossils are interpreted as exoskeletons; they range from less than 1.0 cm. to 1.5 cm. in height. *Hydroconus* Korde from the Lower Cambrian of Tuva resembles Rugosa in having septalike structures interrupted by a fossulalike space but has canals in the central part that are thought comparable with the radial canals of the gastrovascular system in Scyphomedusae. Handfield (1969, p. 782) has suggested that his new genus *Tabulaconus,* which comprises small, solitary, broadly conical to cylindrical skeletons of $CaCO_3$, with a slender, layered wall and crossed by thin, generally complete, but in places incomplete tabulae, belongs to the family Gastroconidae Korde (which lacks axial canals, but which Korde included in the Hydroconozoa). Handfield has doubtfully referred this family and genus to the Antho-

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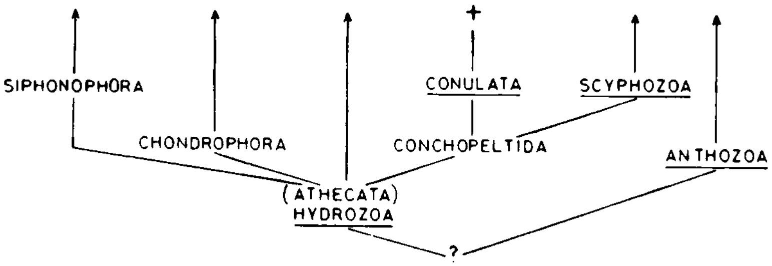

FIG. 308. Evolution: origin. Relations between some Hydrozoa, Anthozoa, Conulata, and Scyphozoa (Glaessner, 1971).

zoa Zoantharia. *Tabulaconus* differs from solitary Rugosa in being aseptate and from aseptate Tabulata in not being colonial. Its relationship to the Tabulata must remain speculative (Fig. 309).

JELL and JELL (1976, p. 194) have named a new Family Lipoporidae for some lower Middle Cambrian problematica from New South Wales and have doubtfully referred them to the Tabulata. They also referred to this family *Coelenteratella* KORDE, 1959, from the lower Middle Cambrian Amgian Stage of the southeast Siberian Platform. *Lipopora* JELL and JELL, 1976, is irregularly fasciculate, the individual skeletons being scolecoid, without tabulae or dissepiments, but with repeated rejuvenescence; its calices have 8 or 16 thin, continuous, short to moderately long septal ridges, which do not appear to have spinose distal edges.

Four Cambrian genera with ?calcareous compound skeletons consisting of contiguous, prismatic, very slender tubuli have been described. *Bija* VOLOGDIN (1932, p. 17) from the ?Lower Cambrian of River Lebed in the Altay of central Asia is said to be of aseptate and atabulate tubuli, with doubtfully porous walls, and 0.06 mm. in diameter. *Cambrotrypa* FRITZ and HOWELL (1959, p. 89) from the Middle Cambrian (*Albertella* Zone) of Montana is described as cerioid, or in part closely fasciculate, of aseptate and atabulate tubuli with relatively thick walls and of 1.0 mm. diameter. *Cambrophyllum* FRITZ and HOWELL (1955, p. 181) from the Upper Cambrian (Dresbachian) of Montana has atabulate thick-walled tubuli elongate in transverse section, with discontinuities in the walls, laminar adaxial extensions from which are interpreted as evidence of adaxial bipartite increase. *Archaeotrypa* FRITZ (1947, p. 434), from the Upper Cambrian Dresbachian of the Ram Range of the Rocky Mountains, Alberta, is doubtfully regarded as a cyclostomatous bryozoan, with some walls zigzag in longitudinal section, and is probably not anthozoan. As SOKOLOV (1962c, p. 208) suggested, the morphology of the first three is like that which might be expected of an ancestor to the Lichenariidae, and indeed to other Tabulata.

Protoaulopora SOKOLOV (1952b, p. 145) from the ?Upper Cambrian of Kazakhstan is of diversely oriented slender tubuli (0.1 mm. in diameter), apparently aseptate and atabulate, with up to three offsets arising simultaneously from the one tube. In spite of their small diameter, SOKOLOV considered these forms probably ancestral to the Auloporicae.

AFFINITIES WITH RUGOSA

FLOWER (1961, p. 31), in considering possible relationship between Rugosa and Tabulata, included microstructure in the morphological features on which he built his scheme. He considered that the simplest walls and septa are composed of parallel fibers formed normal to the secreting surface, and that development of fibers into trabeculae is a derived condition. A somewhat similar view was expressed by SMIRNOVA (1971, p. 79). FLOWER held that the primitive corals possessed a radiofibrous wall, and that septa first developed as processes on the inside of the wall; as septa developed in length and prominence, septal trabeculae developed. Thus the rugosan *Palaeophyllum* could have developed from *Lichenaria* via *Saffordophyllum* and *Foerstephyllum,* and he also speculated that *Strep-*

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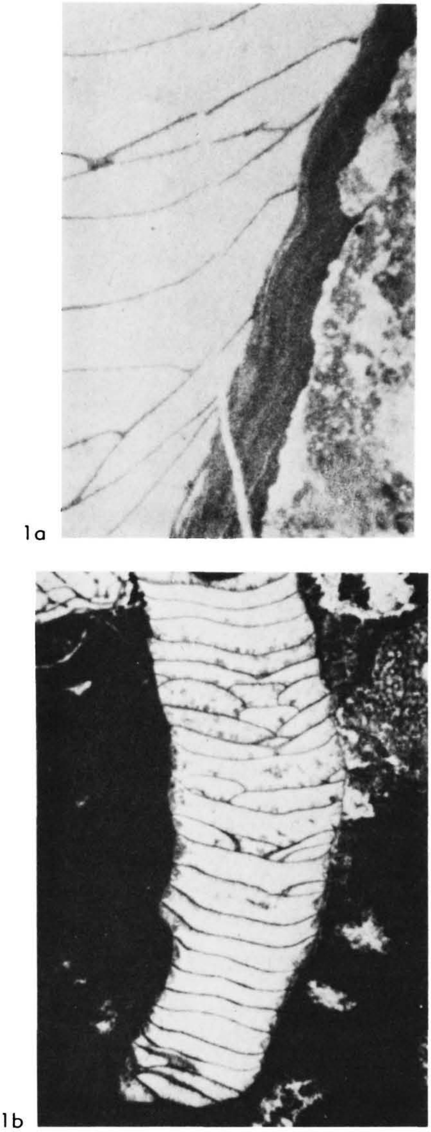

FIG. 309. Evolution: origin.——*1. Tabulaconus kordeae* HANDFIELD; *1a,* paratype, long. sec. showing layered external wall, ×26; *1b,* holotype, long. sec. showing complete and incomplete tabulae, ×4 (after Handfield, 1969).

telasma evolved from *Palaeophyllum.* His scheme for the Ordovician genera he studied is shown in Figure 310. To give credence to FLOWER's phylogenetic scheme we need supporting basic evidence on the order of insertion of the septa in these early Tabulata and Rugosa, and until this and micro- and ultrastructural studies on little altered Early or early Middle Ordovician corals have been supplied, further speculation is supererogatory.

SOKOLOV (1962c, p. 212; Fig. 311) expressed the view that ancient affinities exist between his anthozoan subclasses Rugosa, Tabulata (including Tetradiina, but excluding Chaetetina), and Heliolitida, and had no doubt that these major branches of Paleozoic corals diverged sharply from one another as far back as the early Paleozoic.

ORIGIN OF THE ORDERS (LOWER AND MIDDLE ORDOVICIAN)

Cryptolichenaria SOKOLOV (1955, p. 234) is considered by SOKOLOV and TESAKOV (1963, p. 90) to be characteristic of the Chunya Stage at the top of the Lower Ordovician of the Siberian Platform; it is cerioid, of irregularly prismatic corallites with amalgamated common walls like many Chaetetida, and like them has **adaxial** bipartite increase, which is, however, peripheral and unequal; the tubuli are aspinulate and from 0.3 to 0.5 mm. in diameter. SOKOLOV at first placed this genus in the Lichenariidae, but later transferred it to a new family Cryptolichenariidae, which he considered to be the oldest Tetradiida. In this *Treatise* it is regarded as the oldest genus of the Chaetetida. It could also reasonably be considered to be ancestral to the Tetradiida.

In the Lower Ordovician of North America (Canadian "Beekmantown" of the Appalachian Valley and the Pogonip of Nevada and Texas) are species identified as *Lichenaria* by BASSLER (1950, p. 260) and as *Lichenaria* and *Eofletcheria* by DUNCAN (1956, p. 216).

By the end of the Middle Ordovician the subclass Rugosa and all orders of the Tabulata had entered. It is necessary to indicate where the boundary between Middle and Upper Ordovician is drawn in this review, because the interbasinal and intercontinental correlation of the Ordovician graptolite and shelly faunas is still fluid (WILLIAMS *et al.,* 1972, p. 9). In the United Kingdom it is drawn at the base of the *Dicranograptus clingani* Zone and the base of the Longvillian; in the Baltic States, at the base of the Rakvere (E). In the USSR, NIKITIN's

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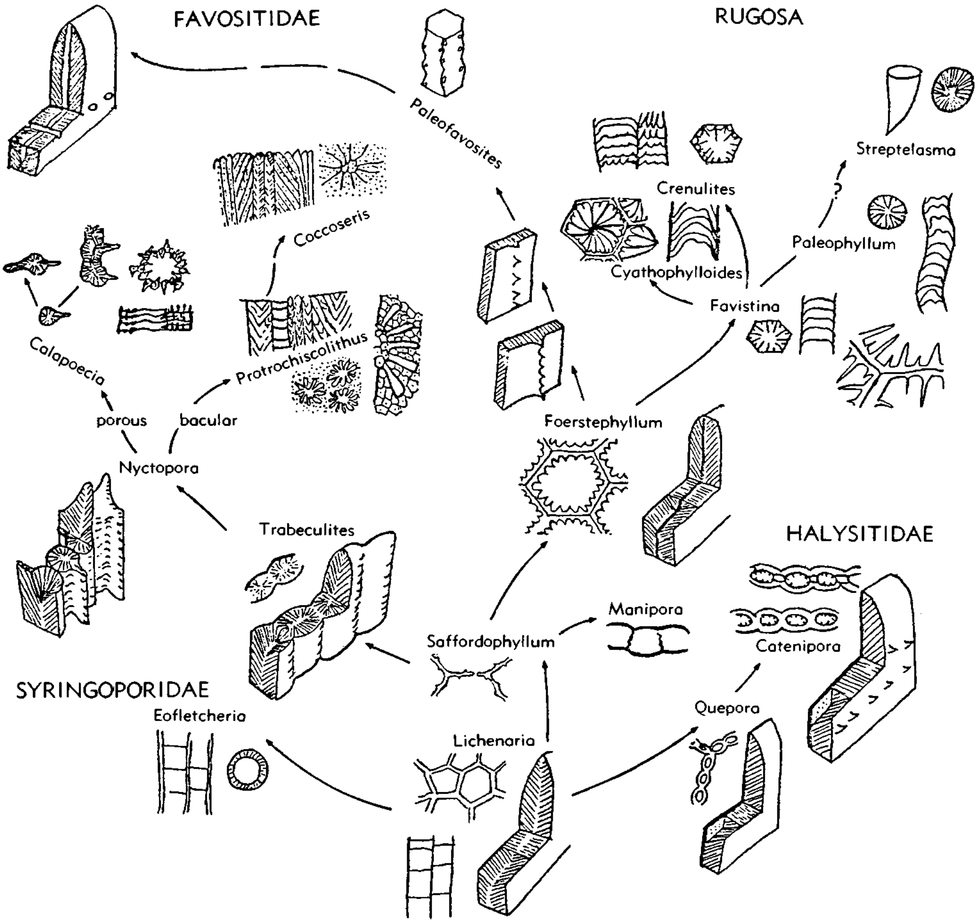

FIG. 310. Evolution: affinities with Rugosa. Inferred relationships of some Ordovician coral genera, by FLOWER (Flower, 1961).

(1971) correlations are used; thus, in Kazakhstan it is drawn at the base of the Anderken horizon; in the Altay, at the base of the Toginian; on the Siberian Platform, at the base of the Dolborian Stage; in northeast USSR at the base of the Kulon and Nalchan suites. In China the boundary is drawn at the base of the Yenwashan and Pagoda limestones; in North America, at the base of the Cincinnatian (base of Eden); and in Australia, at the base of the *Dicranograptus hians* Zone and the Clearview Limestone Member of the Bowan Park Limestone.

Thus, if *Cryptolichenaria* be accepted in the Chaetetida as herein advocated, Chaetetida were already present in the Lower Ordovician. *Chaetetipora* (or *Chaetetella*) is present in the Upper Ordovician Red River Formation of south Manitoba and the Richmondian of Arctic Canada. Tetradiida are present in force and cosmopolitan in the Middle Ordovician. Sarcinulida appeared in the Middle Ordovician in all present continents. *Billingsaria, Nyctopora,* and *Lyopora* at present seem to have entered in that order. Favositida were already represented by *Saffordophyllum* in the Chazyan of North America and by *Paleofavosites* at the very top of the Middle Ordovician of the western slope of the Urals (SOKOLOV, 1951a, p. 38). Of the Auloporida, records of "*Aulopora* spp." exist for the Middle Ordovician of New South Wales (WEBBY & SEMENIUK, 1971, p. 247), but descriptions and figures are required.

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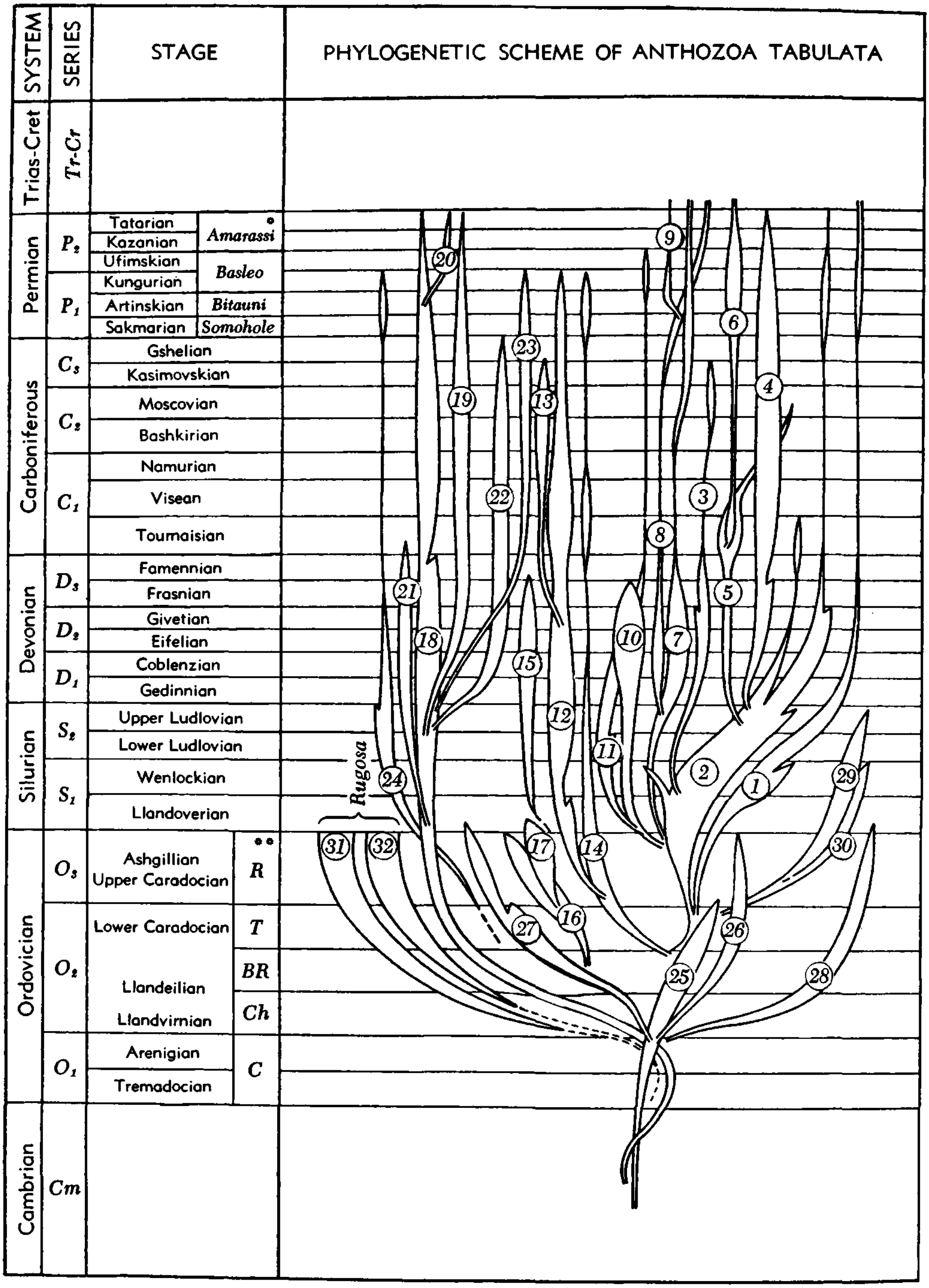

FIG. 311. Evolution: affinities with Rugosa. Phylogenetic scheme of orders and families of Tabulata and Rugosa, by SOKOLOV (Sokolov, 1962c). *, Stratigraphic scheme of Permian deposits of Timor Island. **, Stratigraphic scheme of Ordovician deposits of North America: *R*, Richmond; *T*, Trenton; *BR*, Black River; *Ch*, Chazyan; *C*, Canadian series. Key to numbered branches. TABULATA, *1-30*. Order Favositida, *1-11*; Suborder Favositina, *1-6; 1*, Theciidae, *2*, Favositidae, *3*, Syringolitidae, *4*, Micheliniidae, *5*, Cleistoporidae, *6*, Palaeacidae; Suborder Thamnoporina, *7-9; 7*, Pachyporidae, *8*, Trachyporidae, *9*, Trachypsam-

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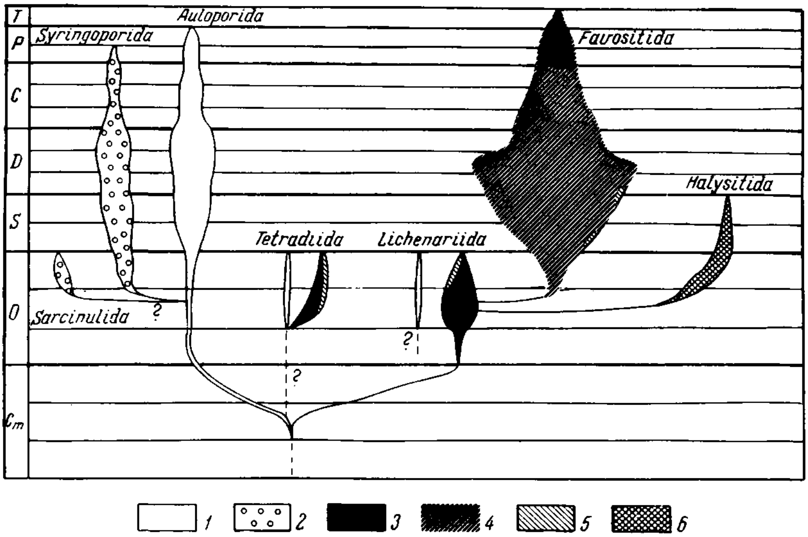

FIG. 312. Evolution: origin of the orders. Phylogeny of Tabulata (after Bondarenko, 1966b). Key. *1,2.* Fruticose type of polypary; *1,* without connective structures; *2,* with connective structures. *3,4.* Massive type of polypary; *3,* without connective structures; *4,* with connective structures. *5,6.* Fruticose-massive polyparies; *5,* tollinoid variant; *6,* halysitoid + tollinoid variant.

Syringoporicae are represented by *Labyrinthites* in the Middle Ordovician of North America. *Praesyringopora* IVANOV in IVANOV and MYAGKOVA (1950, p. 16; 1955, p. 28), previously considered Middle Ordovician, is now (F. E. YANET, written commun. July, 1974) believed to come from post-Ludlovian deposits and may be *Syringopora.* Heliolitina are represented in the Middle Ordovician Cliefden Caves Limestone of New South Wales by *Coccoseris, Heliolites, Propora,* and *Plasmoporella* (HILL, 1957a, p. 101). Halysitina are represented in the Middle Ordovician of North America by *Quepora; Halysites* first occurs in the Bowan Park Limestone of New South Wales in beds correlated with the *Didymograptus hians* Zone (WEBBY & SEMENIUK, 1969, p. 357), considered Upper Ordovician herein.

SOKOLOV (1962c, p. 212; 1971, p. 9) has given considerable thought to the possible interrelations of the major subdivisions of Tabulata. His phylogenetic schemes are chronologically derived and his diagrams show ranges and relative abundance as well as assumed relationships. He placed phylogenetic importance on the development of mural pores and connecting tubuli, considering coralla with such devices to be more advanced than those without such communication. He also placed stress on the development of peripheral stereozones in corallites. He deduced two stems for the Tabulata (without Heliolitina and Chaetetida). One was cerioid and imperforate, typified by *Lichenaria* and the Lichenariidae; the other was fasciculate and incommunicate, typified by *Protoaulopora* and

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FIG. 311. *(Explanation continued from facing page.)*

miidae; Suborder Alveolitina, *10, 11; 10,* Alveolitidae, *11,* Coenitidae. Order Syringoporida, *12-15; 12,* Syringoporidae, *13,* Multithecoporidae, *14,* Tetraporellidae, *15,* Thecostegitidae. Order Sarcinulida, *16, 17; 16,* Syringophyllidae, *17,* Calapoeciidae. Order Auloporida, *18-23; 18,* Auloporidae, *19,* Cladochonidae, *20,* Auloheliidae, *21,* Romingeriidae, *22,* Aulocystidae, *23,* Sinoporidae. *24,* The isolated family Fletcheriidae. Order Lichenariida, *25-27; 25,* Lichenariidae, *26,* Billingsariidae, *27,* Lyoporidae. Order Tetradiida, *28,* Tetradiidae. Order Halysitida, *29, 30; 29,* Halysitidae, *30,* Hexismiidae. RUGOSA, *31, 32. 31,* Favistellidae. *32,* Streptelasmatidae.

