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MORPHOGENESIS OF SYRINGOPORIDA

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General patterns and main trends of syringoporoid morphogenesis are described. Microstructure of corallite wall, connecting elements and tabulae are shown. In syringoporoid evolution similar structures appeared repeatedly, but as a rule not simultaneously at different taxonomic levels. A new system of the order Syringoporida is given.

K e y w o r d s: corals, Tabulata, Syringoporida, morphogenesis.

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The interest displayed by paleontologists in the study of tabulate corals increased in particular after the publication of Sokolov's series of monographs (1950—1962). These works discuss the morphology, systematics and phylogeny of Tabulata. Sokolov was the first to bring together separate syringoporoid genera and unite them into the order Syringoporida.

Investigation of a rich material (more than four thousand thin sections) from all Paleozoic collected in different regions of the USSR, a comparative study of the collections housed in the Moscow, Leningrad, Kiev, Novosibirsk museums, as well as of collections from Sweden, North America (the North-East of Alaska), along with the analysis of published data, allowed me to revise this complex group of corals.

As a result of this investigation systematic composition of the order Syringoporida has been established:

Order Syringoporida: family Syringoporidae, subfamily Syringoporinae, genera: *Syringopora* Goldfuss, 1826; *Troedssonites* Sokolov, 1947; *Syringoporinus* Sokolov, 1952; *Syringocolumna* Stumm, 1969; *Armalites* Tchudinova, 1964; *Syringella* Nowiński, 1970; *Kueichowpora* Chi, 1933; *Gorskyites* Sokolov, 1955; *Syringoalcyon* Termier et Termier, 1945; subfamily Neosyringoporinae, genera: *Chia* Lin, 1958; *Syringocystis* Deng, 1966; *Pleurosiphonella* Tchudinova, 1970; *Enigmalites* Tchudinova, 1975; *Neosyringopora* Sokolov, 1955.

Family Tetraporellidae, genera: *Tetraporinus* Sokolov, 1947; *Arcturia* Wilson, 1931; *Hayasakaia* Lang, Smith et Thomas, 1940.

Family Multithecoporidae, genera: *Spiroclados* Dubatolov, 1969; *Syringoporella* Kettner, 1934; *Multithecopora* Yoh, 1927; *Neomultithecopora* Lin, 1963; *Montanella* Tchudinova, 1979.

Family Thecostegitidae, genera: *Cannapora* Hall, 1852; *Thecostegites* Milne-Edwards et Haime, 1849; *Chonostegites* Milne-Edwards et Haime, 1851; *Fuchungopora* Lin, 1963; *Ortholites* Tchudinova, 1975; *Verolites* Tchudinova, 1975; *Duncanopora* Sando, 1975.

A detailed study of the syringoporoid morphology (the study of astogenesis and blastogenesis) served as the basis for clarifying general patterns of syringoporoid morphogenesis, i.e. made it possible to trace morphological structures as they changed both individually and phylogenetically.

The structure of syringoporoid colonies reveals the entire spectrum of skeleton elements that may be found in tabulate corals. Certain findings of the earliest syringoporoids date back to the Middle Ordovician. The earliest syringoporoids had small massive fasciculate colonies composed of cylindrical-prismatic corallites, with simple horizontal tabulae, short connecting tubes located on corallite ribs, lamellar wall, small and thin septal spines.

During the evolution of the Syringoporida the simple structure of the colonies is replaced by a complex structure. The fascicular type of the colonies typical of all the genera, persisted throughout the Paleozoic.

Corallites forming the colonies are cylindrical-prismatic or cylindrical in shape. This feature developed in two ways: (1) ancestral cylindrical-prismatic corallites persisted throughout the Paleozoic (genera of the family Tetraporellidae; pl. 42: *5*—*7*); (2) the ancestral cylindrical-prismatic corallites (the genus *Troedssonites* of the family Syringoporidae, pl. 42: *1*) were replaced by cylindrical corallites (all the other genera of Syringoporidae, pl. 42: *2*—*4*; the family Multithecoporidae, pl. 42: *8*—*11*; and the genera of the family Thecostegitidae, pl. 42: *12*—*16*). Cylindrical corallites were the most wide-spread among Syringoporida being characteristic of nearly all the syringoporoid genera.