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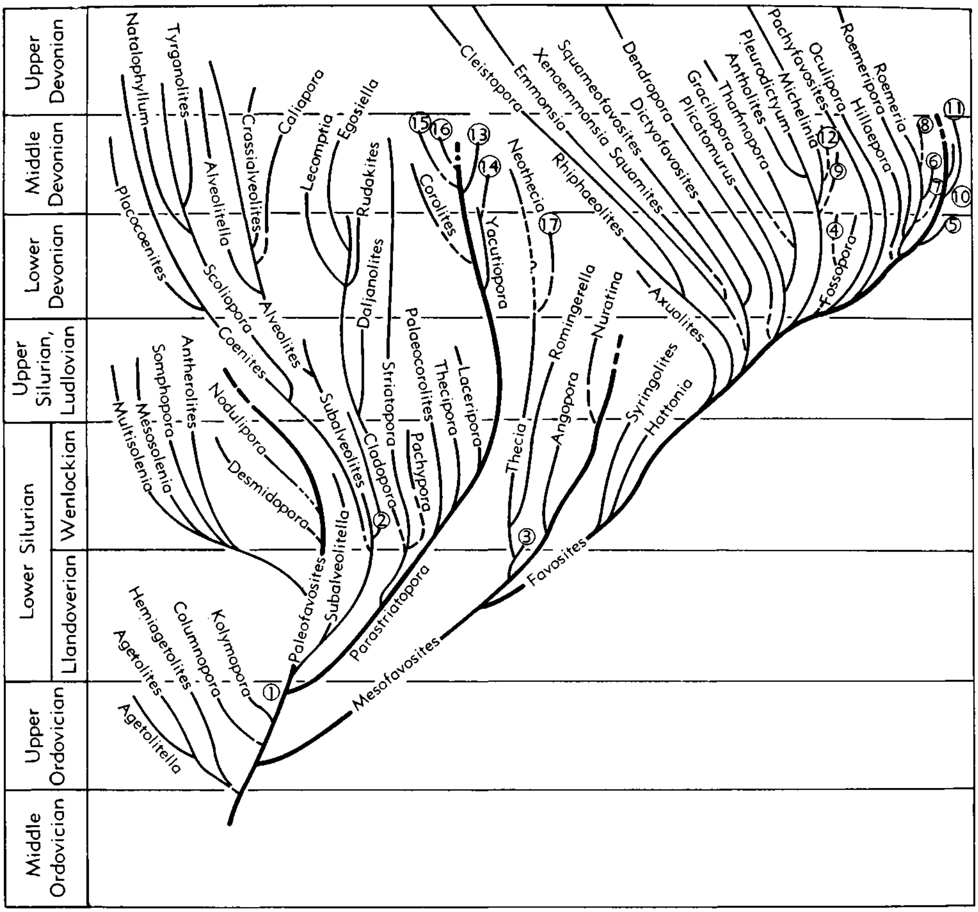

Fig. 313. Evolution: phylogenetic range diagrams. Leleshus' phylogenetic outline of Ordovician, Silurian, and Devonian members of the order Favositida (after Leleshus, 1971c). 1, *Priscosolenia.* 2, *Planalveolites.* 3, *Hemithecia.* 4, *Fossoporella.* 5, *Lamellaeoporella.* 6, *Roemerolites.* 7, *Armalites.* 8, *Neoroemeria.* 9, *Holacanthopora.* 10, *Crenulipora.* 11, *Gephuropora.* 12, *Procteria.* 13, *Fomitchevia.* 14, *Echyropora.* 15, *Trachypora.* 16, *Rachopora.* 17, *Xenothecia.*

Aulopora. He thought that, from the first of these, Billingsariidae and Lyoporinae (both regarded as Sarcinulida in this *Treatise*) evolved near the boundary between Early and Middle Ordovician and that Lyoporinae gave rise to Calapoeciinae and Syringophyllinae[1] during the Middle Ordovician. He thought that Tetradiida derived from it *via Cryptolichenaria* during the Early Ordovician. The cerioid Tabulata with mural pores (e.g., the Favositida) and the fasciculate Tabulata with connecting tubuli (e.g., the Syringoporicae) he thought had a common ancestry within his cerioid incommunicate stock, both groups arising late in Middle Ordovician time. Bondarenko (1966b, p. 14), however, derived the Syringoporicae from the Auloporicae because some Syringoporicae have an early anastomosing, reptant, or auloporoid stage in astogeny (Fig. 312). The Halysitina were thought by both authors to have originated from this same cerioid, incommunicate stock near the end of the Middle Ordovician. Bondarenko considered the Heliolitina to be a separate subclass from the Tabulata, though sharing a common ancestry with the Rugosa.

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[1] The taxonomic names are those applied in this *Treatise*, unless otherwise indicated.

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Sokolov (1962c, p. 275) indicated that one heliolitinan stock, the Coccoseridicae, from which he derived the Helioliticae during the late Middle Ordovician, probably originated in the Early Ordovician. The Proporicae he thought arose in the Middle Ordovician and the Cyrtophyllidae near the end of that epoch. The second fasciculate, incommunicate stem for the Tabulata he conceived as originating in the Cambrian and developing during the Ordovician into the Auloporicae.

PHYLOGENETIC RANGE DIAGRAMS

Authors of range diagrams for the genera placed in the suborders and families of Tabulata have shown speculative and very differing phylogenetic lines based on morphological similarities and differences. I have found no diagrams for Chaetetida, Tetradiida, and Sarcinulida, but for the Favositida there are several. Leleshus (1971c, p. 19; Fig. 313) gave a diagram for the order which differs in several important particulars from that given by Sokolov (1962c, p. 212; Fig. 311). For the Favositicae and Favositidae, Dubatolov (1963, p. 167; 1974a, p. 141), Mironova (1965, p. 81; Fig. 314) and Kim (1971c, p. 143) have offered varying views. Schemes dealing with the Pachyporicae of this *Treatise* have been provided by Chudinova (1959, p. 112) and Dubatolov (1963, p. 173; 1972a, p. 106; see also Dubatolov, 1972b, p. 68). For the Alveolitina, schemes have been drawn up by Dubatolov (1963, p. 180), Chudinova (1964, p. 11), and for a part by Kim (1971b, p. 131); the alternative ultimate derivations suggested are from the problematical *Plasmodictyon* Wilson, 1926, or from *Paleofavosites* Twenhofel, 1914, *via Subalveolites.* The Multisoleniidae are considered by Kim (1971b, p. 127) to have had a common ancestry with the Alveolitina in *Plasmodictyon,* and by Dubatolov (1963, p. 167) and Leleshus (1971c, p. 19) in *Paleofavosites.* Sokolov (1955, p. 146) considered the Theciidae to derive from somewhere close to early Favositidae, whereas in this *Treatise* they are classified as Sarcinulida. The Agetolitidae, herein doubtfully considered Favositida, are regarded by Kim (1971a, p. 40), on the basis of unpublished ontogenetic studies, as hav-

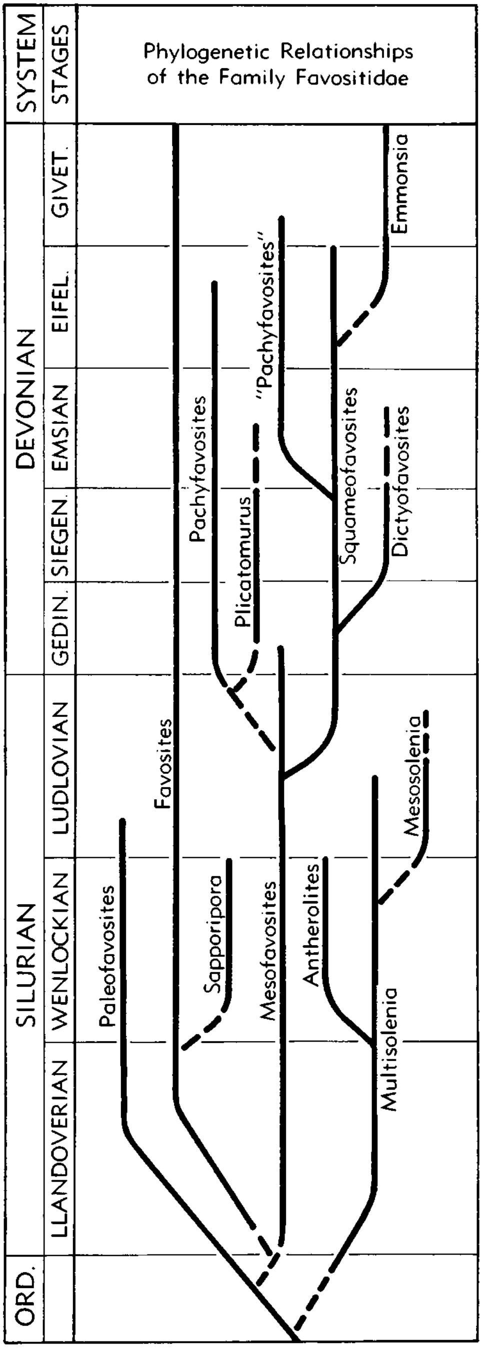

FIG. 314. Evolution: phylogenetic range diagrams. Phylogenetic relationships of the genera of the family Favositidae (after Mironova in Sokolov & Dubatolov, 1965b).

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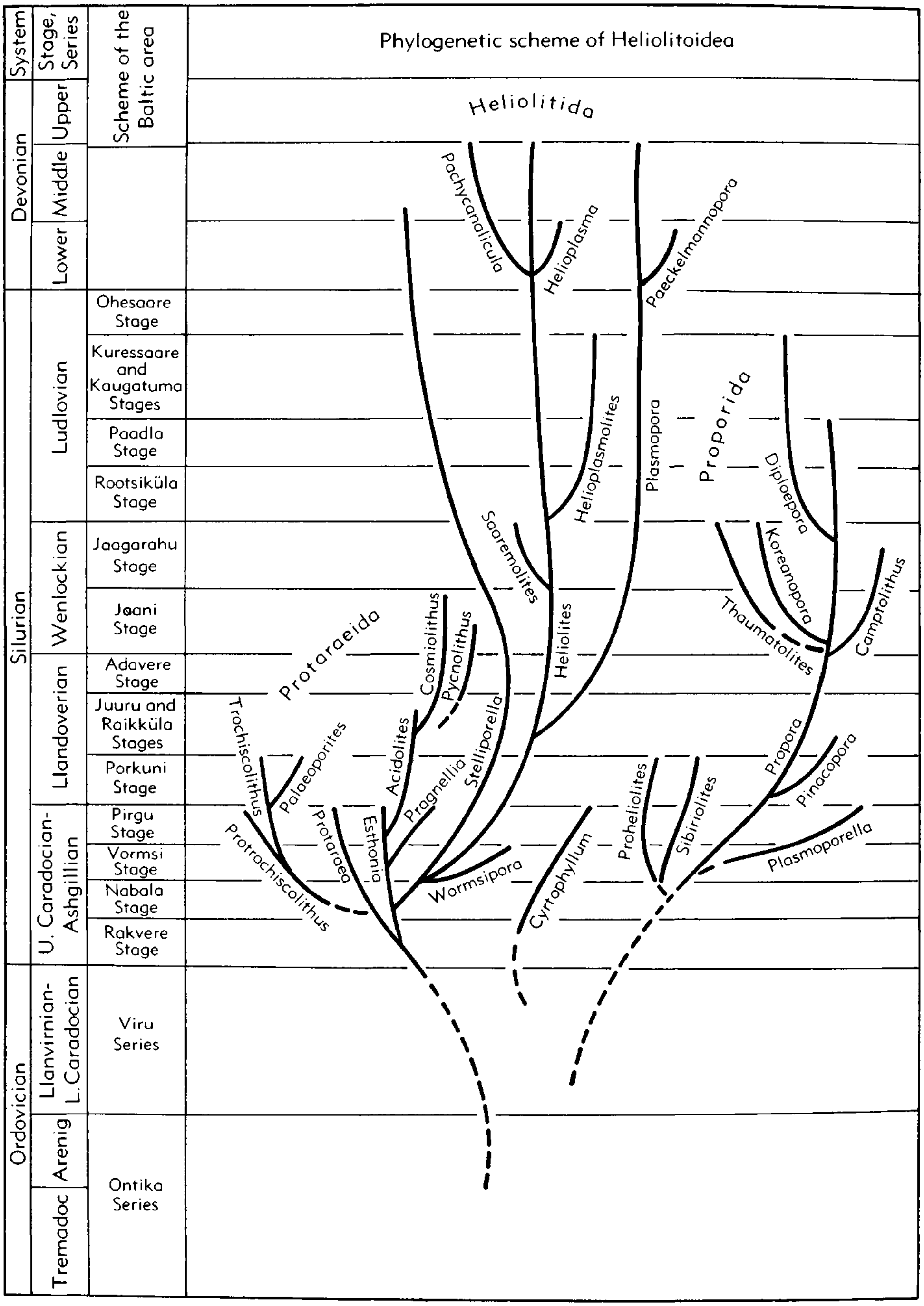

FIG. 315. Evolution: phylogenetic range diagrams. Phylogeny of Heliolitoidea (Sokolov, 1962).

ing rugosan septal insertion and, therefore, Rugosa.

SOKOLOV (1962c, p. 275) has given a diagram of possible generic relations within the Heliolitina (Fig. 315).

No diagrams seem to have been published

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for the Halysitina or the Auloporicae other than the family lineages of SOKOLOV (1962c, p. 212). For part of the group included in this *Treatise* in Syringoporicae, CHUDINOVA (1971a, p. 106; 1974, p. 112) has outlined a scheme. For the Roemeriidae, also regarded herein as Syringoporicae, DUBATOLOV (1963, p. 169; 1974a, p. 146) and CHUDINOVA (1964, p. 16) have offered diagrams.

RATES OF GROUP EVOLUTION

Rates of group evolution for the Tabulata (except Chaetetida and Heliolitina) and for the Heliolitina have been calculated by LELESHUS (1971c, p. 17). Such rates of evolution, *E,* he suggested, might be determined for a group given a knowledge of: 1) the number of genera, x_2, arising in the course of a geological epoch; 2) the duration of the epoch, t; 3) the number of inherited genera, x_1, i.e., those in existence at the beginning of the epoch; and 4) the phylogeny of the group concerned. He took the duration of periods and epochs from HAMILTON (1965) except for the Silurian, where he followed AFANAS'EV *et al.* (1964); he used 10,000,000 years as the unit of time. His formula was a simplified and somewhat modified empirical variant of the formula:

$$E=\frac{x_2}{t\left[x_1+(n_1-y_1)+\frac{(n_2-y_2)(m-1)}{m}+\frac{(n_3-y_3)(m-2)}{m}+\cdot\cdot\right]}$$

in which y_1 is the number of inherited genera which gave rise to other genera during the first burst of evolution in an epoch, and n_1 is the number of new genera so arising; y_2 and n_2 refer to the numbers in the second burst of evolution within the epoch, etc.; m is the number of such bursts. The modification he considered to be desirable because some phylogenetic lines would come to an end within the epoch, and some genera would exist considerably longer than the epoch. The formula thus modified became:

$$E=\frac{x_2}{t\left[x_1+\frac{n_1-y_1}{2}+\frac{n_2-y_2}{4}+\frac{n_3-y_3}{6}+\cdots\right]}$$

On this basis, he obtained the rates of group evolution shown in Table 2.

TABLE 2. *Rates of Evolution of Tabulates and Heliolitoids.*

Geochronological subdivision	Favositida	Tabulata	Heliolitina
Triassic	0.00	0.00	....
Permian	0.20	0.19	....
Middle-Late Carboniferous	0.30	0.29	....
Early Carboniferous	0.26	0.29	....
Late Devonian	?0	0.06	....
Middle Devonian	0.20	0.23	0.00
Early Devonian	0.85	0.89	0.38
Silurian	1.09	1.00	0.84
Late Ordovician	1.14	0.74	1.03

The validity of the results obtained is affected by the subjectiveness of the phylogenies adopted and of the taxonomic units.

From the figures it would appear that very significant changes in the rates of group evolution both of Favositida and Tabulata (less Chaetetida and Heliolitina) took place at the boundary between Early and Middle Devonian, and that a similar change occurred in the evolution of the Heliolitina between Silurian and Devonian. A sharp reduction of rates of evolution is followed some time later by a sharp reduction in abundance and taxonomic diversity. The highest rates occurred in the periods preceding the acme of the group and in the early stages of its flourishing; and the lowest rates occurred in the late stages of evolution. Thus the Favositida, which arose at the end of the Middle Ordovician, had large numbers of individuals, but still only a small number of taxa by the end of the Late Ordovician. They began to flourish in the Silurian and their acme continued into the second half of the Middle Devonian, at which time the favositids were represented by the largest numbers of species, genera, and families in their history and were greatly predominant in numbers of individuals. At the beginning of the Late Devonian they became far more rare and more uniform; from the beginning of the Famennian on to their extinction in the Early Triassic, they were poor in numbers of both individuals and taxa.

TRENDS IN EVOLUTION

Recognition of evolutionary trends in

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Tabulata is a speculative undertaking, is certainly subjective, and has provoked a considerable literature. Parallelism, convergence, and iteration have been noted. The ideas propounded must continue to be tested; they are necessarily closely interwoven with phylogenetic speculation and with deductions on paleoecology. Possible trends involve changes in form of corallum, development of communicating structures between neighboring corallites, development of dissepimental or tubulose coenenchyme, change in form of corallite, development in corallites of a peripheral stereozone, changes in tabulae, and changes in the development of septal elements.

A. Changes in form of corallum.

1) Development of cylindrical branches from cerioid coralla by localization of active increase (e.g., in the Late Ordovician species of *Lyopora* and *Nyctopora*) (Bondarenko, 1962, p. 58); this is commonly associated with skeletal thickening and shortening of the distance between tabulae in the peripheral zone of the branches (e.g., *Paleofavosites* to *Kolymopora* in the Late Ordovician, and *Paleofavosites* to *Parastriatopora* in the Silurian). Leleshus (1972c, p. 42) considered such changes to be adaptive, related to deeper, quieter sea floors, but Preobrazhenskiy (1967b, p. 3) suggested that the peripheral zone of thickening represented the developmental stage of sexual maturity.

2) Cateniform coralla appeared in unrelated stocks, in some apparently derived from phaceloid coralla, but in many apparently from cerioid coralla (Tesakov, 1965, p. 19; Preobrazhenskiy, 1965, p. 21; Bondarenko, 1966b, p. 9); paleoecological control has been suggested.

3) Fasciculate to cerioid, and cerioid to fasciculate, coralla. Bondarenko (1966b, p. 11) considered that the cerioid "Lichenariida" probably developed from the fasciculate auloporoids in the Early Ordovician, as the latter rose above the substrate, like the reptant *Mastopora* in the Devonian and *Aulohelia* in the Permian. But a trend from cerioid to fasciculate is also presumed, as for instance in *Lessnikovaea* in the Ordovician and the Roemeriidae in the Devonian, in which the corallites in at least the peripheral regions of the coralla grow apart and cylindrical.

B. Development of communicating structures between neighboring corallites.

1) Mural pores. Sokolov (1955, p. 281) and Bondarenko (1966b, p. 14) considered that the Favositida arose from the "Lichenariida" by this trend in the Middle Ordovician; later trends in the Favositida involved the arrangement of the pores in the walls and at the angles between the walls.

2) Connecting tubuli. Sokolov (1955, p. 291) considered that early Syringoporicae arose from cerioid incommunicate "Lichenariida" by the development of tubuli as the corallum became fasciculate, but Bondarenko (1966b, p. 14) thought they developed from incommunicate Auloporicae.

3) Connecting platforms and connecting channels or tubuli, in the Ordovician Syringophyllidae, Silurian Chonostegitidae, and the Devonian Roemeriidae and Neoroemeriidae.

C. Development of dissepimental or tubulose coenenchyme, as in some Halysitina and in all Heliolitina.

Coates and Oliver (1973, p. 3) have related developments B and C above to the soft parts and expressed them as "developments in coloniality." They discussed "degrees of integration of individuals within colonies of corals" and gave "scales of integration" based on skeletal features, together with interpretations of the positions of these features on other scales of "tissue level," "extrapolypoidal skeleton and tissue," and "polymorphism." They considered phaceloid coralla with corallites bounded by an imperforate wall to have lower integration of individuals than similar cateniform and cerioid coralla, which were lower than meandroid coralla: all of these had lower integration than phaceloid coralla with a perforate wall (as in *Syringopora*), and such phaceloid coralla were lower than cerioid coralla with mural pores. All the above were at a lower level than coralla in which separating walls were incomplete or lacking between corallites, such as meandroid coralla, and these they regarded as less integrated than coenenchymate coralla (such as in Heliolitina). They adopted Wells' postulate (1971, p. 748) that the

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homomorphous individuals, organically (by soft tissue) or structurally (by skeletal tissue) united in true colonies, as in phaceloid and cerioid epithecate Rugosa, resulted from extratentacular budding of the polyps. It may be possible to extend WELLS' postulate to the fasciculate and cerioid Tabulata, except the Chaetetida and Tetradiida. These two orders, with adaxial growth of dividing walls, may have reproduced by intratentacular budding of their polyps; a similar type of increase may be found in Alveolitina, though in these presumably extratentacular budding would have been dominant.

D. Change in form of corallite.

Alveolitoid corallites may be considered to have evolved from prismatic and contiguous or cylindrical corallites by a change of habit from erect to inclined either to the substrate or to the axis of a branch. LELESHUS (1972c, p. 43) considered such changes to have given rise in the Favositida to Alveolitina; in the "Lichenariidae" to *Baikitolites*; and in the *Tetradiidae* to *Paleoalveolites*. These changes may affect the form and habit of the corallum.

E. Development in corallites of a peripheral stereozone (e.g., *Favosites* to *Pachyfavosites* and *Heliolites* to *Pachycanalicula*; LELESHUS, 1972c, p. 43).

F. Changes in tabulae.

1) Replacement of tabulae by tabellae is found in many unrelated stocks; in some, these tabellae may be confined to a peripheral zone *(Hayasakaia)*.

2) An axial syrinx may develop in unrelated lineages from infundibuliform tabulae (e.g., in *Syringolites*, presumably from *Favosites*; and in *Syringopora*, presumably from *Tetraporella* or other genera).

G. Changes in the development of septal elements.

1) Microstructure. FLOWER (1961, p. 32) has speculated on the evolution of the septa; he held that the primitive corals possessed a fibrous wall, and that septa first developed as processes on the inside of the wall; that is, as trabeculae that may become contiguous to form the septal plates. SCHOUPPÉ & OEKENTORP (1974, p. 165) speculate, however, that the fine septal spines so characteristic of Middle Paleozoic Tabulata developed in a ?retrogressive trend by reduction from the coarse laminar or acanthine septa that are commonest in the early Paleozoic.

2) Development of septal plates from septal spines; e.g., in lineages suggested by LELESHUS (1972c, p. 44) from *Multisolenia* to *Antherolites*; from *Parastriatopora* to *Laceripora*; from *Parastriatopora* to *Palaeocorolites*; and from *Parastriatopora* to *Thecipora*.

3) Development of squamulae; found in many lineages of Favositida in the latest Silurian and Early and early Middle Devonian (YANET, 1971, p. 109).

PALEOECOLOGY

By analogy with living corals it might be supposed that there were deepwater corals as well as reef corals in the Paleozoic; but as far as I am aware there are no published studies proving their existence. The recorded faunas seem without exception to have inhabited epicontinental sea floors or continental shelves or slopes. Accepting then, that the Tabulata were neritic and benthonic, we find that while some are found in the normal argillaceous-arenaceous or volcanic sedimentary facies of the shallow sea floor, they are far more common in carbonate facies, and are particularly abundant in reef facies. However, in the reef facies they are so commonly not the most important frame builders, binders, or dwellers, that it is seldom appropriate to speak of tabulate coral reefs. Nevertheless, Tabulata may be the most common component of some of the biostromes developed in reefal complexes, particularly in those of the Late Ordovician, Silurian, and Devonian.

Paleozoic reefs consist of a framework of animal and algal skeletons that rose above the surrounding sea floor to a greater or lesser height; the interstices of the framework are more or less filled by skeletons of reef-dwelling organisms and by bioclastic and biogenetic carbonates; the framework

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may or may not have been rigid due to contiguous growth of its constructors, which may be algae of many kinds, stromatoporoids, tabulate or rugose corals, bryozoans, or sponges; rigidity may be imparted by binding of debris and framework by encrusting skeletons of Bryozoa, stromatoporoids, blue-green or coralline algae, or corals, or by stromatactoids or stromatolites. Bodies so constructed may be bounded laterally by contemporaneous or penecontemporaneous bedded clastics and may then be called bioherms; similarly constructed biostromes that do not rise above the level of their surroundings but are laterally extensive commonly form part of the reef complex, and on the margins of platforms they may greatly increase in thickness to become barrier reefs. Coarse to fine detritus derived from the reefs by wave or current action or by reef-boring organisms may be spread widely between and around the reefs, and forms part of the reef complex. In the forereef areas such bioclastic material may form steeply dipping talus slopes populated by a rich epibiont fauna and flora. In reef-fringed or reef-studded carbonate platforms, intratidal or shallow subtidal mud or sand may be deposited and in some such lagoons with restricted circulation, evaporites may be deposited. Reef growth, even on shallow platforms, is inhibited by influxes of terrigenous sediment.

Some Paleozoic reefs, particularly those of lenticular biohermal form and of considerable height, show vertical zonation that has been explained as due to the upward growth of the reef into zones of wave action at a rate greater than the rate of subsidence of the sea floor (or rise in sea level). Silurian and Devonian examples are quite numerous. Many such reefs began on hard ground made by the skeletons of solitary Rugosa or small tabulate colonies, or by crinoids or crinoidal debris. The first framework organisms based on this hard ground are, in the Silurian, not infrequently Tabulata that form rather loose skeletal networks, such as *Syringopora* or *Halysites*. As the reef is traced upward, more massive cerioid coralla such as *Favosites* and Heliolitina may predominate, and more genera, species, and individuals are present, indicating that the shallow reef environment was more favorable to growth of Tabulata than the earlier nonreef environment. The species characteristic of the different zones may also be found in associated reefal biostromes where the physical conditions and supply of food were similar; controlling physical factors appear to have been turbidity and rate of settling of mud or sand, force and direction of wave or tidal currents, nature of substrate, depth, and, in some places, salinity.

It is clear from the above summary that the reefal facies have multitudinous subfacies, and each is likely to have its own community; and so ultimately the paleoecological study of any reef complex or reef archipelago must be a matter of detailed field, subsurface, and laboratory observations and analyses. However, the most detailed studies of the last decade have devoted acute attention to one aspect only, usually the sedimentological aspect; maximum benefit to the science will not be obtained unless close and skilled taxonomic work accompanies the sedimentology.

An aspect of reef studies that occupies considerable space in the literature is the adaptation of the growth form of a corallum to a particular reef niche. Many generalizations have been made, but owing to the number of controlling factors the number of exceptions to a suggested norm is great. Thus, slenderly branching coralla are not necessarily characteristic of either quiet or deep water; indeed, they may be found in most reef environments except perhaps the reef crest exposed to the full force of breakers. Similarly, stubby or knobby coralla are not necessarily indicative of the surf zone; they may also be found in areas where much mud settles. Although particular species or genera may be found commonly in particular environments, it cannot be assumed that they always indicate that environment.

The biological character of Paleozoic reefs changed during the era. In the Early Cambrian, algae were dominant, with Archaeocyatha their most important associates, both as reef dwellers and builders. In later Cambrian and Early Ordovician time, sponges took the place of the Archaeocyatha. In the Middle Ordovician, bryozoans, pelmatozoans, stromatoporoids, and tabulate and rugose corals to a large extent replaced the sponges.

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The reef ecology of Ordovician Tabulata is perhaps best exemplified by the Middle Ordovician (Chazyan) mounds, commonly called bioherms, of eastern North America (PITCHER, 1971, p. 1341). Earlier than this epoch only sporadic Tabulata are recorded. These mounds, seldom more than 20 by 30 by 100 to 300 feet and mostly smaller, were built up by bryozoans, stromatoporoids, encrusting Tabulata *(Billingsaria)*, and algae acting mostly as binders. Some corals such as the cerioid *Lamottia heroensis* and the closely fasciculate *Eofletcheria incerta,* some bryozoans, and some sponges contributed as frame builders in a few mounds. Few, if any, Ordovician reefs can properly be called coral reefs. However, mounds in the Carters Limestone of Tennessee are interpreted by ALBERSTADT, WALKER, and ZURAWSKI (1974, p. 1171) as "patch reefs" developed in the four stages of reef growth: stabilization; colonization; diversification, chiefly of frame-building corals and stromatoporoids; and domination by stromatoporoids. On the whole, Ordovician Tabulata are found mostly in shallow, subtidal, level-bottom communities on the carbonate platforms, like the Black River *Foerstephyllum halli* community in New York. A wave-baffle community of *Tetradium cellulosum* has been described from the shallow calcareous mudflats of the Blackriveran sea floors of New York State (WALKER, 1972b, p. 2509). WALKER (1972a, p. 82) has also analyzed the various Black River communities in terms of their feeding (trophic) relationships.

In the Upper Ordovician Boda reefs of Sweden (see JUX, 1966a, p. 153), corals lived mainly near the margins of the reefs and appear to have been less important builders than the algae.

LOWENSTAM (1957, p. 232) reviewed the Silurian reefs of North America. He considered that reefs may have begun following localized reduction by weak currents of the amount of mud settling on the sea floor. In one such incident the pioneer reef populations were large boss-shaped specimens of *Syringopora* (dominant) and *Favosites*; as reef growth began, lamellar forms of *Favosites* were the dominant constructors. In this quiet-water stage, the endemic reef elements (stromatactoids and locally stromatoporoids) also participated as trappers and binders. The populations were small, and terrigenous detritus at first commonly outweighed bioclastic debris in filling the interstices of the frame.

The second stage of reef growth was the semirough-water stage, from the depth of the deepest storm wave penetration (that is, with occasional agitation of the water), to about normal surf base. Reef construction during this stage was in the form of an open lacy network; stromatactoids were still dominant, but stromatoporoids increased in importance while Tabulata (*Favosites, Halysites, Heliolites,* and *Syringopora,* their coralla usually being small, low-lying bosses) were now only accessory builders. In general, the upward increase in turbulence was accompanied by a similar increase in numbers of species and individuals of reef dwellers, including those living on the flanks; many Tabulata of considerable size were involved in the later phases of this growth stage; they may be found also in the interreef facies. The fill in the interstices was dominantly bioclastic (Fig. 316).

The rough-water or wave-resistant stage also involved both reef builders (including binders) and reef dwellers. It was profusely populated, abounding in species and individuals, and represented the climax of reef enrichment. Of the reef builders, stromatoporoids greatly increased in proportion to stromatactoids and there was an increase in Tabulata and Rugosa. Tabulata functioning primarily as stabilizing elements for skeletal debris in frame-building zones included *Thecia,* alveolitids, and, as effective sediment-catching accessories on protected reef surfaces, *Fletcheria* and *Coenites.* LOWENSTAM postulated that sheetlike *Thecia* partly replaced stromatoporoids on reefs where there was settling of greater amounts of terrigenous matter.

LOWENSTAM (1957, p. 237) considered the reef corals to have been derived initially from semirough- to rough-water open shelf stocks, and that many of them were morphologically preadapted and able to occupy reef environments with little change. Adjustment in growth form to direct wave impact was mostly by reduction of surface area in the vertical dimension. Many frame

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builders were horizontally expanded; others were bracket-shaped with sturdy low pillars proximally, raising the calical surface sufficiently above the substrate to prevent injury or burial by shifting skeletal sands.

Paleoecological studies on the Silurian reefs of Gotland, Great Britain, and the USSR in general have given similar results; on the whole stromatoporoids, stromatactoids, and algae were more important than Tabulata as constructors (builders and binders), but locally Tabulata were dominant. Commonly Tabulata were important reef-dwellers.

Manten (1971) considered that in Gotland turbidity and the resultant settling of mud may have had more influence on the composition of reef communities and on the growth-forms of their species than degree of wave action (turbulence) and depth. In this connection, Philcox (1971, p. 338) has related the settling of sediment to variability in the direction and volume of growth of *Favosites* coralla in an American reef. All Gotland reefs are thought to have developed in less than 50 meters of water, and the Hoburgen (Wenlockian) reefs in less than 30 meters. Scoffin (1971, p. 173) has given an exemplary account of the sedimentology of Wenlockian reefs in Great Britain; these are small (average width 12 m. and thickness 4.5 m.) and the water was probably never more than 30 meters deep, although reefs were not broken up by wave or current action. Very few beds of reef-derived talus occur; reef surfaces were small and convex and reached heights of only 50 centimeters to 3 meters above the seabed (Fig. 317, 318). The Wenlock reefs differ from the average North American and Gotland reefs in that Tabulata, massive and branching Heliolitina and *Favosites,* and the lettucelike *Halysites* are the dominant framework organisms, and the laminar Alveolitidae and *Thecia* as reef binders were subordinate only to stromatolites.

Naumenko (1970, p. 60) has discussed the tabulate communities of the Llandovery bioherms and perireef and interreef biostromes of the carbonate facies of the Western Sayan in Siberia, and Ivanova, Belskaya, and Chudinova (1964), those of the Silurian and Devonian of the Kuznetsk, Minusinsk, and Tuva basins, and all have

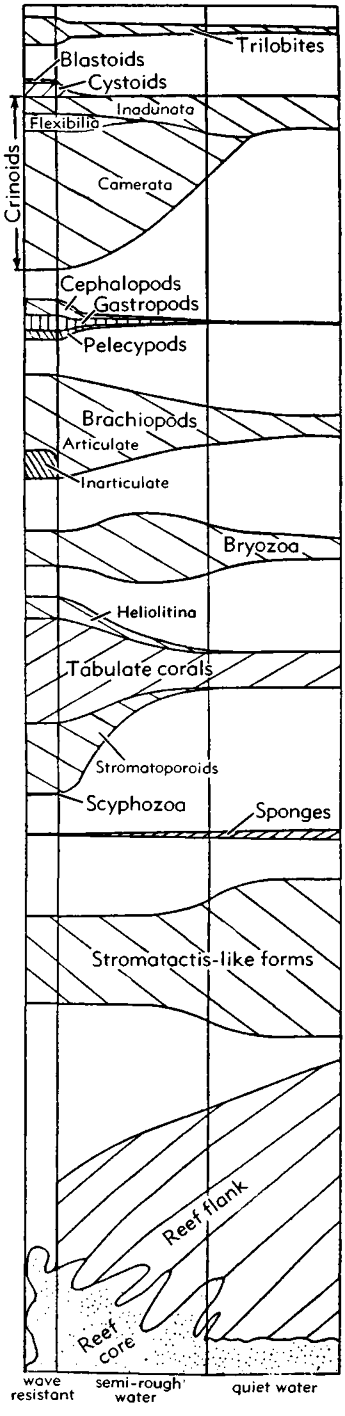

Fig. 316. Paleoecology; changes in population structures of Niagaran reef biota plotted as a function of reef upgrowth, shown schematically by classes and orders (after Lowenstam, 1957).

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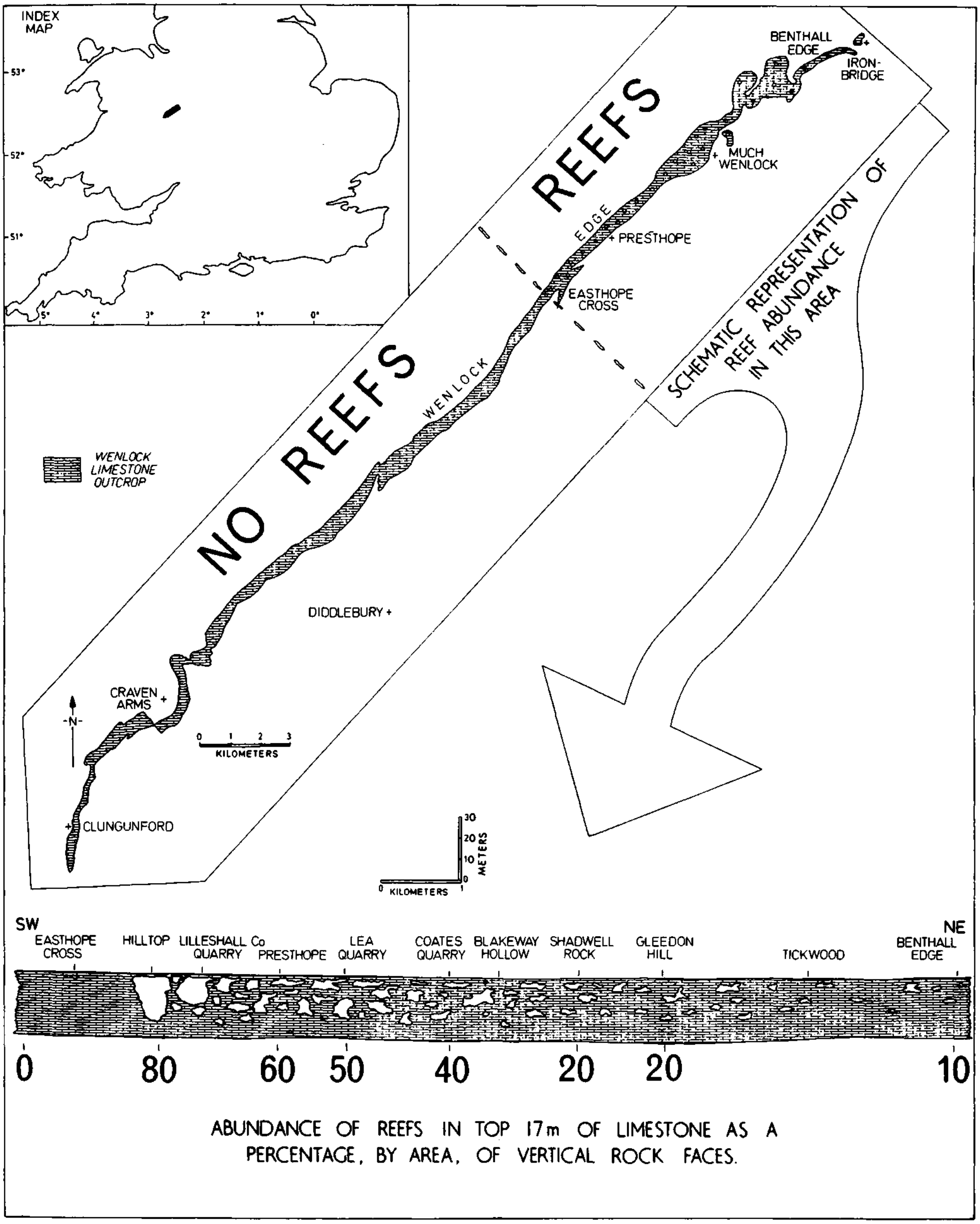

Fig. 317. Paleoecology; section showing shape and abundance of reefs in top 17 meters of Wenlock Limestone in northern part of Wenlock Edge (Scoffin, 1971).

obtained results consistent with those of Lowenstam.

Lithofacies and associated biofacies of Devonian reefs are the subject of a considerable literature. Lecompte (1959, 1960), followed by Tsien (1971, p. 123), studied the Middle and Upper Devonian (Frasnian) reefs of Belgium and Struve (1963, p. 252; Fig. 319) reviewed earlier work on those of the Eifel. Both related their observations to water turbulence, which in turn, particularly in the more rapidly subsiding basins,

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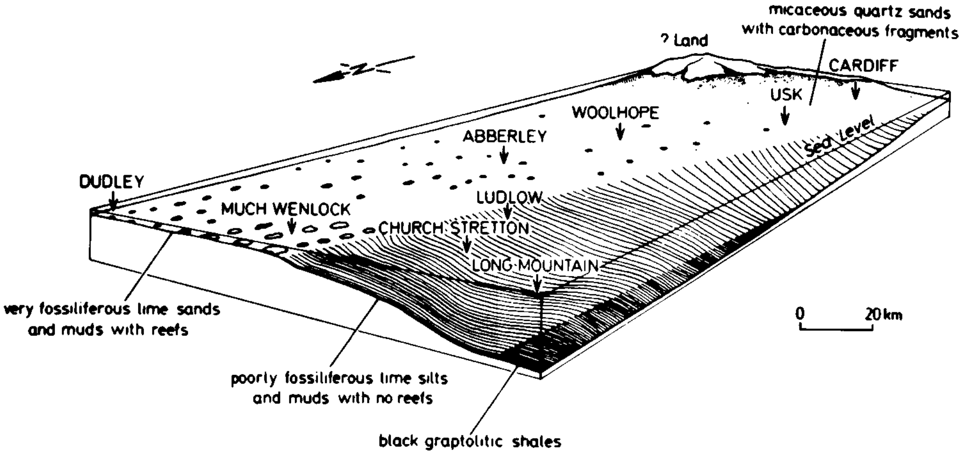

FIG. 318. Paleoecology; schematic reconstruction of the regional paleoenvironments during Wenlock Limestone times (Scoffin, 1971).

was related to bathymetry. Thus, LECOMPTE's *Zone sous-turbulente* corresponded to part at least of LOWENSTAM's quiet-water stage, his *Zone sub-turbulente* (WEDEKIND's and STRUVE's *Rasen-Riff,* turf-reef, and possibly also their *Knollen-Block-Riff*) to the semirough-water zone of LOWENSTAM, and his *Zone turbulente* (and STRUVE's *Stromatoporoiden-Bankriff* and possibly also his *Knollen-Block-Riff*) to LOWENSTAM's rough-water stage. It was recognized that on the more stable regions that subsided less, water movement would be less, on the whole, particularly in environments protected behind upslopes that would take the main force of wave action, and that there turbidity would be varied. Lamellar *Alveolites* replaced lamellar *Thecia* in its various niches, and the branching *Thamnopora* is found in all environments except, very rarely, in the reef core exposed to the maximum break of the waves.

The association of petroleum with Devonian reefs in Canada has led to subsurface studies as well as field studies, and KLOVAN (1964) among others has applied water-turbulence theory in reconstructions of the environments of deposition. After comparing Canadian Devonian reefs with those present-day reefs that have considerable elevation above the floor of the open-marine Yucatan shelf (see LOGAN, 1969), EMBRY and KLOVAN (1971, p. 738) have suggested that the boundary between the underturbulent and subturbulent zones represents the threshold at approximately 75 feet, at the base of storm wave action, and that the boundary between subturbulent and turbulent zones represents the threshold to strong normal wave action (rough-water stage) at about 30 feet. The angle of slope of the reef profiles and the width and shallowness of the shelf are factors that could modify the depth of the thresholds in any one part of the reef complex, and might vary the sequence of growth forms or of communities expected (DOLPHIN & KLOVAN, 1970, p. 289).

The general absence of the stromatoporoids from Carboniferous and Permian reefs together with a great reduction in Tabulata in these two periods, make these reefs very different in aspect from the earlier reefs. But the stromatolites, stromatactoids, bryozonas, and other algae continue as binder-builders, and are accompanied in some Russian reefs by hydractinoids and in some Permian reefs by sponges. In the Carboniferous and Permian atoll of Akiyoshi in Japan, lamellar coralla of *Chaetetes,* some with hummocky upper surfaces, act as builders and binder-builders.