Wall. — Syringoporida were observed to have two types of microstructure of the corallite wall sclerenchyme: the lamellar (earlier) type and the fibrous (later) type. The replacement of the first type by the second occurred in all phylogenetic branches of Syringoporida at different stages of their evolution. In the phylogenetic branch of the family Multithecoporidae the lamellar microstructure of corallite walls persisted till the Late Carboniferous (*Spiroclados*, Silurian-Devonian; *Syringoporella*, Devonian-Carboniferous; *Neomultithecopora*, Carboniferous, pl. 46: 2). It was not until the Early Permian that there appeared multithecoporids with a fibrous wall microstructure (*Multithecopora*, Permian, pl. 46: 1). In three other phylogenetic branches (the families Syringoporidae, Tetraporellidae and Thecostegitidae) the lamellar type of wall microstructure (*Syringoporinus*, Ordovician, pl. 43: 1) was replaced by the fibrous microstructure either in the Early Devonian or in the Early Carboniferous (*Pleurosiphonella*, Devonian, pl. 44: 1; *Enigmalites*, *Neosyringopora*, Carboniferous-Permian, pl. 45: 1—3).

The syringoporid septal apparatus is represented by spines arranged in vertical rows in the sclerenchyma of corallite walls. The spines vary in their shape and size: from short, scarcely visible inside the wall and slightly projecting into the visceral chamber of corallites to long, almost reaching the center and sometimes forming discontinuous columella (*Syringocolumna*). The lamellar microstructure of the septal spines is older, while the trabecular one is younger. In corals with a lamellar wall the spines have either lamellar or trabecular structure (holacanths are found in some species of the genus *Syringopora*, pl. 43: 2, monacanths — in the genera *Armalites* from the Early Devonian, pl. 44: 2 and *Syringoalcyon* from the Early Carboniferous, pl. 44: 3). In corals with a fibrous wall structure trabecular spines are developed (— monacanths, *Enigmalites* from the Late Carboniferous and Permian, pl. 45: 2).

Syringoporoids display typical connecting structures. They are developed in the form of tubes, plates and, occasionally, pores. This feature evolved in four ways: (1) the older connecting formations in the form of short tubes located on corallite ribs persisted throughout the Paleozoic (genera of the family Tetraporellidae, pl. 42: *5—7*; pl. 45: 4); (2) connecting tubes moved away from the ribs to become sporadically located. This feature was most widely represented as it enhanced the viability of colonies (the genera of the family Syringoporidae: *Syringopora, Syringoporinus, Syringocolumna, Armalites, Syringella, Kueichowpora, Gorskyites, Syringoalcyon, Chia, Syringocystis, Pleurosiphonella, Enigmalites, Neosyringopora*, pl. 42: *2—4*); (3) as a result of the fusion of connecting tubes, connecting plates are formed (the genera of the family Thecostegitidae, pl. 42: *12—16*). This feature was most strongly pronounced in the Thecostegitidae during the Early Carboniferous. During the period of flourishing and decline of thecostegitids some highly specialized genera appeared among them with connecting plates, tubes and, more rarely, with pores (*Fuchungopora, Duncanopora, Verolites, Ortholites*, pl. 47: 3); (4) gradual disappearance of connecting formations during the Paleozoic (genera of the family Multithecoporidae, pl. 42: *8—11*). In older genera (*Spiroclados*, Silurian-Early Devonian) connecting tubes are arranged closely and sporadically and then progressively become more widely separated (*Multithecopora*, Carboniferous-Permian). In the colonies of such kind the lateral offsetting is observed more frequently. This trend is characterized by the development of zooid individuality, while the other three are marked by an increasing degree of coloniality.

Tabulae. — The development of this feature was accomplished in several ways. The earlier Syringoporoids had horizontal, concave, incomplete tabulae. The first way is characterized by the maintenance of the earlier, primitive structure of tabulae (the genera of the family Multithecoporidae, pl. 42: *8—11*). This feature is observed virtually throughout the Paleozoic, it was towards the end of this family evolution that the genus *Neomultithecopora* evolved more complex tabulae that were concave and in some parts funnel-shaped. The second way is marked by both the maintenance of the older structure and its complication, the tabulae being evolved from concave to funnel-shaped (the genera of the family Thecostegitidae, pl. 42: *12—16*). For the third way complication of tabulae is typical; concave and incomplete tabulae in the axial zone are surrounded by the vesicular ring at the corallite periphery (the genera of the family Tetraporellidae, pl. 42: 5—7; pl. 45: 4). In the last trend, a maximum variety of tabulae structures is observed (some genera of the family Syringoporidae). The earlier syringoporoid genera have well-developed, horizontal, concave tabulae (*Troedssonites*, Ordovician; *Syringoporinus*, Ordovician-Early Silurian, pl. 43: 1); concave tabulae evolving into funnel-shaped ones (*Syringopora*, Silurian-Early Carboniferous, pl. 43: 2*b*); funnel-shaped tabulae with an axial tube (*Kueichowpora*, Early Carboniferous, pl. 43: 4); funnel-shaped tabulae with a lateral tube (*Pleurosiphonella*, Early Carboniferous; pl. 45: 1); funnel-shaped tabulae with a vesicular zone at the corallite periphery (*Chia*, Early Carboniferous) and vesicular tabulae (*Neosyringopora*, Carboniferous-Early Permian, pl. 44: 1).