Tabulata are absent to occasional *(Syringopora)* in the Early Carboniferous "Waulsortian" reef knoll facies. In the Visean reef complexes developed on the margins of the more stable platforms of Derbyshire, England, algal barrier reefs occur as a dis-

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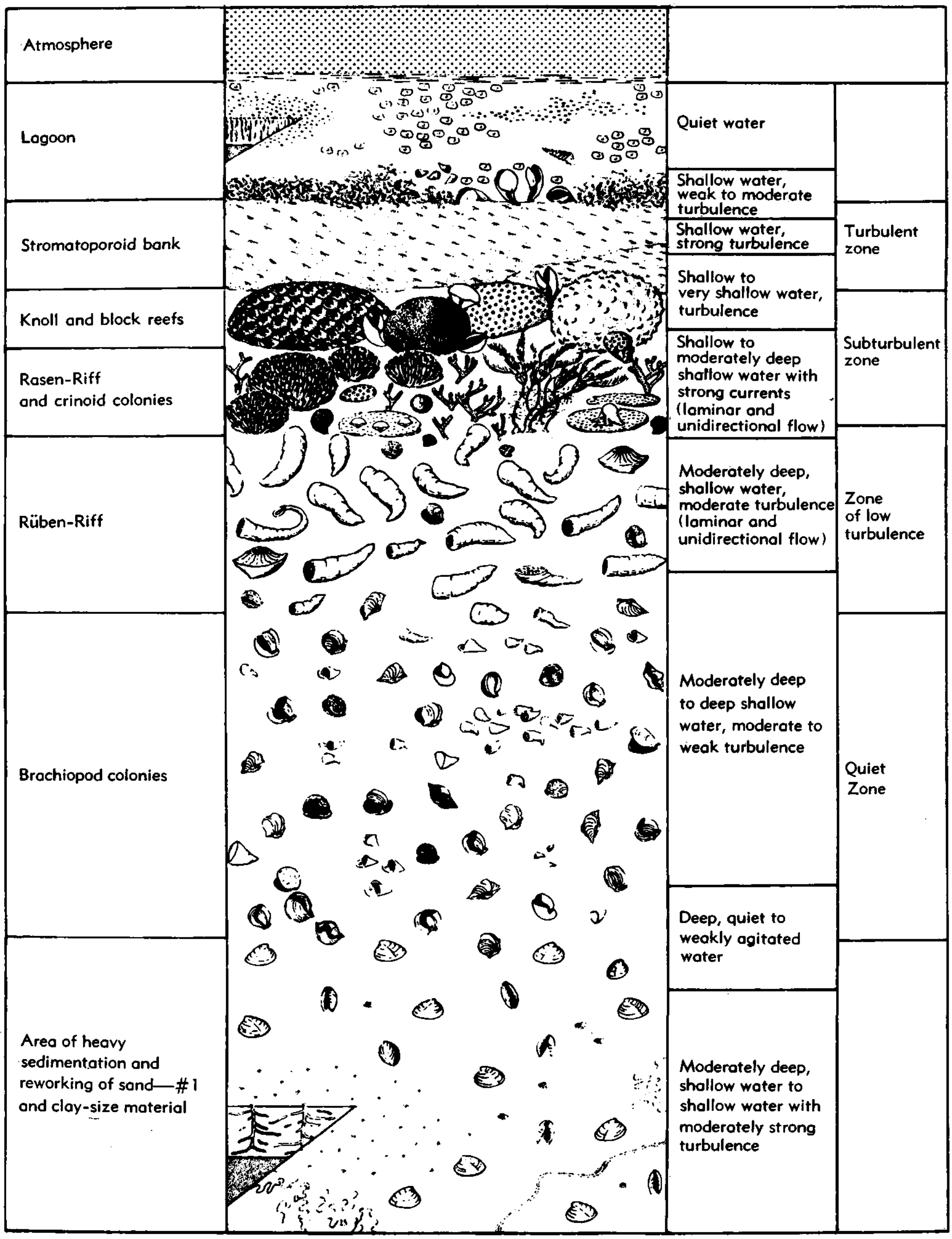

Fig. 319. Paleoecology; environments of the Eifelian reefs (Struve, 1963).

continuous wall-like mass of limestone with abundant stromatolitic algae, sponges, and occasional *Chaetetes depressus* (and Rugosa); steeply dipping (30°) forereef beds are very fossiliferous; cerioid *Michelinia* is dominant in a zone not far below the reef crest (=algal barrier reef) (Broadhurst & Simpson, 1973, p. 367); and *Chaetetes septosus* and *Syringopora* may be found at somewhat lower levels on the slope. The

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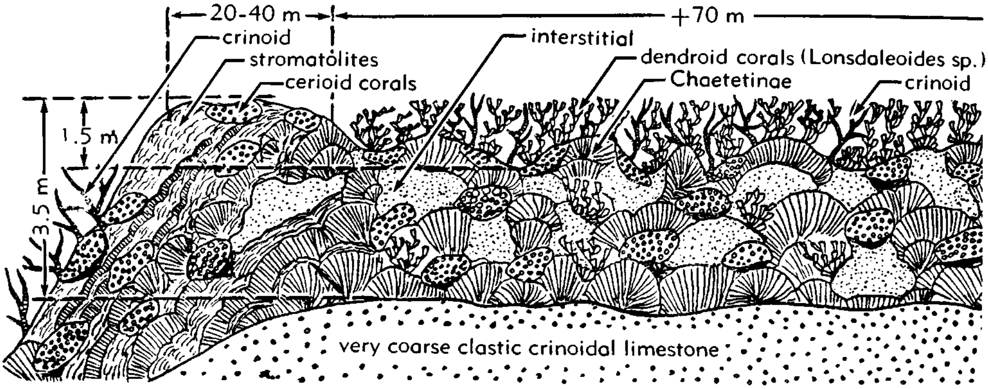

FIG. 320. Paleoecology; schematic reconstruction of a reef-mound of the Carboniferous and Permian atoll of Akiyoshi, in Sumitomo Quarry (after Ota, 1968).

backreef limestones include some biostromes and grade laterally into the standard shelf limestones; reef dwellers are very numerous and most species occur in the shelf limestones, backreef limestones and biostromes, and forereef beds, including the tabulatans *Chaetetes septosus* and *Syringopora*; Rugosa are, however, more important (see Wolfenden, 1958, p. 894; Stevenson & Gaunt, 1971).

In the Middle and Upper Carboniferous of the Moscow Basin (Ivanova, 1958, p. 62), Chaetetida favored neither the littoral nor the coastal shallow water with terrigenous matter, nor the relatively deep sea floors with the special physicochemical regime that led to dolomite deposition. They were especially characteristic of the shallower and rougher parts of the sea, distant from terrigenous sources, e.g., around shoals or islands; colonies were relatively small, with diameters of from 5 to 20 centimeters, rarely of half a meter, and spherical or ovate; in the shelf zone of the open sea and the inner slopes, colonies were mainly tabular and large. Syringoporidae favored the quieter conditions of relatively deep water with a normal regime and soft bottom, although they were also distributed in the neritic zone; they flourished in algal bioherms. Auloporicae (including Cladochonidae) are encountered sporadically, encrusting brachiopods and sponges and other corals, and also on boulders and rocky outcrops. They generally inhabited shallow regions with clean mobile water and also the coastal shallows with unstable regime, and were not affected by terrigenous matter.

In the Carboniferous and Permian atoll of Akiyoshi in Japan, Ota (1968, p. 10) and Ota, Sugimura, & Ota (1969, p. 7) distinguished five types of limestone in a "true-reef" facies; of these, one has a framework of stromatolites and sheetlike *Chaetetes* with some Rugosa and some encrusting Foraminifera; another has a framework mainly of dendroid and cerioid Rugosa and hemispherical *Chaetetes* with minor hexagonellid bryozoans and encrusting foraminifers; the other facies regarded as true reef is bioclastic limestone, largely of crinoid and bryozoan debris, and oolitic limestone (Fig. 320).

Thus Tabulata, like Rugosa, did function as builders and binders in Paleozoic reefs, but they were seldom dominant in these roles; they flourished better in reef environments than in nonreef environments, and they reached their maximum diversity and profusion not far below surf base. Although members of the shelf (?and upper slope) benthos, they were generally unimportant in argillaceous and arenaceous environments. Whether they had upper and lower critical temperature limits, as do the Scleractinia of today, is unknown.

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BIOSTRATIGRAPHY

Considerable biostratigraphic correlation by Tabulata has been undertaken in the USSR, where this aspect of their study has been of great value in geological mapping. An important work by Tesakov (1978) on the place of Tabulata in biologic and biogeologic assemblages and their significance in stratigraphy was received too late for inclusion in this review.

Sokolov (1962a, p. 53) has discussed the sequence and distribution of tabulate faunas through the Paleozoic of the USSR, using genera only. Sokolov and Tesakov (1963, p. 112) exemplified the use of successive faunal assemblages of tabulate species found in the stages and horizons recognized on stratigraphical and other faunal grounds for some sections of the Silurian and Ordovician of the Siberian Platform. The assemblages they listed have proved very useful in correlation; for instance, Rozman *et al.* (1970, p. 223, 228) distinguished successive tabulatan assemblages in sections through the Upper Ordovician of northeastern USSR and correlated them with those of the Siberian Platform and, indeed, of the rest of the USSR and the world. A similar study, based on the Heliolitina of the Ordovician, Silurian, and Lower Devonian of Kazakhstan, has been presented by Bondarenko (1967).

Klaamann (1970b, p. 115) has found that the classical horizons of the Silurian of Estonia are characterized each by an assemblage of tabulate species, and has used the name of one of the more significant species of each such assemblage as a zonal name. Thus in the Llandoverian he recognizes in unit G_{1-2} a zone of *Paleofavosites paulus,* in unit G_3 a zone of *Parastriatopora celebrata,* and in unit H a zone of *Mesofavosites obliquus.* In the Wenlockian he recognizes in unit J_1 a zone of *Favosites jaaniensis* and in unit J_2 a zone of *Coenites juniperinus.* In the Ludlovian in unit K_1 is the *Parastriatopora commutabilis* Zone and in unit K_2 the *Thecia swinderniana* Zone. The Downtonian units K_{3-4} include the *Favosites effusus* Zone. Several of these Estonian zones are now known in other regions.

Hill (1967) reviewed the sequence and distribution of the Upper Silurian, Lower Devonian, and lower Middle Devonian coral faunas (including Tabulata) of the USSR. For the Devonian, Dubatolov (1959, p. 247) has provided a sequence of tabulatan zones based on successive assemblages in the Kuznetsk Basin, and (Dubatolov, 1972c) has given a comprehensive and, indeed, indispensable account of the tabulatan biostratigraphy of the Devonian of Eurasia. Some of the zones have proved identifiable in more than one basin or more than one biogeographical province; for instance, the zone of *Favosites regularissimus,* first recognized as the basal zone of the Eifelian Stage as then understood on the eastern slopes of the Urals, has since been identified in the Taymyr Peninsula, the Tien Shan, the Altay, and in the Kuznetsk Basin; it is now correlated with the Upper Emsian or Zlichovian of western and central Europe, though Dubatolov (1972c, p. 34) continues to include it in his Middle Devonian; the zonal name is alternative to a binomial in which a geographical name appropriate to the depositional region is coupled with the word "horizon."

Tabulatan biostratigraphy of the Carboniferous and Permian has had comparatively little attention, mostly as a very minor component of joint studies with Rugosa or other invertebrates. Classical work on the Lower Avonian of Hook Head, Eire, by Smyth (1930) set a useful standard and showed that many of the large-celled favositinans of the epoch had short ranges in time; as he extended his work it became clear that some of them had considerable geographic extension as well and were useful index fossils.

Degtyarev (1973b, p. 206) included Tabulata in his biostratigraphical account of the Carboniferous corals of the Urals. Vasilyuk, Kachanov, and Pyzhyanov (1970, p. 45) used biostratigraphical data, though only at a generic level, in reviewing the paleobiogeography of the Carboniferous and Permian Coelenterata and so did Hill (1948, 1957b, 1973). Some special studies have been made, for example, by Sokolov (1939, p. 411), on the Chaetetina of the Carboniferous of Russia, and by Nelson

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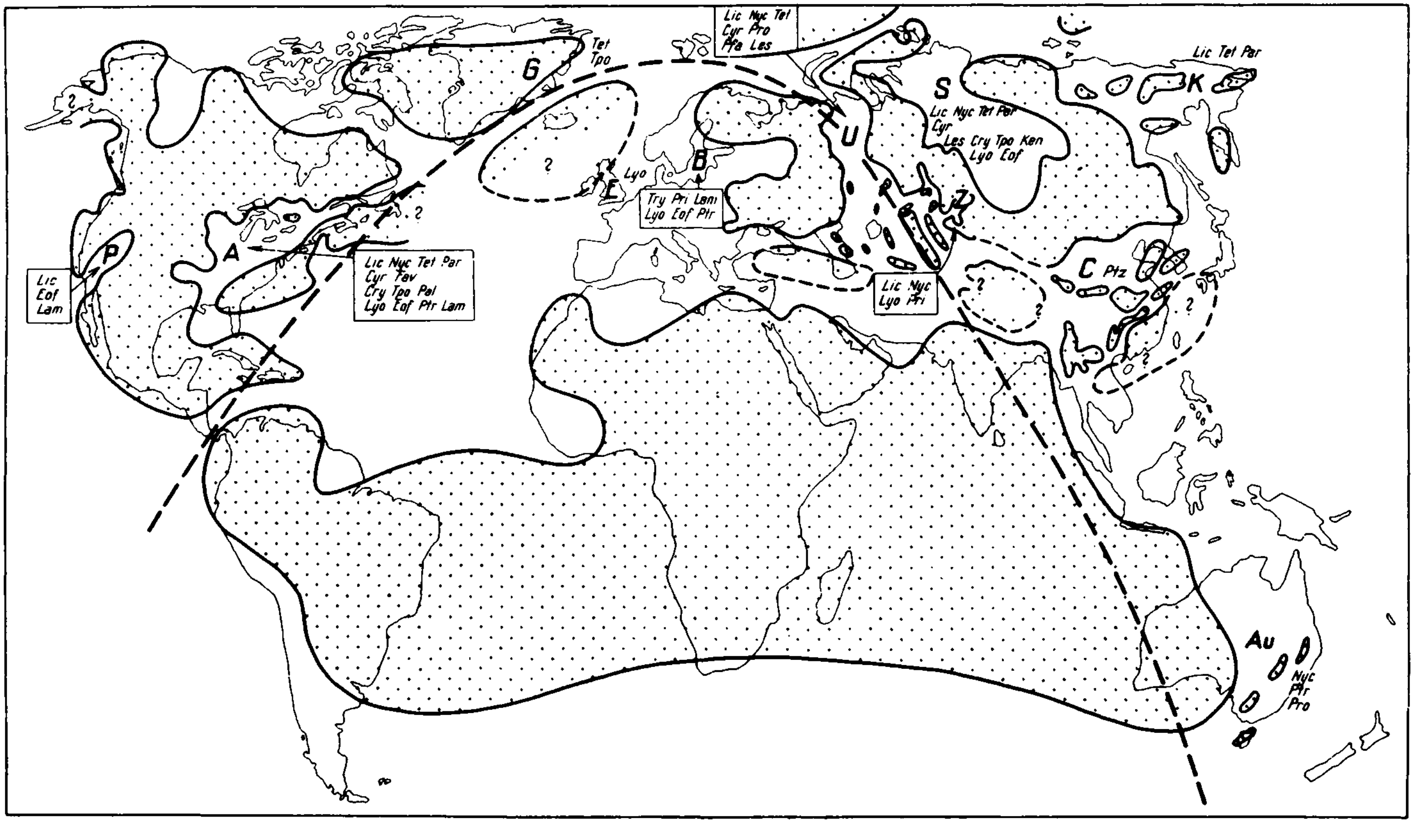

FIG. 321. Paleozoogeographic provinces; distribution of selected Middle Ordovician genera (after Kaljo & Klaamann, 1973). Legend: *A*, North America; *Au*, Australia; *B*, Baltic and Scandinavia; *C*, China; *E*, Great Britain; *G*, Greenland; *I*, Iran; *K*, northeastern USSR; *M*, Bohemia and Podolia; *P*, California; *S*, Siberia; *T*, Tadzhikistan; *U*, the Urals; spotted areas, land; white areas, seas. Where the abbreviated names of genera appear on four different lines, the first line names tabulate corals characteristic for the province, the second line heliolithoids and rugose corals characteristic for the province, the third line genera of restricted geographic range, and the fourth line some additional genera. Abbreviations: Cry, *Cryptolichenaria*; Cyr, *Cyrtophyllum*; Eof, *Eofletcheria*; Fav, *Favistella*; Ken, *Kenophyllum*; Lam, *Lambeophyllum*; Les, *Lessnikovaea*; Lic, *Lichenaria*; Lyo, *Lyopora*; Nyc, *Nyctopora*; Pal, *Palaeophyllum*; Par, *Paratetradium*; Pfa, *Paleofavosites*; Pri, *Primitophyllum*; Pro, *Propora*; Ptr, *Protaraea*; Ptz, *Protozaphrentis*; Tet, *Tetradium*; Tpo, *Tetraporella*; Try, *Tryplasma*.

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(1962, p. 442) on the Syringoporidae of the Lower Carboniferous of southwestern Canada. Late Paleozoic Tabulata are clearly in need of intensive biostratigraphic study and this work should be aided by the bibliographic index of North American rugose and tabulate coral species by Wilson (1974, p. 598), and the checklist of North American late Paleozoic coral species by Sando (1974).

PALEOZOOGEOGRAPHIC PROVINCES

Coral paleozoogeographic provinces have attracted considerable interest lately in debates on continental drift and plate tectonics. Tabulatan studies are areally unbalanced, the amount of detailed work done in the USSR greatly exceeding that in the rest of the world. Nevertheless, it is possible to draw a few inferences of limited value from the presently known distributions of genera, even if there is still much room for argument on both systematics and stratigraphic ranges. Evidence from species would be more valuable, and has been used within the confines of the USSR, but elsewhere the low order of knowledge precludes its use.

Records of Tabulata earlier than Middle Ordovician are too scanty for paleozoogeographic analysis. For the Middle Ordovician, recent analyses exist by Sokolov (1962a, p. 55), Leleshus (1970d, p. 84), and Kaljo and Klaamann (1973, p. 38). The somewhat inconsistent level of the boundary between Middle and Upper Ordovician leads to uncertainty regarding the first appearance of many genera; perhaps the most pressing of these questions is the age of the Cliefden Caves Limestone of New South Wales, in which many genera of the Heliolitina are at present considered Middle Ordovician, though elsewhere they characterize the Upper Ordovician. Kaljo and Klaamann considered it possible to distinguish two faunal provinces in the Middle Ordovician, North American-Siberian and Eurasiatic; but Leleshus, who used a statistical analysis based on degrees of difference, concluded that only one province was recognizable, the Sibero-American. He noted that there were generic differences between the Ural, the Baltic, and the Australian faunas, but thought them still closely tied to the North American (Fig. 321).

The Upper Ordovician faunas, that is, those correlated with the Upper Caradocian and Ashgillian and including the equivalents of the Baltic unit F_2, are much richer, and have been analyzed in the three papers quoted above. Kaljo and Klaamann distinguished American-Siberian and Eurasiatic provinces. Leleshus recognized 1) a Baltic Province comprising the Baltic, Scandinavia, and western Europe, dominated by sarcinulidans and heliolitinans and without cyrtophyllids and agetolitids, 2) a Central Asian Province (Kazakhstan, the Sayan, the Altay, and China), linked fairly closely with the Baltic but with agetolitids characteristic; 3) a Siberian Province (Siberian Platform, southwest Siberia) with cyrtophyllids and endemic sarcinulidans; and, most isolated from the Baltic Province but closely linked with it, 4) the Arctic Province consisting of northeastern USSR, Arctic USSR, the Urals, and North America, all with *Troedssonites.* Both authors supplied tables listing genera and their occurrences. Many cosmopolitan genera occur in the Upper Ordovician, *Calapoecia, Paleofavosites,* and tetradiids being perhaps the most abundant (Fig. 322). A different analysis for the Upper Ordovician is given by Rozman *et al.* (1970, p. 268), based on all faunas. Rozman distinguished four roughly parallel belts, which he considered of climatic significance. These were 1) Canadian-Siberian, 2) European, 3) Kazakhstan-Appalachian, and 4) Kolymian-Alaskan, arranged more or less symmetrically about the Canadian-Siberian belt, which he considered close to equatorial.

The Lower Silurian tabulatan faunas are very different, due to the extinction of nearly all the earlier endemic genera and of the Tetradiida, Syringophyllidae, Cyrtophyllidae, *Coccoseris,* and Agetolitidae. Leleshus as well as Kaljo and Klaamann regarded them as forming a single worldwide province. By the latest Llandovery, the new families Theciidae, Multisoleniidae, Alveolitidae, and Pachyporidae were cosmopolitan, and the fauna was quite rich.

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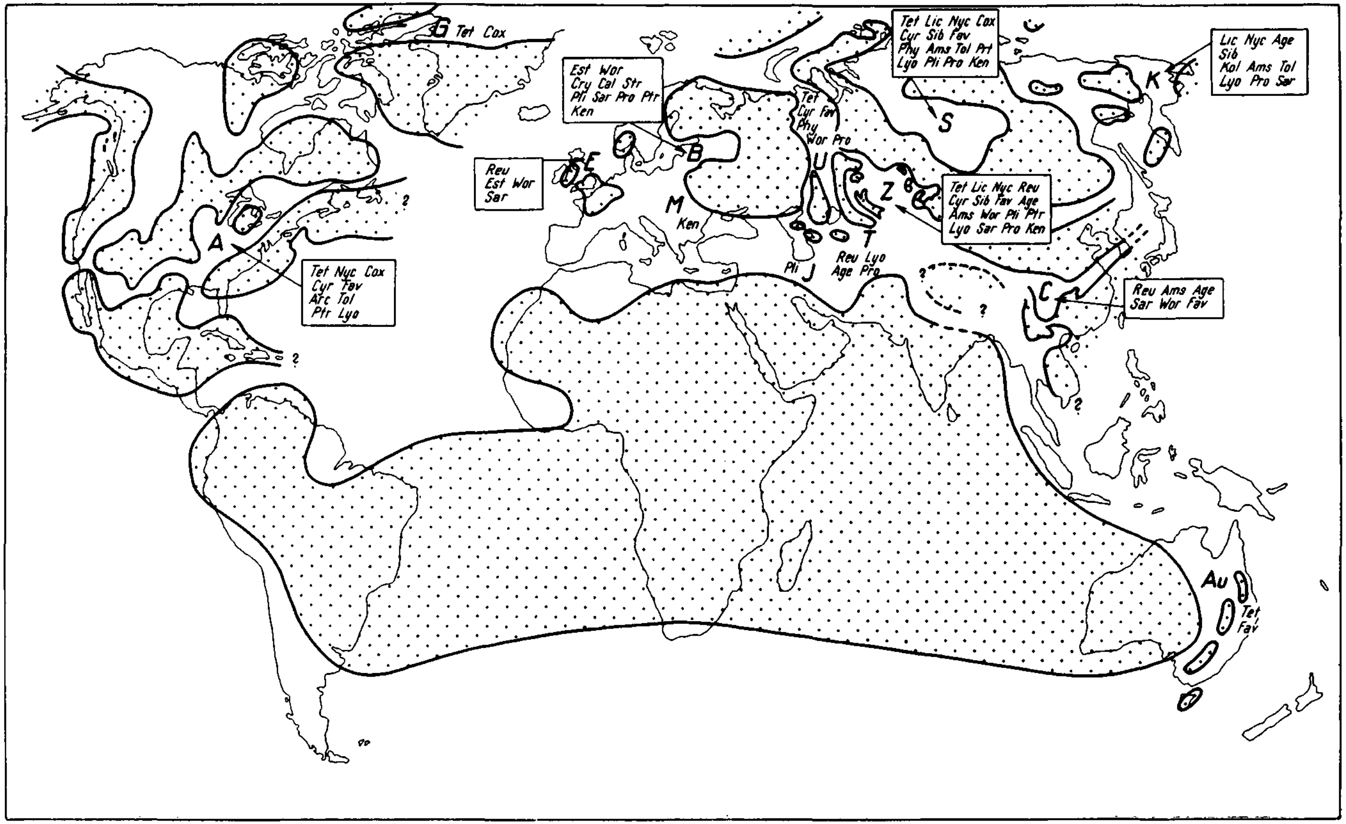

FIG. 322. Paleozoogeographic provinces; distribution of selected Late Ordovician corals (after Kaljo & Klaamann, 1973). Legend as in Figure 321. Abbreviations: Age, *Agetolites*; Ams, *Amsassia*; Arc, *Arcturia*; Cal, *Calostylis*; Cox, *Coxia*; Cry, *Cryptolichenaria*; Cyr, *Cyrtophyllum*; Est, *Esthonia*; Fav, *Favistella*; Ken, *Kenophyllum*; Kol, *Kolymopora*; Lic, *Lichenaria*; Lyo, *Lyopora*; Nyc, *Nyctopora*; Phy, *Phytopsis*; Pli, *Paliphyllum*; Pro, *Propora*; Prt, *Proterophyllum*; Ptr, *Protaraea*; Reu, *Reuschia*; Sar, *Sarcinula*; Sib, *Sibiriolites*; Str, *Strombodes*; Tet, *Tetradium*; Tol, *Tollina*; Wor, *Wormsipora.*

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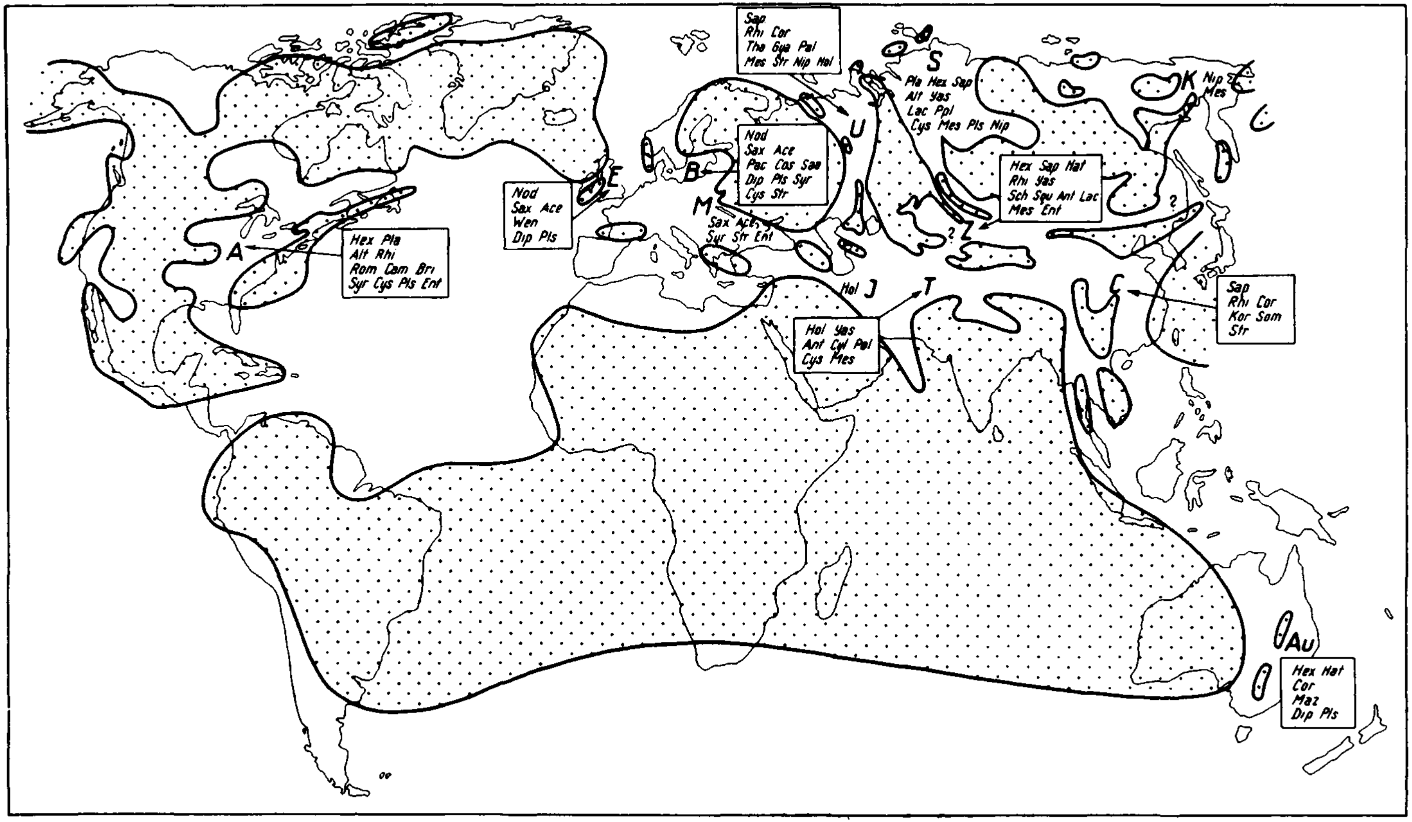

FIG. 323. Paleozoogeographic provinces; distribution of selected Wenlockian corals (after Kaljo & Klaamann, 1973). Legend as in Figure 321. Abbreviations: Ace, *Acervularia*; Alt, *Altaja*; Ant, *Antherolites*; Bri, *Briantelasma*; Cam, *Camptolithus*; Cor, *Coronoruga*; Cos, *Cosmiolithus*; Cyl, *Cylindrostylus*; Cys, *Cystihalysites*; Dip, *Diploepora*; Ent, *Entelophyllum*; Gya, *Gyalophyllum*; Hat, *Hattonia*; Hex, *Hexismia*; Hol, *Holmophyllum*; Kor, *Koreanopora*; Lac, *Laceripora*; Maz, *Mazaphyllum*; Mes, *Mesosolenia*; Nip, *Nipponophyllum*; Nod, *Nodulipora*; Pac, *Pachypora*; Pal, *Palaeocorolites*; Pla, *Planalveolites*; Pls, *Plasmopora*; Ppl, *Protopilophyllum*; Rhi, *Rhizophyllum*; Rom, *Romingeria*; Saa, *Saaremolites*; Sap, *Sapporipora*; Sax, *Syringaxon*; Sch, *Schedohalysites*; Som, *Somphopora*; Squ, *Squameofavosites*; Str, *Strombodes*, Syr, *Syringolites*; Tha, *Thaumatolites*; Wen, *Wenlockia*; Yas, *Yassia*.

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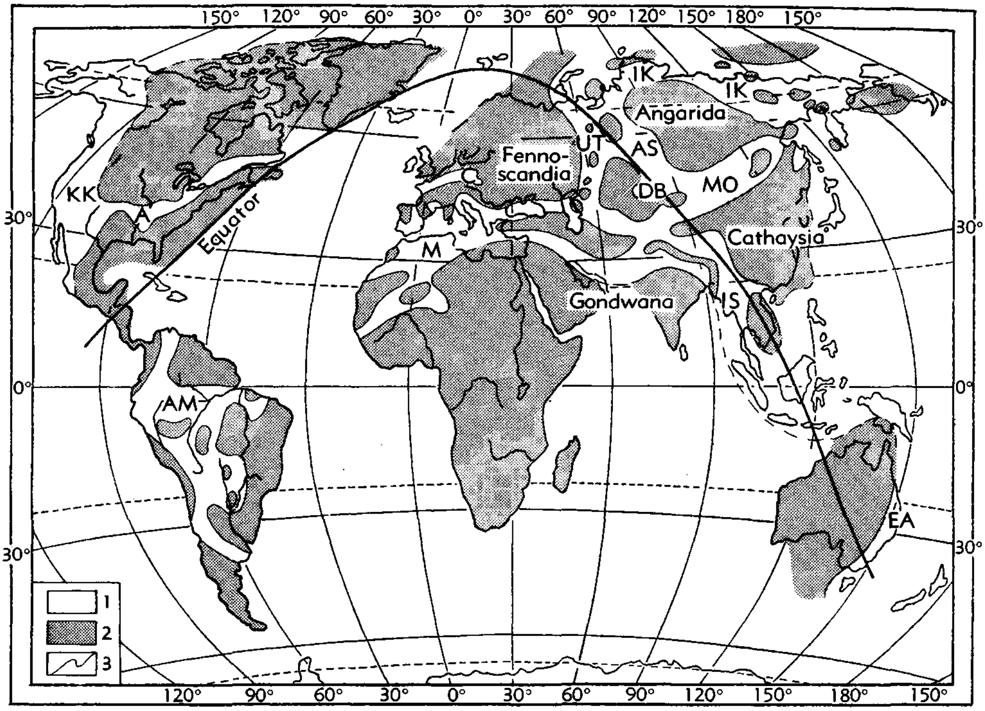

Fig. 324. Paleozoogeographic provinces; zoogeographic subdivision into regions of the world oceans in the Early Devonian (after Dubatolov, 1972c). Legend: 1, ocean basin; 2, land; 3, boundary between land and sea. Provinces: *A,* Appalachian; *AM,* Amazonian; *AS,* Altay-Sayanian; *DB,* Dzhungaro-Balkhashian; *EA,* East Australian; *IK,* Indigiro-Kolymian; *IS,* Indosinian; *KK,* Californo-Canadian; *M,* Magribian; *MO,* Mongolo-Okhotskian; *UT,* Urals-Tien Shanian.

Nearly all genera continued into the Middle Silurian, but in Leleshus' view, provinces were not clearly delimited then. Hill (1959, p. 167) considered that although in the Silurian there were suggestions of Asian-Australian and North American provinces, on the whole, the Silurian coral faunas of the world were cosmopolitan. Kaljo and Klaamann maintained that a weak differentiation suggested in the Upper Llandovery became somewhat stronger in the Middle Silurian with weakening of North American connections with Siberia (Fig. 323). Provincial distinction became sharper in the Upper Silurian (including Pridolian), and Leleshus distinguished four provinces, 1) Baltic, Podolia, Bohemia, and the Soviet Arctic, 2) the Urals, southwestern Siberia, Kazakhstan, and Central Asia, 3) Australia, and 4) North America, whereas Kaljo and Klaamann distinguished only two, European and Asiatic (including the Urals and possibly China).

At the beginning of the Early Devonian, in the Gedinnian, according to Leleshus, only one world province existed for Tabulata. The Halysitina had become extinct. Lower and Middle Devonian tabulatan faunas flourished, and are the richest of all. Devonian tabulatan biostratigraphy of Eurasia has been considered in detail by Dubatolov (1972c), who used this background to develop his paleozoogeographical and climatic analysis of the Devonian world. Early Devonian provinces he identified are 1) Amazonian, 2) Californo-Canadian (=western North America), 3) Appalachian (=eastern North America), 4) Magribian (North Africa), 5) Mediterranean (=Tethyan; including western and central Europe, Asia Minor, the Pamirs, Iran, and the Himalaya), 6) Ural-Tien Shanian (Urals, Tien Shan, central Asia, Novaya Zemlya, and possibly northwest China), 7) Dzhungaro-Balkhashian (Pribalkhash, Dzhungarian Alatau, and possibly China),

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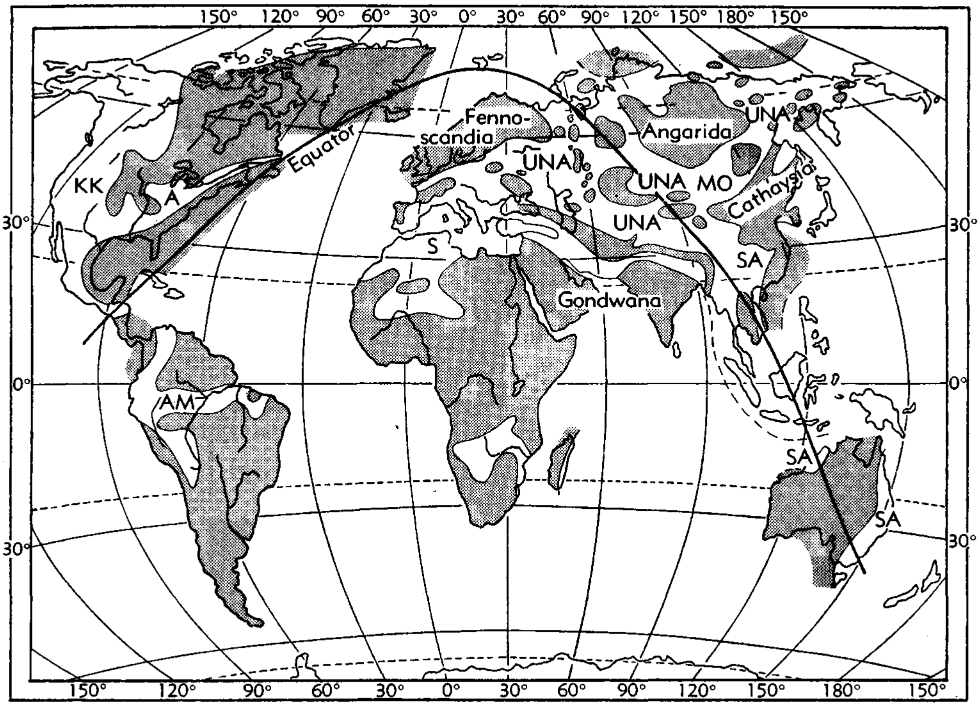

Fig. 325. Paleozoogeographic provinces; zoogeographic subdivision into regions of the world oceans in the Middle Devonian (Eifelian-Givetian) (after Dubatolov, 1972c). Legend as in Figure 324. Provinces: *A*, Appalachian; *AM*, Amazonian; *KK*, Californo-Canadian; *MO*, Mongolo-Okhotskian; *S*, Mediterranean; *SA*, Sino-Australian; *UNA*, Uralo-North Asian.

8) Altay-Sayanian (Altay, Salair, Kuznetsk Basin), 9) Indigiro-Kolymian (=Taymyr-Kolymian) with distinguishable subdivisions for Tas-Khayakhtakh, Ormulev-Kolyma, and Sette-daban and the Taymyr Peninsula, 10) Mongolo-Okhotskian (Transbaikalia, Far Eastern USSR, East Mongolia, and Japan), 11) Indosinian (southwest China, Indochina), and 12) East Australia (Australia, New Zealand). In the resultant map (Fig. 324), Dubatolov indicated the position he deduced for the equator. The twelve provinces, he considered, might form four groups: Australo-Eurasiatic, Appalachian, North Pacific, and Atlantic.

For the Zlichovian, which he included in the Middle Devonian, he found the same provinces to be present. But for the later Eifelian and Givetian he grouped those entities numbered 4 and 5 above as Mediterranean, 6, 7, 8, and 9 as Uralo-North Asian, and 11 and 12 as Sino-Australian; he did not discuss western North American or South American arrangements. That is, for the Middle Devonian he deduced considerable merging of provinces, large numbers of genera being polyprovincial (Fig. 325). Hill (1957b, p. 49) had earlier indicated a migration of Eurasaustralasian fauna to Pacific North America at the beginning of the Givetian.

In the Late Devonian (Frasnian), by which time the number of genera and species had greatly decreased with the extinction of the Heliolitina and many families of Favositicae, faunas were dominated by Alveolitidae and *Thamnopora,* and Dubatolov recognized only two provinces, North American and Australo-Eurasiatic (Fig. 326). During Famennian times Tabulata were very scarce and subsequently remained greatly subordinate to Rugosa.

For Carboniferous and Permian coral provinces, results from Tabulata are combined in the literature with those from the predominant Rugosa. Thus, Hill (1973, p. 133) deduced three provinces for the Lower Carboniferous, those of North Amer-

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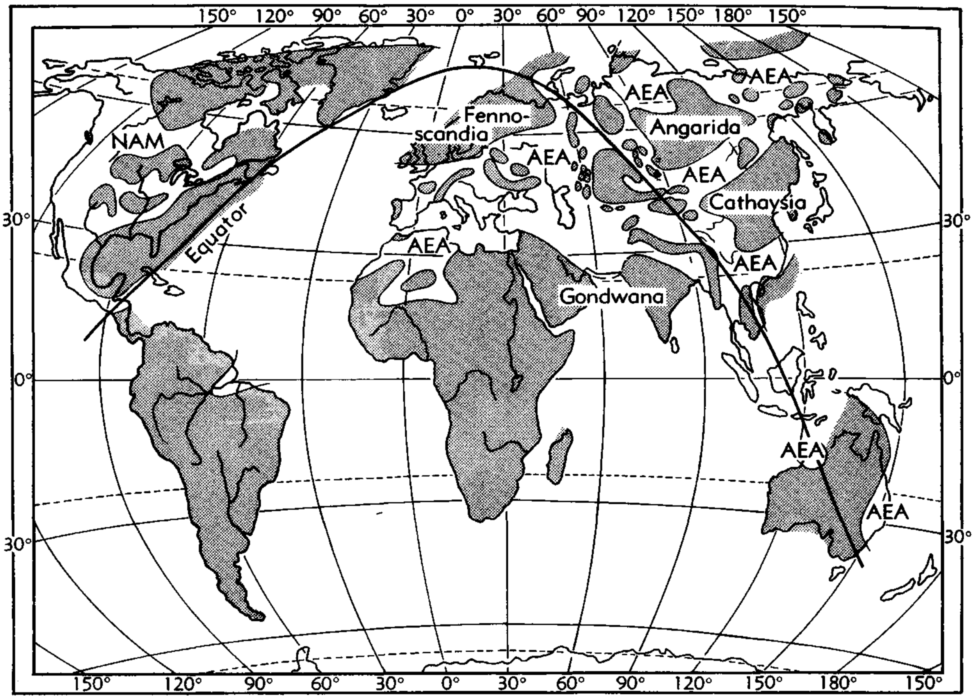

Fig. 326. Paleozoogeographic provinces; zoogeographic subdivision into regions of the world oceans in the Late Devonian (Frasnian) (after Dubatolov, 1972c). Legend as in Figure 325. Provinces: *AEA,* Australo-Eurasian; *NAM,* North American.

ica, Eurasia, and Australia (Fig. 327). The eastern and western ends of the Eurasian Province were distinct, and in the western subprovince is included Nova Scotia and northwestern Africa. However, Vasilyuk, Kachanov, and Pyzhyanov (1970, p. 45) recognized, in Eurasia, in the Tournasian, five provinces: 1) Western European, 2) Eastern European-Siberian (including subprovinces of the Urals, Novaya Zemlya, Siberia, East Siberia, Pamirs, eastern Europe, and Asia Minor), 3) Central Kazakhstan, 4) Kuznetsk, and 5) China. In the Visean, provinces 1, 3, and 5 were still distinguished, but the Eastern European-Siberian grouping was considered to form three provinces: 1) the East European (Moscow Basin, Urals, Novaya Zemlya), 2) the Donetz Basin with Central Asia, and 3) Eastern Siberia, with which the Kuznetsk Province (4 above) was merged, comprising eastern Taymyr, northeastern USSR and the Kuznetsk Basin. In the Namurian, they recognized only two Eurasian provinces, Eastern European-Siberian (central Europe, Moscow Basin, Urals, Novaya Zemlya and East Taymyr) and Mediterranean (Donetz Basin, Asia Minor, central and South Kazakhstan, central Asia, and Pamirs), but the only tabulatan they mentioned was *Chaetetes pinnatus.*

For the Middle Carboniferous they recognized, like Hill (1957b), two provinces in Eurasia, East European (Urals, Moscow Basin, Novaya Zemlya) and Mediterranean (Spain, Czechoslovakia, Donetz Basin, Tien Shan, Pamirs, China, Japan). The North American Province was still distinctive, as it was also in the Upper Carboniferous. For the Upper Carboniferous the same authors distinguished in Eurasia, the Ural-Arctic (Spitsbergen, Novaya Zemlya, Urals, eastern parts of Russian Platform) and the Mediterranean (Carnic Alps, Donetz Basin, Pamirs, China, Japan) provinces (Fig. 328). No Middle or Upper Carboniferous Tabulata have been recognized in Australia.

For the Permian, Vasilyuk, Kachanov, and Pyzhyanov (1970) considered the Uralo-Arctic Province again to be distin-

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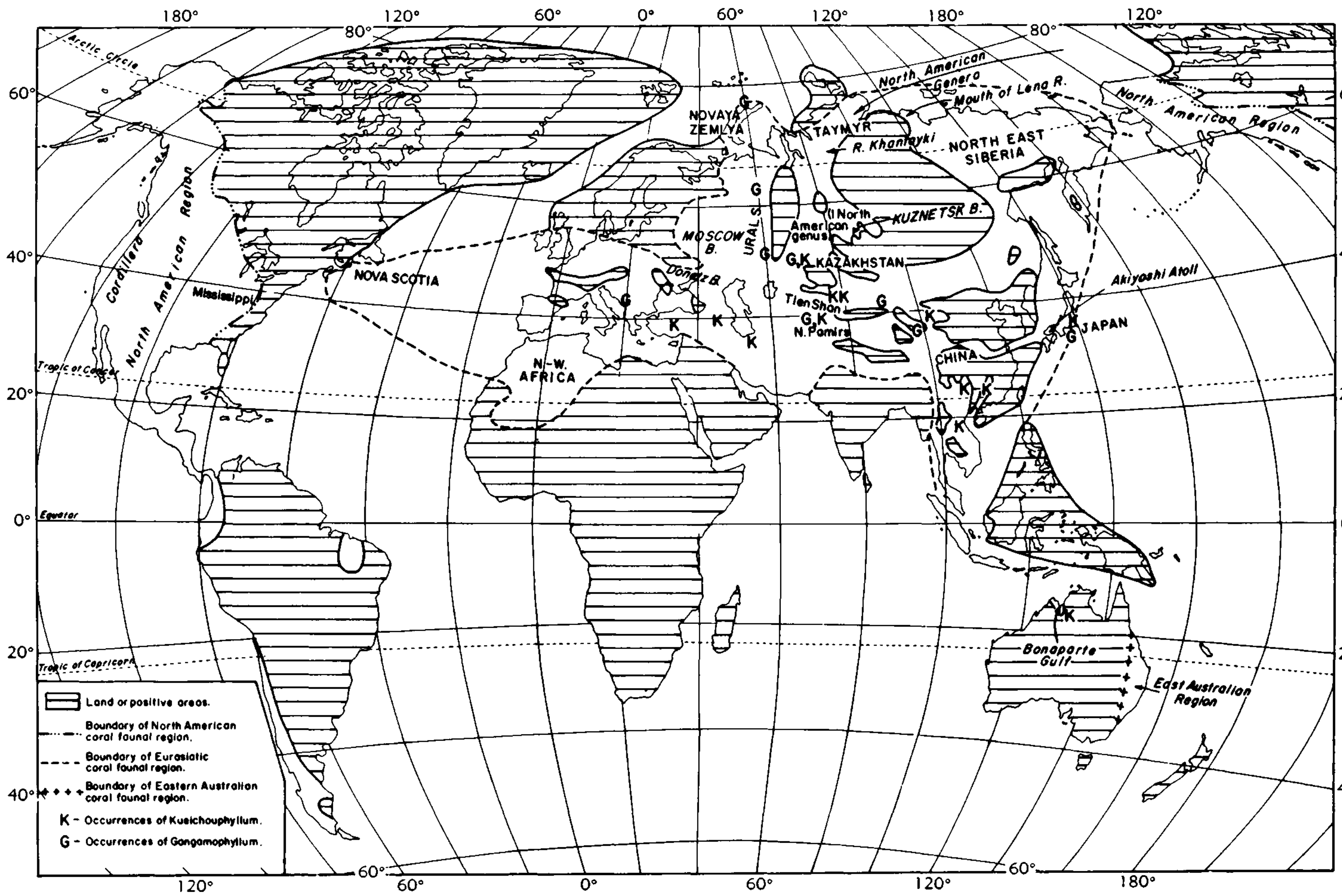

FIG. 327. Paleozoogeographic provinces; Lower Carboniferous coral faunal regions and provinces (Hill, 1973).