The evolution of syringoporoids repeatedly witnessed similar morphological structures that appeared in parallel, but not simultaneously.

The entire variety of morphological structures made the Syringoporida adaptable to different environmental conditions and provided for their rapid evolution and extremely wide distribution in space and time.

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EXPLANATION OF THE PLATES 42—47

Plate 42

Morphogenetical trends in Syringoporida

h Hypothetical auloporid; *1—4* family Syringoporidae: *1* ***Troedssonites***, *2* ***Syringoporinus***, *3* ***Syringopora***, *4* ***Neosyringopora***; *5—7* family Tetraporellidae: *5* ***Tetraporella***, *6* ***Tetraporinus***, *7* ***Hayasakaia***; *8—11* family Multithecoporidae: *8* ***Spiroclados***, *9* ***Syringoporella***, *10* ***Multithecopora***, *11* ***Neomultithecopora***; *12—16* family Thecostegitidae: *12* ***Cannapora***, *13* ***Thecostegites***, *14* ***Chonostegites***, *15* ***Verolites***, *16* ***Ortholites***.

Plate 43

1. *Syringoporinus celebratus* Preobrazhensky. *a* Transverse section, ×15; *b* longitudinal section, ×15. (PIN AN USSR, N 2534/13), Southern USSR, riv. Iasechnaja, Ashgillian.

2. *Syringopora lindströmi* Tchernyshev. *a* Transverse section: corallite, lamellar wall and trabecular spines of holacanth type. ×15; *b* longitudinal section, ×15. (ZNGR, USSR, N 5256/26), O. Vajgach-Dolgij, Ludlovian.
3. *Syringopora weiningensis* Chi. Transverse section: corallite, lamellar wall and trabecular spines of monacanth type, ×15. (PIN AN USSR, N 3460/4), Kazakhstan, Mt. Sadiadir, north Karaganda; Tournaisian.
4. *Kueichowpora patula* Tchudinova. Longitudinal section: funnel-shaped tabulae with an axial tube, ×15. (PIN USSR, N 2333/823). The Middle Urals, Grand Sopljask riv., Viséan.

Plate 44

1. *Pleurosiphonella crustosa* Tchudinova. *a* Transverse section: fibrous corallite wall, ×10; *b* longitudinal section: funnel-shaped tabulae with a lateral tube, ×10. (PIN, USSR, N 2189/369), Transcaucasus, Mt. Sari-Pap, Tournaisian.
2. *Armalites novellus* Tchudinova. *a* Transverse section: lamellar corallite wall and trabecular spines of monacanth type, ×15; *b* longitudinal section, ×15; holotype. (PIN, AN USSR, N 1396/2586), Kusbass, Ur riv., Novopesterevo, Eifelian, Schandian beds.
3. *Syringoalcyon unicum* Tchudinova. *a* Transverse section: lamellar corallite wall and trabecular spines of monacanth type, ×15; *b* longitudinal section, ×15; holotype. (PIN USSR, N 2668/34), the South Urals, Novotroick, Ankermanovka, Viséan.