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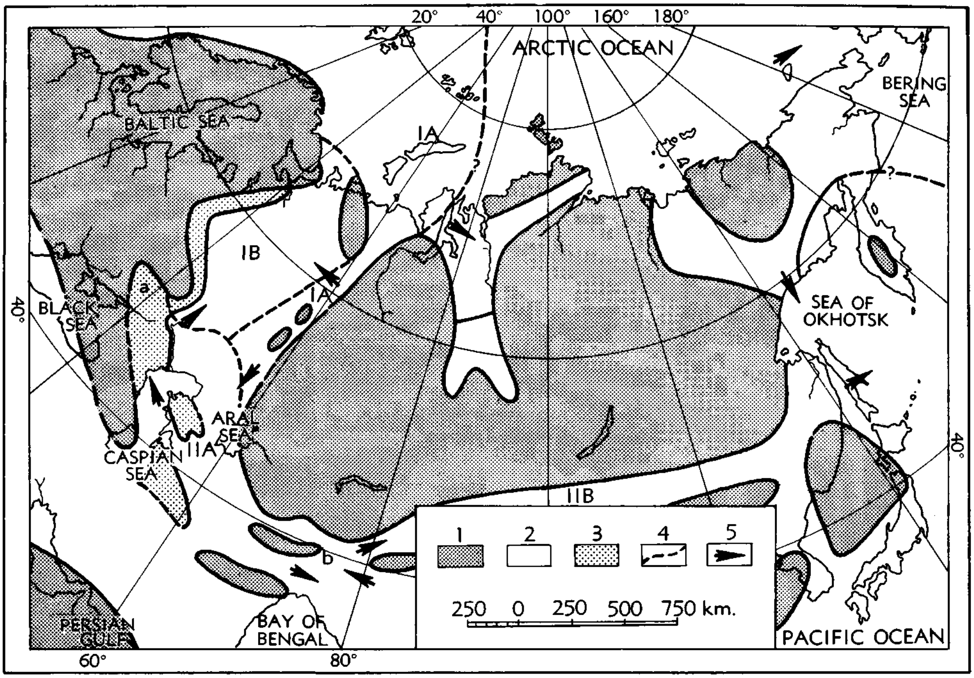

Fig. 328. Paleozoogeographic provinces; paleobiogeographic regions based on coelenterate faunas in the Moscovian (Vasilyuk, Kachanov, & Pyzhyanov, 1970). Legend: 1, land; 2, sea; 3, alternating marine and continental conditions; 4, boundary between provinces; 5, probable direction of migration. Provinces: *I,* East European; *II,* Mediterranean. Subprovinces: *IA,* Uralian; *IB,* Moscow Basin; *IIA,* Central Mediterranean (regions: *a,* Donbas; *b,* Pamirs); *IIB,* Chinese.

guishable, and to include the European Arctic, the western slopes of the Urals and Priurals, and the Moscow Basin; the Mediterranean Province comprised in its central parts the Donetz Basin, Asia Minor, the Pamirs, and in its eastern parts the Primorye, China and Japan, Indonesia, and New Zealand (and presumably Australia). In the Permian the North American coral complex is close to that of the Uralo-Arctic Province (Fig. 329).

More intensive taxonomic work and more work on distributional patterns are required before students of tabulates will be able to make significant pronouncements for or against continental drift or specific uses of plate tectonics theory in paleogeographic reconstructions.

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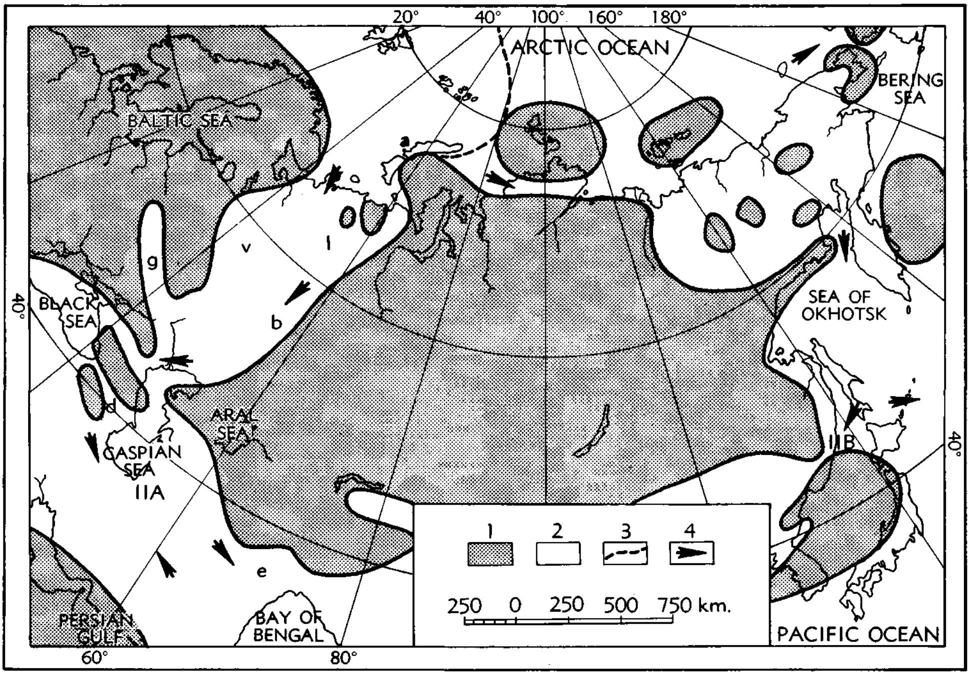

FIG. 329. Paleozoogeographic provinces; paleobiogeographic regions based on coelenterate fauna in the Early Permian (Vasilyuk, Kachanov, & Pyzhyanov, 1970). Legend as in Figure 329. Provinces: *I,* Uralo-Arctic (regions: *a,* European-Arctic; *b,* western slopes of Urals and Priurals; *v,* Moscow Basin); *II,* Mediterranean. Subprovinces: *IIA,* Central Mediterranean (regions: *d,* Transcaucasia; *e,* Pamirs; *g,* Donbas); *IIB,* Eastern Mediterranean.

CLASSIFICATION

HISTORY

The Tabulata are well served with historical reviews of which the most useful are those of MILNE-EDWARDS (1857a, b, c; 1860), NICHOLSON (1879), POČTA (1902), OKULITCH (1936b) and SOKOLOV (1950a, 1955, 1962c, 1971).

During the eighteenth century, fossils now included in Tabulata were considered to be related to the corals, which at that time were called zoophytes because of the long-noted resemblance of the tentaculate polyps to flowers. During the century in which LINNÉ's "Systema Naturae" appeared, many descriptive studies of living corals were published, revealing their animal nature. During the first half of the nineteenth century pioneers such as LAMARCK and DE BLAINVILLE incorporated the results of such studies in the evolving system of classification of the animal kingdom, thus laying the foundations of the system for corals set out in several works published between 1848 and 1860 by MILNE-EDWARDS & HAIME and by MILNE-EDWARDS, and based primarily on tentacular and mesenterial features.

MILNE-EDWARDS & HAIME referred the bulk of the then known Tabulata to the Zoantharia Tabulata; two, *Aulopora* and *Pyrgia* (=*Cladochonus*), comprised their Zoantharia Tubulosa; earlier, MILNE-EDWARDS & HAIME (1850, p. lxxvi) had referred these genera to the Alcyonaria; a few were placed in either the Zoantharia Aporosa or the Zoantharia Perforata (which today together comprise the Zoantharia Scleractinia); one genus, *Syringophyllum,* they included in the Zoantharia Rugosa; forms without calcareous skeletons comprised their Zoantharia Malacodermata.

After this first phase, ending in 1857, a second phase, one of reappraisal of the Tabulata, followed. MILNE-EDWARDS &

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Haime had included a number of recent genera which, because their tentacles and mesenteries could be studied, soon betrayed themselves as other than Tabulata. First, Agassiz (1858) noted the hydrozoan nature of *Millepora,* but unfortunately drew the corollary that all Tabulata were Hydrozoa. Verrill (1867, 1870, 1872) did not agree with such a wholesale transfer, but noted that the recent *Pocillopora* was of the Zoantharia Perforata, and suggested that the Favositidae were Poritidae and thus Zoantharia Perforata. In 1872, Duncan discussed these ideas but retained the Zoantharia Tabulata, removing from it to the Alcyonaria, *Chaetetes, Monticulipora, Dania, Stellipora,* and *Labechia.* Lindström (1873a, 1876) and Dollfuss (1875) entirely abandoned the Tabulata as a distinct division of corals. Lindström removed *Labechia* to the Hydrozoa, and *Monticulipora, Fistulipora,* and some others to the Bryozoa, moves which have met with complete acceptance, but the Favositidae he considered Zoantharia Perforata, the Helioporidae a special group of uncertain systematic position, and some (*Fletcheria, Michelinia,* and *Syringopora*) he regarded as Zoantharia Rugosa. Moseley (1877, 1881) studied the recent *Millepora* and *Heliopora,* showing *Millepora* to be a true hydrozoan and *Heliopora* an alcyonarian. But he drew the corollary that *Heliolites* was also dimorphic and an alcyonarian, and tended to the view that all Tabulata were Alcyonaria, a view in general espoused by Nicholson (1879) in a work which was widely accepted as authoritative and which referred informally to those tabulatan genera and families that, by their soft parts, could not be referred to Hydrozoa or to the Zoantharia Perforata or Zoantharia Aporosa, or, by their septal symmetry, to the Zoantharia Rugosa, as the "Tabulate Corals." Nicholson considered that neither the Auloporidae (=Zoantharia Tubulosa) nor the Tetradiidae could at that time be reliably placed in any known order; the Halysitidae and Theciidae he thought found their nearest allies in the Helioporidae (in which he included *Heliolites*), and he considered them better removed to the Alcyonaria. The Chaetetidae he judged genuine Actinozoa (=Anthozoa), and thought they had more affinity with Alcyonaria than with any other group.

This agnostic attitude became fairly generally adopted and by 1913 von Zittel in his textbook was treating two groups as appendices to the Alcyonaria: Heliolitida and Tabulata, the latter comprising Favositidae, Chaetetidae (including *Tetradium*), Syringoporidae, Halysitidae and Auloporidae. However, Bourne (1895), Sardeson (1896), and several others advocated including them all in the Alcyonaria.

The third and present phase began in the 1930's, when a new interest in Tabulata became manifest. Okulitch (1935, 1936b), in considering the Tetradiidae, was impressed by the general similarity between them and the Chaetetidae and the tubular coenenchyme of Heliolitidae; he grouped all these slender corals with adaxial increase into a new subclass of Anthozoa, the Schizocoralla, of equal value with the Rugosa and Hexacoralla (=Scleractinia); the remaining tabulates he referred to the Alcyonaria. Weissermel (1937), however, maintained the integrity of the Tabulata. He pointed out that increase in the corallites of Heliolites was coenenchymal; adaxial division as in the corallites of Chaetetidae and Tetradiidae occurred only in the coenenchymal tubuli, and he also noted that Heliolitidae were constantly 12-septate, whereas the Chaetetidae and Tetradiidae were dominantly aseptate. He considered heliolitids to be linked to the other Tabulata through *Proheliolites.*

Lecompte (1939), after very detailed study of Middle Devonian tabulates, also rejected the subclass Schizocoralla. He treated the Tabulata as a subclass of Anthozoa like Rugosa and Hexacoralla, but described no Heliolitida in this subclass. However, in 1952, he treated the Tabulata and Heliolitida as two suborders of the order Madreporaria of the subclass Actinanthides of the class Anthozoa.

The dominant worker on tabulates in this phase is Sokolov. Beginning with a detailed study of Carboniferous chaetetids (Sokolov, 1939), he founded a most fecund Russian school, with large numbers of specialists, who proved the Tabulata to be an extremely useful group in working out the

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geology of the vast regions of the USSR. Two publications by SOKOLOV (1950a, 1955) have been particularly influential. He distinguished four groups—Chaetetida, Heliolitida, Tabulata Communicata, and Tabulata Incommunicata. He was impressed by the distinctive features of the Chaetetida: their slender, aporose corallites with adaxial bipartite increase. He compared the uniserial longitudinal monacanthine trabeculae seen in the walls of some and the meandroid habit seen in others with the clinogonally radially fibrous longitudinal columns and irregularity of habit found in the Hydrozoa Stromatoporoidea. Believing Chaetetida to be aseptate, he treated them as a distinct group with a closer relationship to the Hydrozoa than to the Anthozoa, tentatively in 1950, more definitely in 1955 and 1962.

The coenenchyme of the Heliolitida, their coenenchymal increase, their fixed number of 12 equal septa, and the trabecular construction of the septa, walls, and longitudinal elements of the coenenchyme, led him to conclude (SOKOLOV, 1950a, 1955) that this was a distinct group of Anthozoa and in 1962 he adopted BONDARENKO's (1958, p. 202) subclass Heliolitoidea for them.

The remainder of the tabulates SOKOLOV (1950a, 1955) grouped in two divisions of the subclass Tabulata of the class Anthozoa, divisions Communicata and Incommunicata. Under the first he included (1950a) as orders, Favositacea with their mural pores and Syringoporacea (including sarcinulids) with their connecting tubuli or canals or tunnels. Under the second he grouped the orders Auloporacea, Halysitacea, Tetradiacea, and Lichenariacea. Later (1962c, p. 208), however, he omitted the divisional taxa as redundant, stating that these two clearly differentiated groups should not be regarded as phylogenetically valid superorders. Communication between corallites appeared and evolved independently in different phylogenetic branches. He recognized seven orders of Anthozoa, subclass Tabulata.

SOKOLOV (1971) appeared to feel that there might be value in once more uniting his conceptions of Tabulata and of Heliolitoidea, and more doubtfully, Chaetetoidea, as superorders in a taxon to be rated as a subclass (presumably of Anthozoa), and that might be called either Tabulata or Tabulatomorpha. He noted the common possession of baculi (=longitudinal monacanthine trabeculae) in all three, and the possession of adaxial increase in more of his Tabulata than suspected earlier.

JONES and HILL (1940) in describing the Australian heliolitids, reviewed the Heliolitida and, like SOKOLOV in 1950 and 1955 and LECOMPTE in 1952, and for much the same reasons, concluded that they were a group distinct from the rest of the Tabulata. However, HILL & STUMM (1956) were more impressed by their similarities than by their dissimilarities, and reunited the Heliolitidae with the Chaetetidae and the rest of the tabulates in the order Tabulata of the Anthozoa Zoantharia, dividing the order into six families.

MIRONOVA (1974b, p. 110) combined the coenenchymate orders Sarcinulida, Halysitida *(s.s.)*, and Heliolitida into a subclass Heliolitoidea.

In this *Treatise*, the Heliolitina and the Halysitina are united in the order Heliolitida, and this is united with the orders Chaetetida, Tetradiida, Sarcinulida, and Auloporida (comprising Auloporicae and Syringoporicae) to form the subclass Tabulata of the Cnidaria Anthozoa, for reasons set out below.

SYSTEMATIC POSITION

For Tabulata we have only skeletons from which to deduce systematic position. The primary evidence is therefore presented by:

1) The skeleton as a whole. This is calcareous and compound, and thus invites comparison with Cnidaria, Bryozoa, and Archaeocyatha. The distinctive inner and outer walls and porosity of the septa, tabulae, and walls of the latter speak against any assignment of the Tabulata to the Archaeocyatha. Bryozoa commonly show polymorphism, absent in Tabulata, and their zooecia are characteristically more slender than the corallites of Tabulata. Of cnidarians, Scleractinia and Rugosa resemble Tabulata in having fasciculate and massive (dominantly cerioid) coralla; the Tabulata have two genera that are homeomorphs of Octocorallia (=Alcyonaria), *Heliolites* with the coenothecalian *Heliopora,* and *Syringopora*

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with the stoloniferan *Tubipora*. There is no real resemblance between Tabulata and the coenostea of the Hydrozoa (Hydractinia and Stromatoporoidea).

2) Microstructure and ultrastructure. Considerable postmortem alteration is characteristic of Paleozoic Tabulata; nevertheless, traces of primary microstructure and even ultrastructure may be found in less altered parts of the skeletons. The currently accepted reconstruction of the microstructure (Hill & Stumm, 1956, p. F446; Kato, 1968b, p. 54) and ultrastructure (Oekentorp & Sorauf, 1970, p. 292; Oekentorp, 1972, p. 41) of the thickening of transverse skeletal elements is a fibrous, radiolamellar microstructure and a microtufted radiolamellar ultrastructure; in the longitudinal skeletal elements this is modified into a trabeculate microstructure. These types are known elsewhere at present only in Scleractinia and Rugosa, and perhaps in the Octocorallia (the coenothecalian *Heliopora* only). The ultrastructure of the cyclostomatous and trepostomatous bryozoan wall appears quite different; it lacks trabeculae (unless pseudopunctae represent trabeculae altered by diagenesis) and is more like that in brachiopods, since the growth lamellae consist of layers of platy crystals of calcite alternating with thinner layers of protein or chitin (Tavener-Smith & Williams, 1972, p. 122). Research in biocrystallization is in its infancy, but as far as it has gone, it appears to deny that Tabulata could be Bryozoa, and to affirm that Tabulata could be Anthozoa Zoantharia.

3) The corallite. a) The plates. Longitudinal skeletal elements dividing the individual calcareous conical skeletons radially are known otherwise only in Rugosa and Scleractinia; they are trabeculate in all three; the wall is composite, of trabeculae and nontrabeculate fibroradiate growth lamellae; the tabula in many Tabulata is extremely thin and may correspond only to the base plate of the tabulae of Scleractinia, but in those Tabulata where it is thick the layers of thickening are identical with those of Scleractinia and Rugosa. The septa are all of one order of size in Tabulata, except in some Theciidae and some Cyrtophyllidae, and occasionally in the Micheliniidae, where longer and shorter septa alternate. Except in Heliolitina and Halysitina, and in some Favositina, where the number is 12, the septa increase in number as the corallite increases in diameter.

b) The symmetry of the corallite. This is indicated by the arrangement of its septal elements, which appears to be radial but could be radiobilateral. A bilateral arrangement is suggested in some, but no order of insertion has yet been determined. The symmetry is consistent with a position within the Anthozoa, or indeed within the Zoantharia, but excludes inclusion of Tabulata in either Scleractinia or Rugosa, although a plane of bilateral symmetry is acquired in the calices of Alveoliticae and some Favositina.

c) Increase. The dominant type of increase in Tabulata is lateral, as it is in the Zoantharia Rugosa. A second type, longitudinal bipartite and quadripartite increase by the adaxial growth of opposed new walls (Chaetetida and Tetradiida) or septal combs (Alveoliticae) seems peculiar to Tabulata; a similar effect is created in some trepostomatous Bryozoa, but in these the wall dividing a new zooecium from an old one is a complete partition from the beginning.

Thus, from the skeletal characters, it seems appropriate to consider the Tabulata as exoskeletons secreted by polyps and, therefore, to refer them to the Cnidaria Anthozoa. Whether they should be regarded as a subclass of Anthozoa or an order of the subclass Zoantharia is arguable and depends on subjective judgments on the relation of septal elements to presumed mesenteries in the polyps, and on their order of insertion. If we judge that there were six protosepta, related to the first six mesenteric pairs, and that subsequent mesenteries were inserted in pairs, then we would refer the Tabulata to the Zoantharia, for such an arrangement is diagnostic of Zoantharia. This was assumed in the first edition of the *Treatise*; however, a considerable consensus has subsequently developed that it is better to treat the Tabulata as a subclass of Anthozoa as was done by Sokolov (1962c), and perhaps first suggested by Abel (1920). In the absence of studies on septal insertion in the Tabulata, this edition of the *Treatise* joins the consensus.

Flügel (1976a, p. 405) has recently spec-

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ulated that the formation of wall pores in Favositidae may be similar to that of astrorizae in Sclerospongiae, and that the Favositidae may thus be considered to be Porifera.

SUBDIVISIONS

As set out above in the history of the study of Tabulata, there has been considerable discussion and uncertainty on the systematic position of the various groups which came to be distinguished among them.

Morphologically simplest are the groups represented by *Chaetetes* and *Tetradium*. Their compound skeletons of slender prismatic tubes are appropriate to either Tabulata or trepostomatous Bryozoa; or they might possibly be solenoporacean algae. The microstructure and ultrastructure is insufficiently known.

In *Chaetetes* itself, illustrations provided by Struve (1898) and by Lafuste and Fischer (1971) show an aporose common wall between tubuli constructed of laterally contiguous, clinogonally fibrous, longitudinal trabeculae, and no continuous median suture in the wall. Such a structure is seen in the recent coenothecalian octocoral *Heliopora*; also, each trabecula is like a single column in some Hydrozoa Stromatoporoidea. However, in thick-walled chaetetids, like *Litophyllum,* the fibers appear to radiate from the entire midplane of the wall. Septal spinules are present in *Rhaphidopora* Nicholson & Thomson and in the Cretaceous *Acanthochaetetes* Fischer [1970, p. 199 (51)]. Fischer considered that the combination of longitudinal trabeculae and latilaminae and sometimes meandroid arrangement of tubuli confirmed the placement of Chaetetida by Sokolov in the Hydrozoa next to the Stromatoporoidea. He considered the spinules of *Acanthochaetetes* to be pseudoseptal; but they do not appear to me to differ from favositid spinules, or from those of the Middle Devonian *Chaetetes lonsdalei* Etheridge and Foord, as figured by Lecompte (1939, pl. 21, fig. 1,2). Sokolov (1962c) considered that the Chaetetida should be removed from the Tabulata because they lacked septal elements and had adaxial longitudinal bilateral increase which when incomplete gave meandroid coralla, and because of the trabecular structure of the wall, which in some consisted of discrete pillars. However, in my opinion, chaetetid spinules, though not general in occurrence, are like those of Favositida; adaxial longitudinal increase by growth of septal combs occurs in Alveoliticae, and quadripartite adaxial longitudinal increase by adaxial growth of two pairs of opposed walls occurs in Tetradiida, which Sokolov regarded as Tabulata; and a trabeculate wall structure is seen in parts of some *Trabeculites.* Although all these features serve to unite the chaetetids as a group, they do not show that the group is hydrozoan rather than tabulatan.

The Tetradiida are very like the Chaetetida in having slender aporose walls. The walls are aspinulate and in my experience are so recrystallized that I have not been able to deduce their original microstructure. Their type of increase differs from that found in Chaetetina only in being quadripartite rather than bipartite. The absence of mural pores serves to distinguish both groups from the Favositida, but should not require their separation from the Tabulata, since an aporose condition is seen in the walls of early Sarcinulida and in many Auloporicae.

I regard both Chaetetida and Tetradiida as Tabulata.