Plate 45

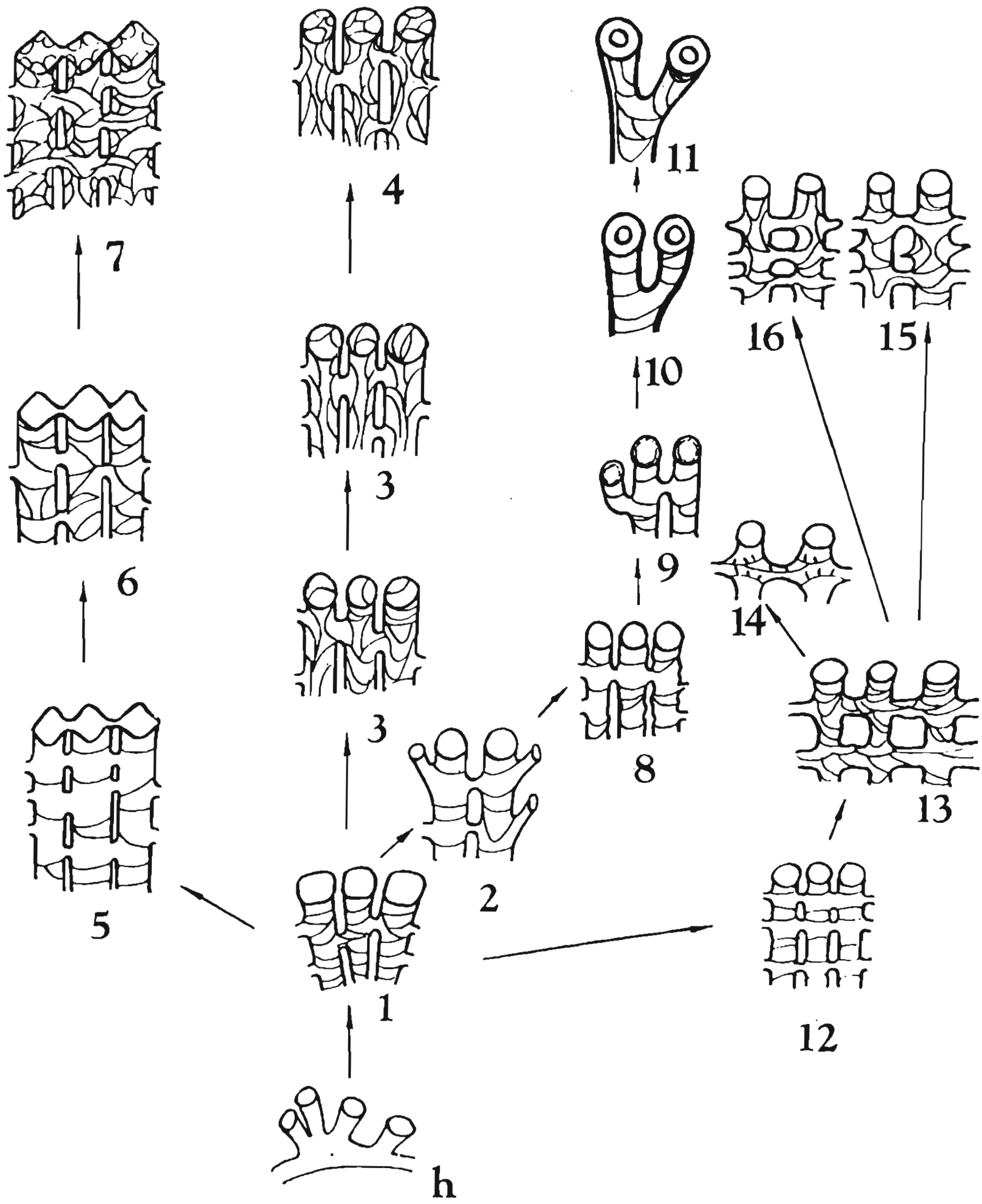
1. *Neosyringopora copiosa* Tchudinova. *a* Transverse section, ×15; *b* longitudinal section, ×15; holotype. (PIN USSR, N 3494/8), the Middle Urals, Kin riv.; Gzelian.
2. *Enigmalites lectus* Tchudinova. Transverse section: fibrous corallite wall and trabecular spines of monacanth type, ×15; holotype. (PIN USSR, N 3494/3), the Middle Urals, Kosva riv.; Sakmarian.
3. *Enigmalites lautus* Tchudinova. Longitudinal section, ×10; holotype. (PIN USSR, N 3494/1), the Middle Urals, Kosva riv.; Asselian.
4. *Tetraporinus singularis* Sokolov. *a* Transverse section, ×15; *b* longitudinal section, ×15. (PIN USSR, N 3494/59), the Middle Urals, Kosva riv.; Viséan.

Plate 46

1. *Multithecopora delicata* Tchudinova. *a* Transverse section: fibrous corallite wall, ×15; *b* longitudinal section, ×10; holotype. (PIN USSR, N 3498/3), Southern Primorie, Peischula riv.; Kasanian.
2. *Neomultithecopora berkhi* (Gorskyi). *a—c* Transverse sections: lamellar corallite wall and trabecular spines of monacanth type, *d* longitudinal section; ×10. (PIN) USSR, N 2333/820), the Middle Urals, Patok riv.; Viséan.
3. *Multithecopora eplicata* Tchudinova. Transverse section: lamellar corallite wall and trabecular spines of monacanth type, ×10. (PIN USSR, N 3494/6), the Middle Urals, Kosva riv.; Asselian.
4. *Multithecopora* sp. Longitudinal section, ×10 (PIN USSR, N 2333/914), the Southern Urals, Belaja riv.; Bashkirian.