The Heliolitina and Halysitina are herein united in the order Heliolitida of the Tabulata, though Jones & Hill (1940, p. 189) had earlier considered the Heliolitina to be a separate zoantharian group apart from the Tabulata. They have in common 12 equal septal combs to each corallite and a coenenchyme that may be dissepimentate or tubulose or both. Their microstructure is basically the same as that of the Sarcinulida, the Favositida, the Auloporida, the Scleractinia, and the Rugosa; their ultrastructure has not yet been reported. The three superfamilies of the Heliolitina are the Helioliticae, the Proporicae, and the Coccoseridicae.

Of the remaining Tabulata, the Sarcinulida, the Favositida, and the Auloporida, the Sarcinulida as understood herein includes the Billingsariidae and *Nyctopora,* both regarded as "Lichenariida" by Sokolov (1962c, p. 247). The "Lichenariida" is rejected as an order, not only because the characters of *Lichenaria* itself require eluci-

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dation, but because its other components appear better placed elsewhere in the Tabulata.

The Favositida, the dominant order of Tabulata, are divisible into two major divisions, the Favositina and Alveolitina, which are considered suborders, although there are a few genera such as *Oculipora* whose allocation to one or the other of the suborders is arguable. The ramose Favositina with peripheral stereozones, the Pachyporicae, are herein considered a superfamily rather than a suborder, because there are several genera such as *Kolymopora, Pachyfavosites,* and *Striatoporella* with characters placing them between the extreme favositicans and the extreme pachyporicans.

The Auloporida are divisible into two major groups, the Auloporicae and the Syringoporicae, the superfamily status being preferred because of lack of sharp dividing lines between them.

BIOSTATISTICS AND NUMERICAL TAXONOMY

The small number and simplicity of the architectural elements of the skeletons of the Tabulata make it very difficult clearly to distinguish one species from another and one genus from another. This same simplicity and scarcity of morphological features, however, make it possible to examine them biometrically and to analyze the results statistically by punch card systems, by electronic calculating machine, and by computer, but so far only a few biostatistical works have appeared. A punched card system to encode data on tabulate coral morphology and to carry written and pictorial data on species has been described by PREOBRAZHENSKIY (1967a, p. 121).

Work so far has concentrated on Favositina. BOROVICZENY and FLÜGEL (1962, p. 7) concluded that biometry forms an exact basis for separation and definition of species in *Favosites.* TESAKOV (1968, p. 14; 1971a, p. 103), on the other hand, concluded that the quantitative indices of a favositid character depended largely on individual peculiarities of the corallum and on ecological conditions and cannot be used as key criteria in establishing species; he considered the role of numerical indices to be grossly overstated in contemporary practice, but in his diagnoses he included numerical values that indicate the established minimum and maximum limits within which the various formae of a species existed. LELESHUS (1968, p. 50; 1969, p. 50; 1970c, p. 34; 1971b, p. 64) has reported the taxonomic results, for species of *Favosites* and *Paleofavosites,* of his evaluation of degrees of difference, and of his subsequent comparisons of diagnoses, descriptions, and photographs, taking geochronological and paleogeographical features into consideration.

Biometric work, electronic machine calculations, and computer programming are laborious, but if they can be proved to give results of consistent stratigraphic value, then, no doubt, tabulatan systematists will use them.

OUTLINE OF CLASSIFICATION OF THE SUBCLASS TABULATA

The following outline of the subclass Tabulata summarizes taxonomic relationships, geologic occurrence, and numbers of recognized genera and subgenera in each suprageneric group from order to subfamily. A single number refers to genera; where two numbers are given, the second indicates subgenera additional to nominotypical ones.

?Order Chaetetida, 20;2. *Ord., ?L.Sil.-U.Perm.* (Paleozoic range).
  Chaetetidae, 10;2. *U.Ord., ?Sil.-?L.Dev., M.Dev.-Perm.* (Paleozoic range).
    Chaetetinae, 7;2. *U.Ord., ?Sil.-?L.Dev., M.Dev.-Perm.*
    Chaetetiporinae, 2. *?U.Ord., M.Dev., Carb.*
    Moskoviinae, 1. *Carb.*
  Cryptolichenariidae, 3. *Ord.*
  ?Desmidoporidae, 3. *U.Ord., M.Sil., M.Dev.*
  ?Tiverinidae, 2. *M.Sil.-L.Dev.*
  ?Lamottiidae, 1. *M.Ord.*
  ?Lichenariidae, 1. *M.Ord.*
Order Tetradiida, 5. *M.-U.Ord.*
  Tetradiidae, 4. *M.-U.Ord.*
  Paleoalveolitidae, 1. *M.Ord.*
Order Sarcinulida, 28;1. *?L.Ord., M.Ord.-Dev.*
  Billingsariidae, 4. *M.Ord., ?U.Ord.-L.Sil.*
    Billingsariinae, 1. *M.Ord.-low.U.Ord.*
    Foerstephyllinae, 3. *M.Ord., ?U.Ord.-L.Sil.*
  Syringophyllidae, 15. *?L.Ord., M.Ord.-L.Sil.*
    Lyoporinae, 10. *?L.Ord., M.Ord.-L.Sil.*
    Calapoeciinae, 2. *M.-U.Ord.*
    Syringophyllinae, 3. *U.Ord.*
  Theciidae, 9;1. *L.Sil.-L.Dev., M.Dev.*

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- Order Favositida, 124;1. *M.Ord.-U.Perm.*
- Suborder Favositina, 103;1. *M.Ord.-U.Perm.*
- Superfamily Favositicae, 76;1. *M.Ord.-U.Perm.*
  - Favositidae, 32. *M.Ord.-L.Perm.*
    - Favositinae, 15. *U.Ord.-M.Dev.*
    - Paleofavositinae, 4. *M.Ord.-L.Dev.*
    - Pachyfavositinae, 3. *U.Sil.-U.Dev.*
    - Emmonsiinae, 10. *U.Sil.-M.Dev., L.Carb.-L.Perm.*
  - Pseudofavositidae, 2. *U.Perm.*
  - Syringolitidae, 2. *L.-M.Sil., L.Dev.*
  - Favositids with commensals, 5.
  - Multisoleniidae, 5. *U.Ord.-?L.Dev.*
    - Multisoleniinae, 4. *U.Ord.-U.Sil., ?L.Dev.*
    - Antherolitinae, 1. *M.Sil.*
  - Agetolitidae, 3. *U.Ord.-?L.-M.Sil.*
  - Micheliniidae, 14;1. *U.Sil.-U.Perm.*
    - Micheliniinae, 11. *U.Sil.-U.Perm.*
    - Granulidictyinae, 3;1. *L.-M.Dev.*
  - Cleistoporidae, 9. *U.Sil.-M.Dev., ?U.Dev., Carb.*
  - Vaughaniidae, 1. *L.Carb.*
  - Palaeacidae, 3. *L.Carb.*
- Superfamily Pachyporicae, 27. *U.Ord.-U.Perm.*
  - Pachyporidae, 21. *L.Sil.-U.Perm.*
  - Parastriatoporidae, 6. *U.Ord.-M.Dev.*
- Suborder Alveolitina, 21. *L.Sil.-U.Dev.*
  - Alveolitidae, 17. *L.Sil.-U.Dev.*
    - Alveolitinae, 8. *L.Sil.-U.Dev.*
    - Caliaporinae, 6. *L.Sil., U.Sil.-M.Dev.*
    - Natalophyllinae, 3. *L.-M.Dev.*
  - Coenitidae, 3. *Up.L.Sil.-M.Dev.*
  - Family uncertain, 1.
- Order Heliolitida, 76. *M.Ord.-M.Dev.*
- Suborder Heliolitina, 65. *M.Ord.-M.Dev.*
- Superfamily Helioliticae, 24. *M.Ord.-M.Dev.*
  - Heliolitidae, 9. *M.Ord.-M.Dev.*
  - Taeniolitidae, 3. *M.-U.Ord., L.Dev.*
  - Stelliporellidae, 8. *U.Ord.-M.Dev.*
  - Pseudoplasmoporidae, 4. *U.Ord.-L.Sil., U.Sil.-?M.Dev.*
- Superfamily Proporicae, 32. *M.Ord.-?L.Dev.*
  - Proporidae, 9. *M.Ord.-U.Sil.*
  - Sibiriolitidae, 3. *U.Ord., ?M.Sil.*
  - Plasmoporidae, 5. *?M.Ord., L.Sil.-L.Dev.*
  - Plasmoporellidae, 7. *M.-U.Ord., L.-M.Sil.*
  - Proheliolitidae, 5. *U.Ord., U.Sil.*
  - ?Cyrtophyllidae, 3. *?M.-U.Ord.*
- Superfamily Coccoseridicae, 9. *M.Ord.-M.Sil.*
  - Coccoserididae, 3. *M.-U.Ord.*
  - Pycnolithidae, 1. *L.* or *M.Sil.*
  - Palaeoporitidae, 3. *?M.-U.Ord.*
  - Family uncertain, 2.
- Suborder Halysitina, 11. *M.Ord.-U.Sil.*
  - Halysitidae, 11. *M.Ord.-U.Sil.*
    - Cateniporinae, 3. *M.Ord.-U.Sil.*
    - Halysitinae, 8. *M.-?U.Ord.-U.Sil.*
- Order Auloporida, 79. *L.Ord.-U.Perm.*
- Superfamily Auloporicae, 40. *L.Ord.-U.Perm.*
  - Auloporidae, 7. *L.Ord.-U.Perm.*
  - Bajgoliidae, 1. *M.-U.Ord.*
  - Kozlowskiocystiidae, 1. *M.Dev.*
  - Fletcheriellidae, 4. *U.Ord.-M.Sil., M.Dev.*
  - Pyrgiidae, 5. *U.Sil., M.Dev.-U.Perm.*
  - ?Trachypsammiidae, 3. *Perm.*
  - Auloheliidae, 1. *U.Perm.*
  - Romingeriidae, 4. *?L.-U.Sil., M.Dev., ?L.-U.Miss.*
  - ?Palaeofavosiporidae, 1. *M.Sil.*
  - Aulocystidae, 9. *L.Sil., L.Dev.-U.Penn., U.Perm.*
  - ?Sinoporidae, 3. *L.Sil., M.Carb.-Perm.*
  - ?Khmeriidae, 1. *?Carb., Perm.*
- Superfamily Syringoporicae, 39. *M.Ord.-Perm.*
  - Syringoporidae, 10. *U.Ord.-L.Perm.*
  - Periphaceloporidae, 1. *M.Dev.*
  - Tetraporellidae, 7. *M.Ord.-M.Dev., L.Carb., L.-U.Perm.*
  - Multithecoporidae, 4. *L.-M.Sil., L.-?U.Dev.-U.Perm.*
  - Roemeriidae, 6. *?L.Sil., L.-M.Dev., L.Carb., L.Perm.*
  - Thecostegitidae, 6. *U.Sil.-U.Carb.*
  - Chonostegitidae, 1. *L.-M.Dev.*
  - Gorskyitidae, 4. *L.Sil., L.Carb.-L.Perm.*
- Order uncertain, 2.

RANGES OF TAXA

Only records accompanied by illustrations of type specimens and type species, myself reasonably sure that the generic identifications are correct have been incorporated in the range data that follow the diagnosis of each genus. Nevertheless, these data are still defective. Preparation of the diagnoses from the literature has made it clear to me that the greatest impediments to precise taxonomy are the incompleteness of descriptions and imperfection of illustrations from which I have been able to make and the lack of analyses of variation in topotypes. A very great improvement in our knowledge would result from critical redescriptions and new figures by specialist officers of museums housing such types. Without precise taxonomy, little of real value can be contributed to current debates on plate tectonics and continental drift. Uncritical use of "faunal lists" is merely stultifying.

The stratigraphic distribution of orders, suborders, superfamilies, families, and subfamilies of Tabulata recognized in the *Treatise* is indicated graphically in the tables that follow (compiled by JACK D. KEIM).

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TABLE 3. *Stratigraphic Distribution of Tabulata.*

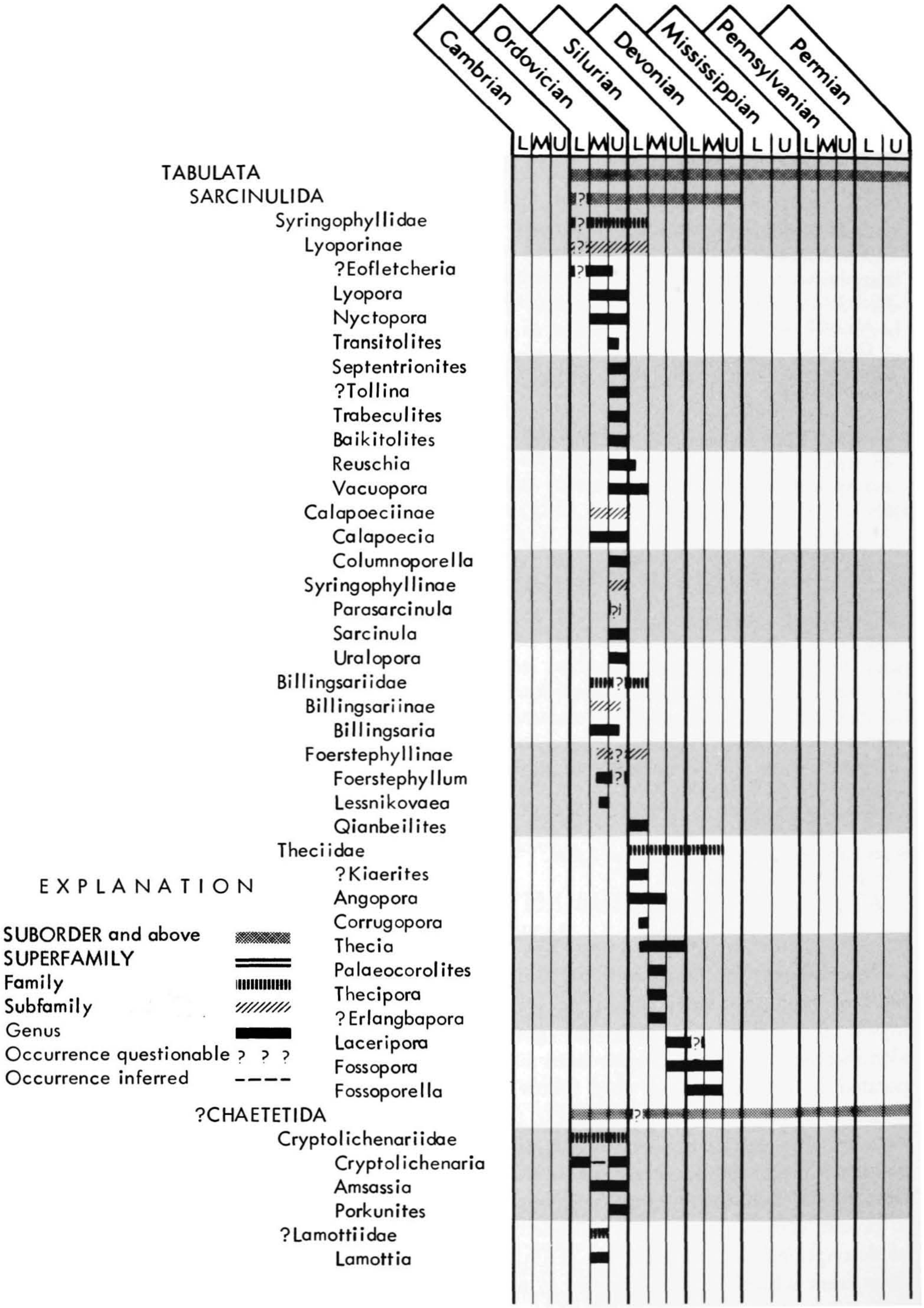

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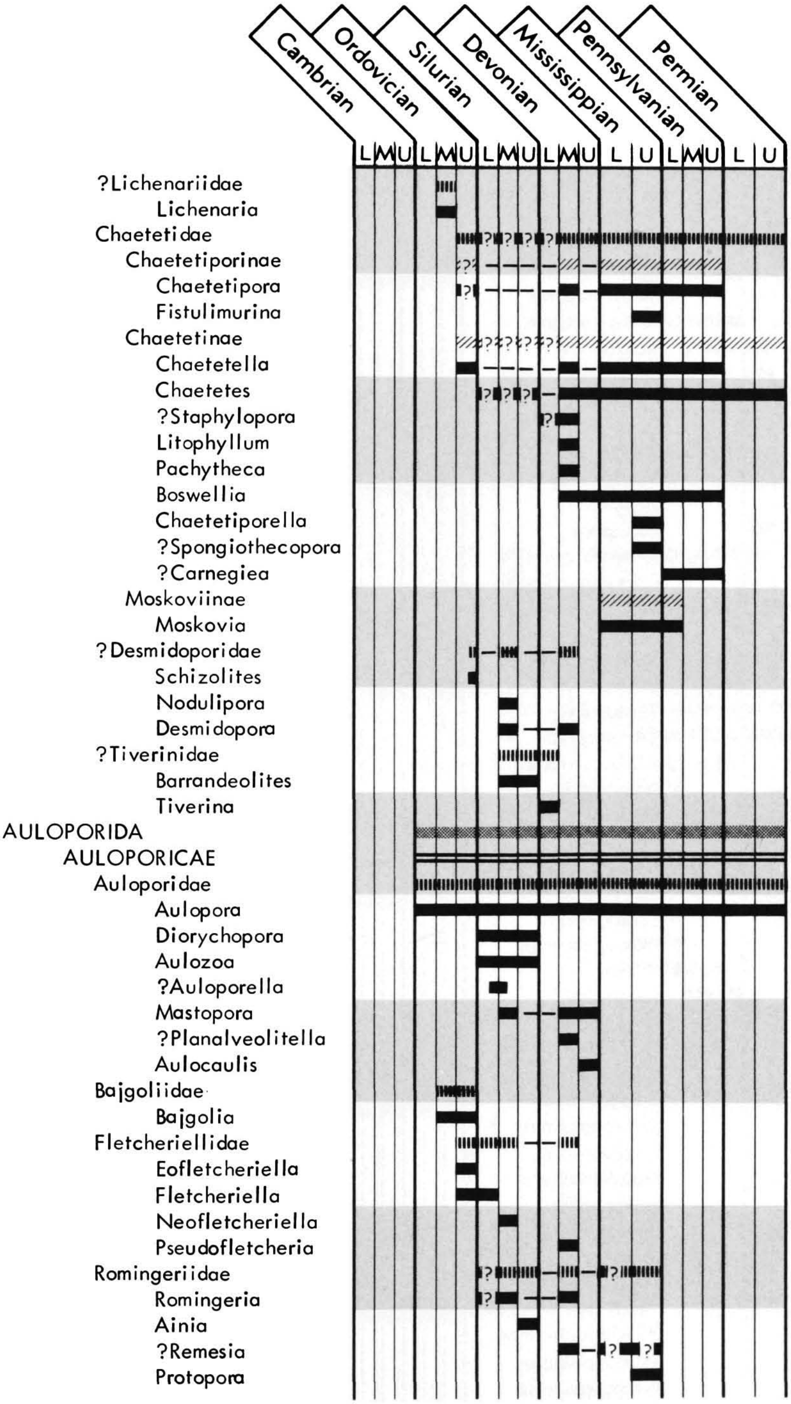
TABLE 3. *(Continued)*



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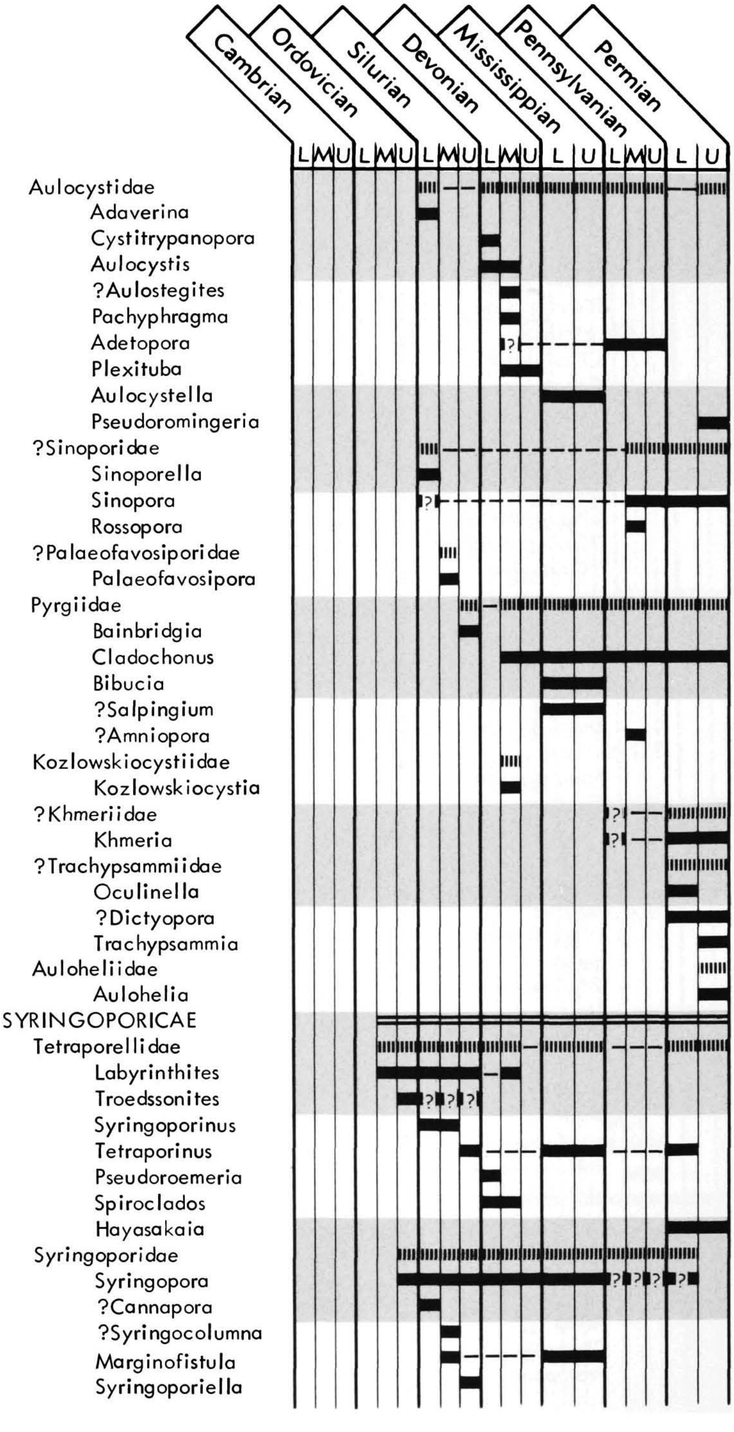

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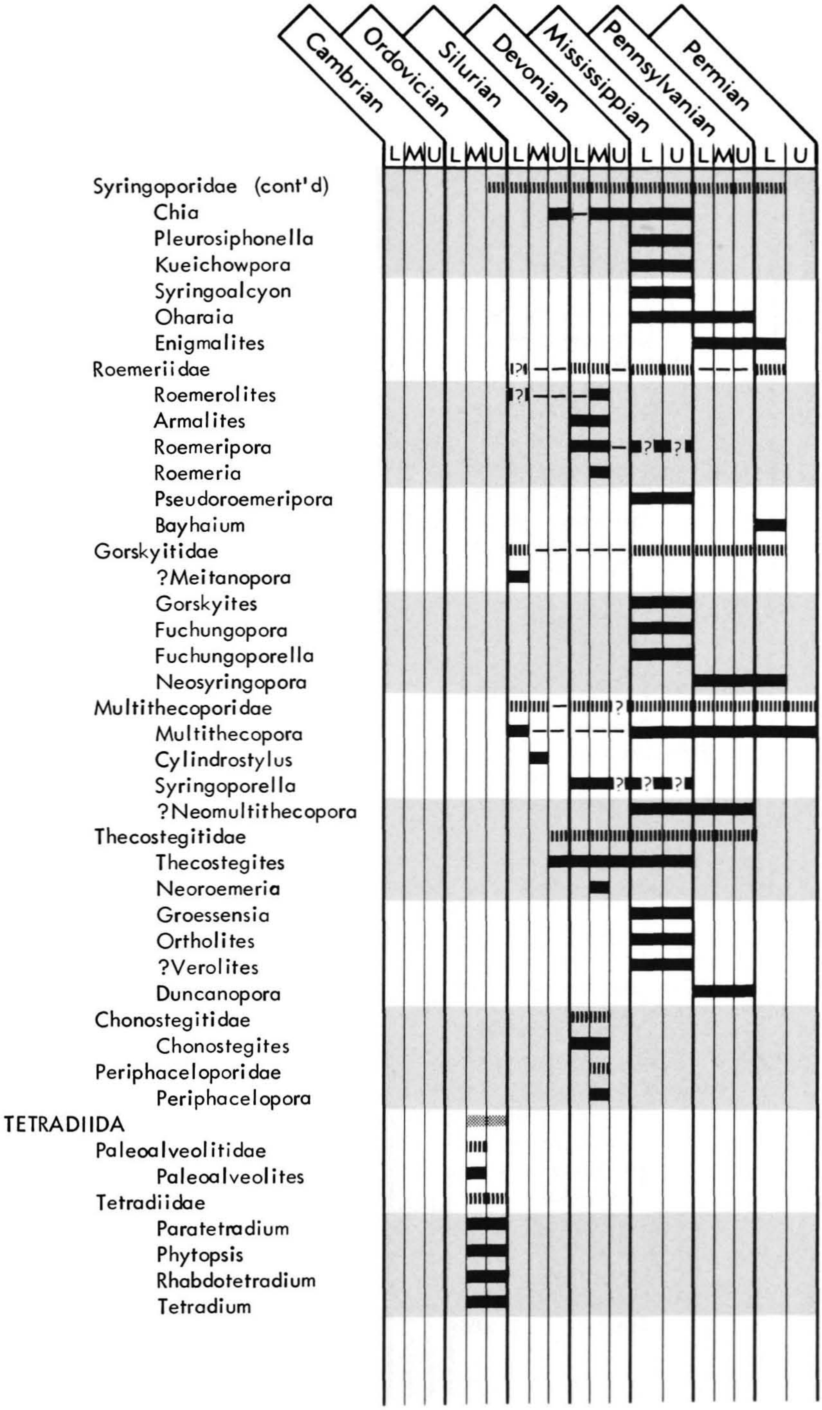

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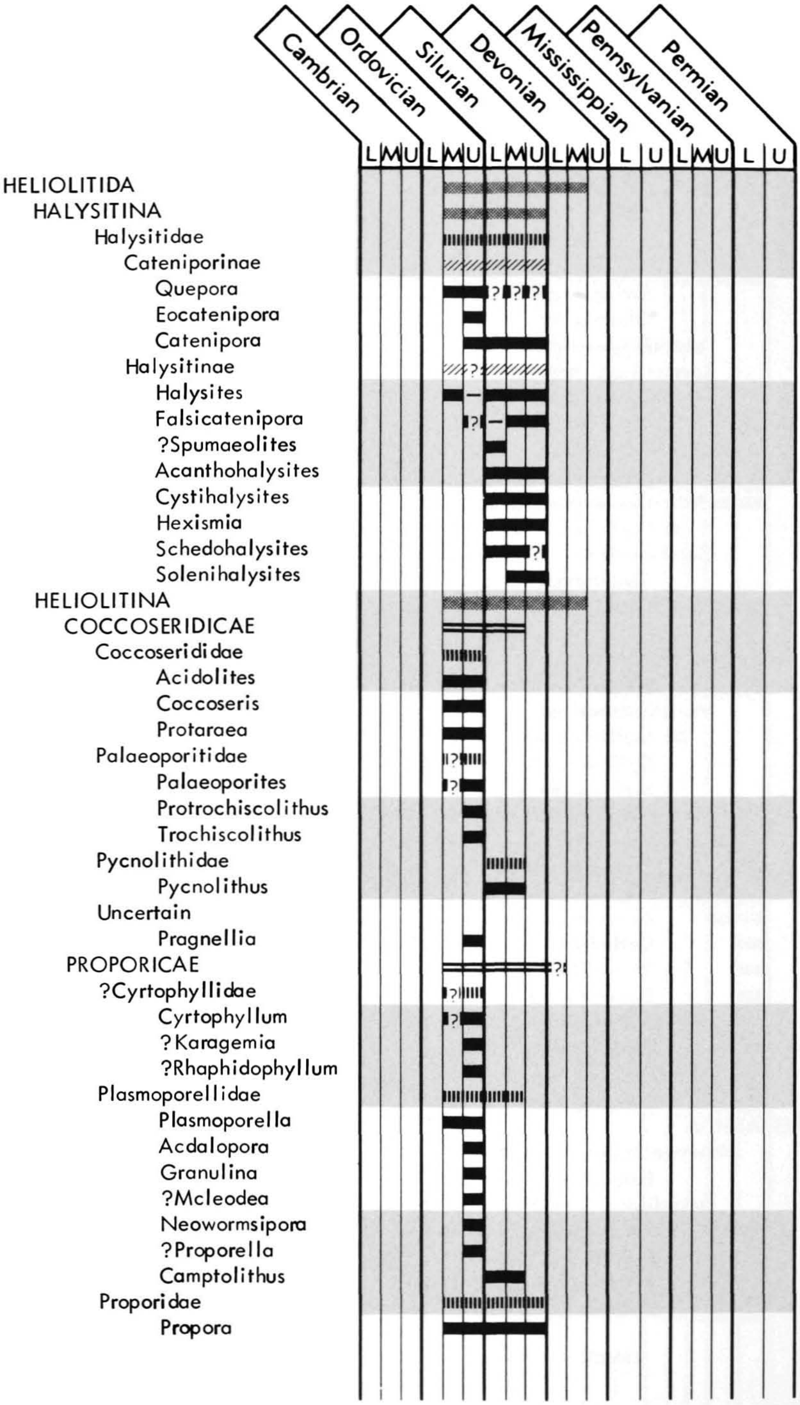

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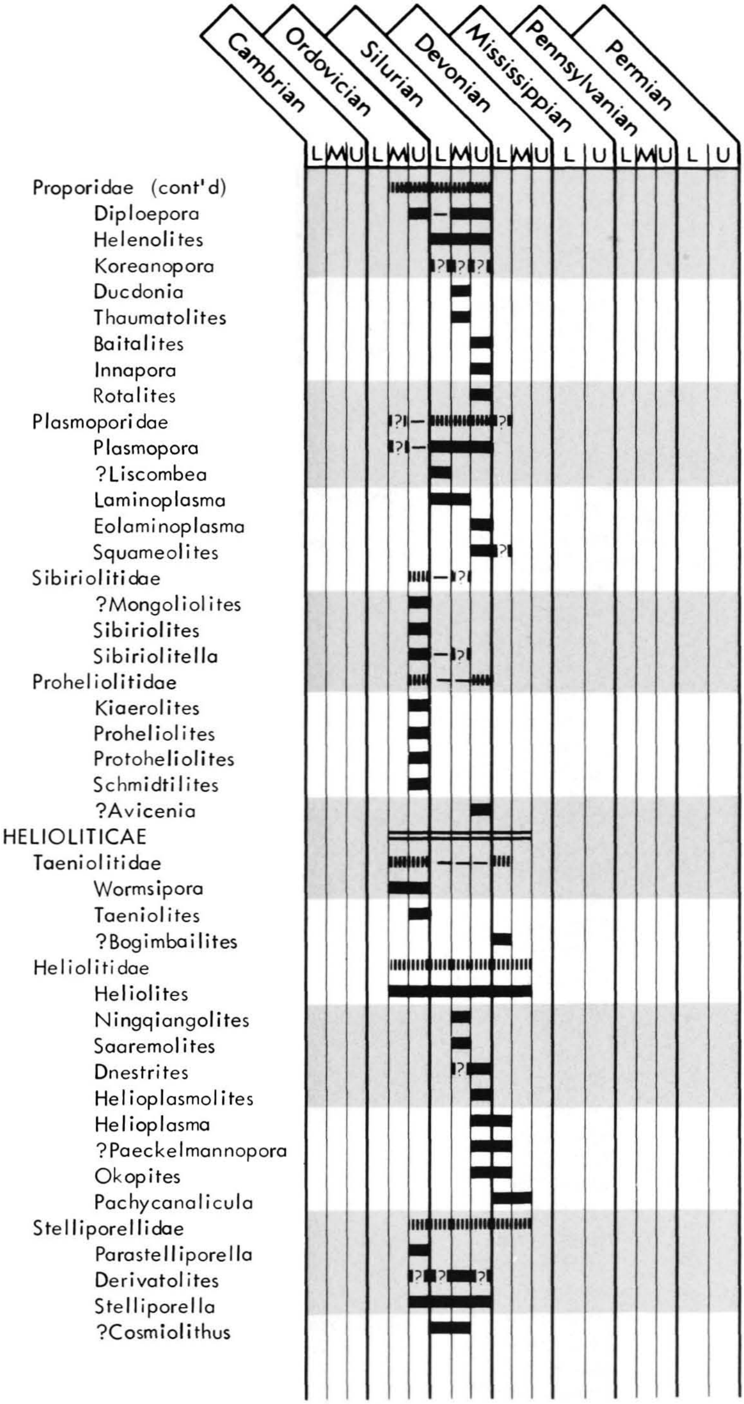

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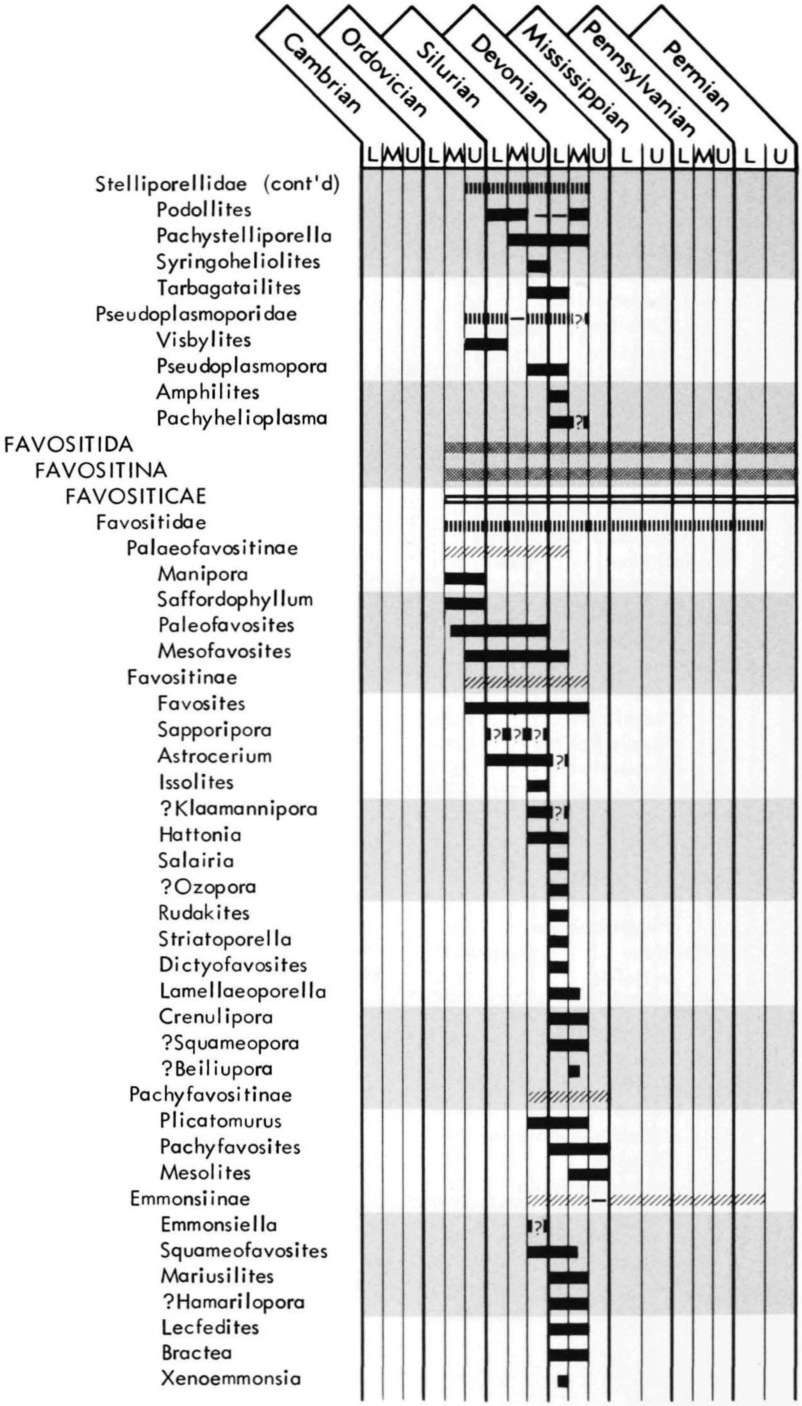

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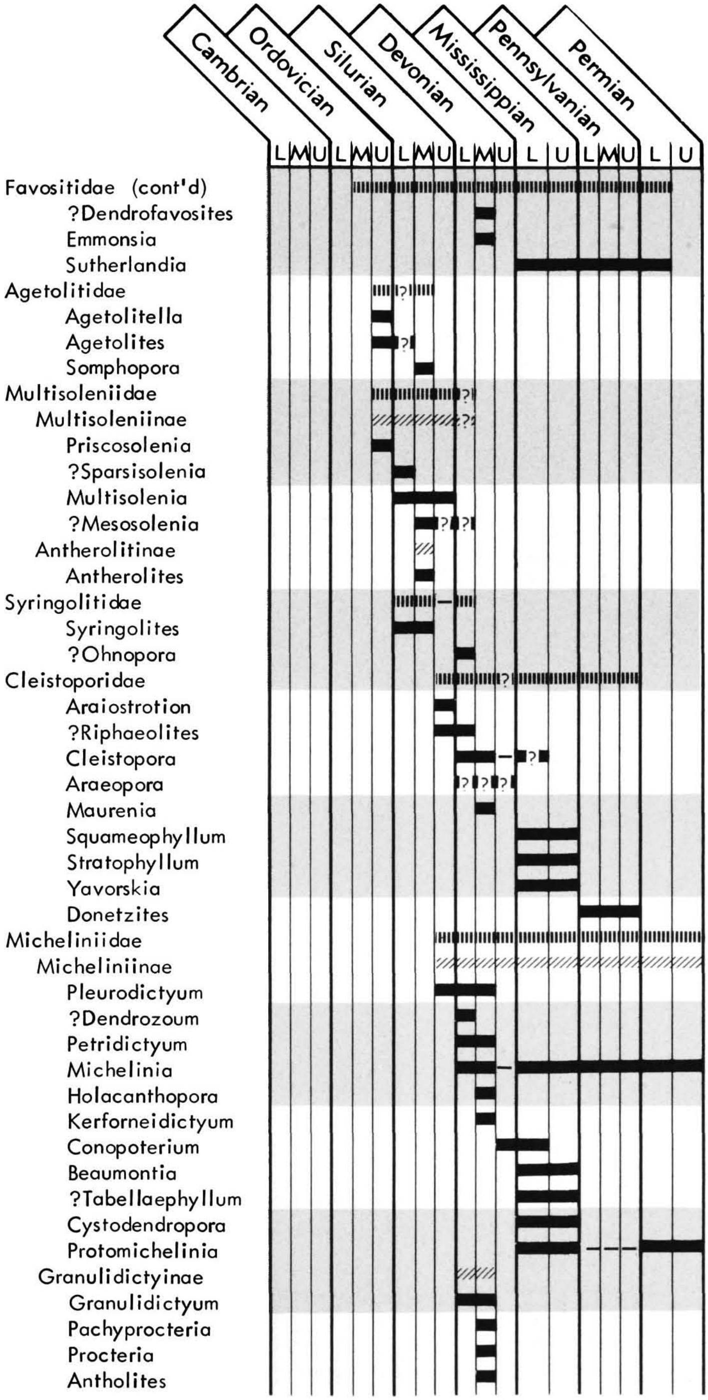

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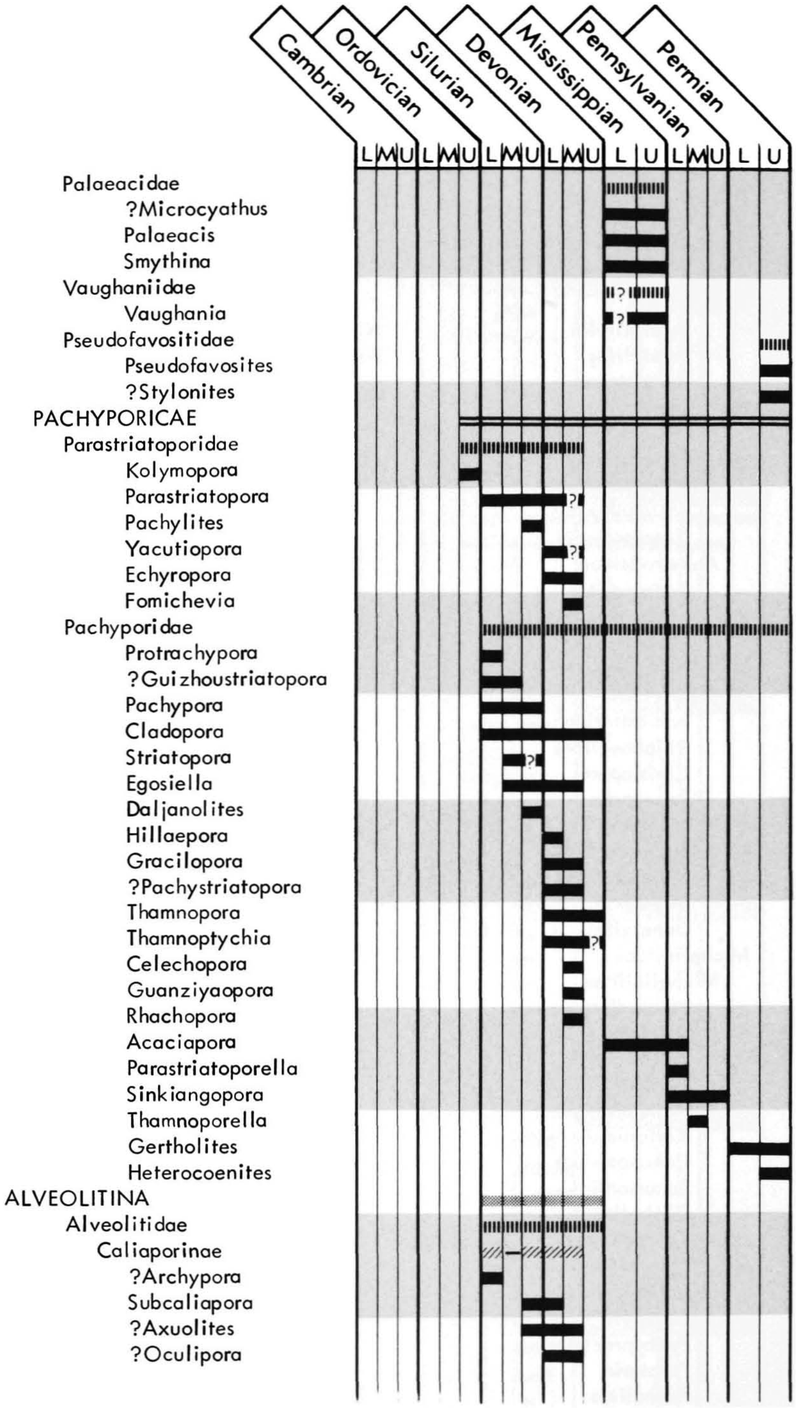

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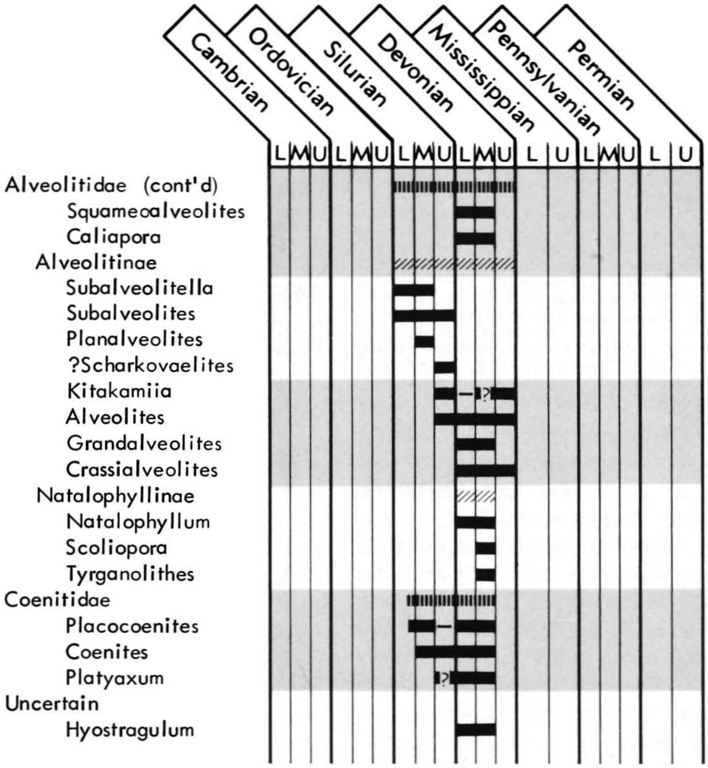

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