Plate 47

1. *Thecostegites infundibuliferus* (Tchernychev). Transverse section: fibrous corallite wall and trabecular spines, ×15. (PIN USSR, N 875/131), Rudnyj Altaj, Smeinogorsk; Eifelian.
2. *Thecostegites* sp. Longitudinal section, ×15. (PIN USSR, N 2333/761), the North Urals, Grand Patok riv.; Tournaisian.
3. *Ortholites nexus* Tchudinova. Longitudinal section: the connecting plates, tubes, and scanty pores, ×10. (PIN USSR, N 3460/1), Kazakhstan, Karasu riv.; Tournaisian.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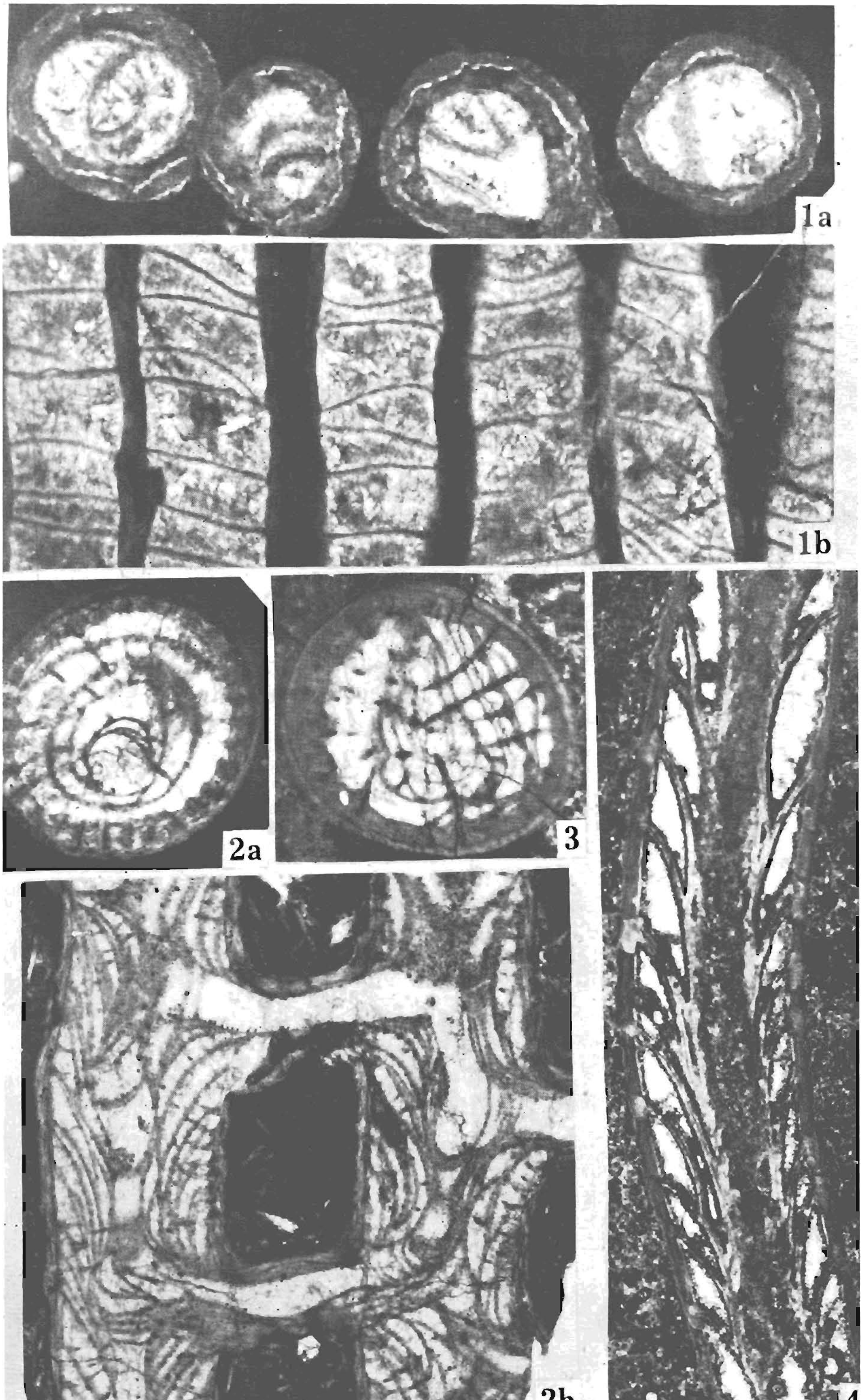
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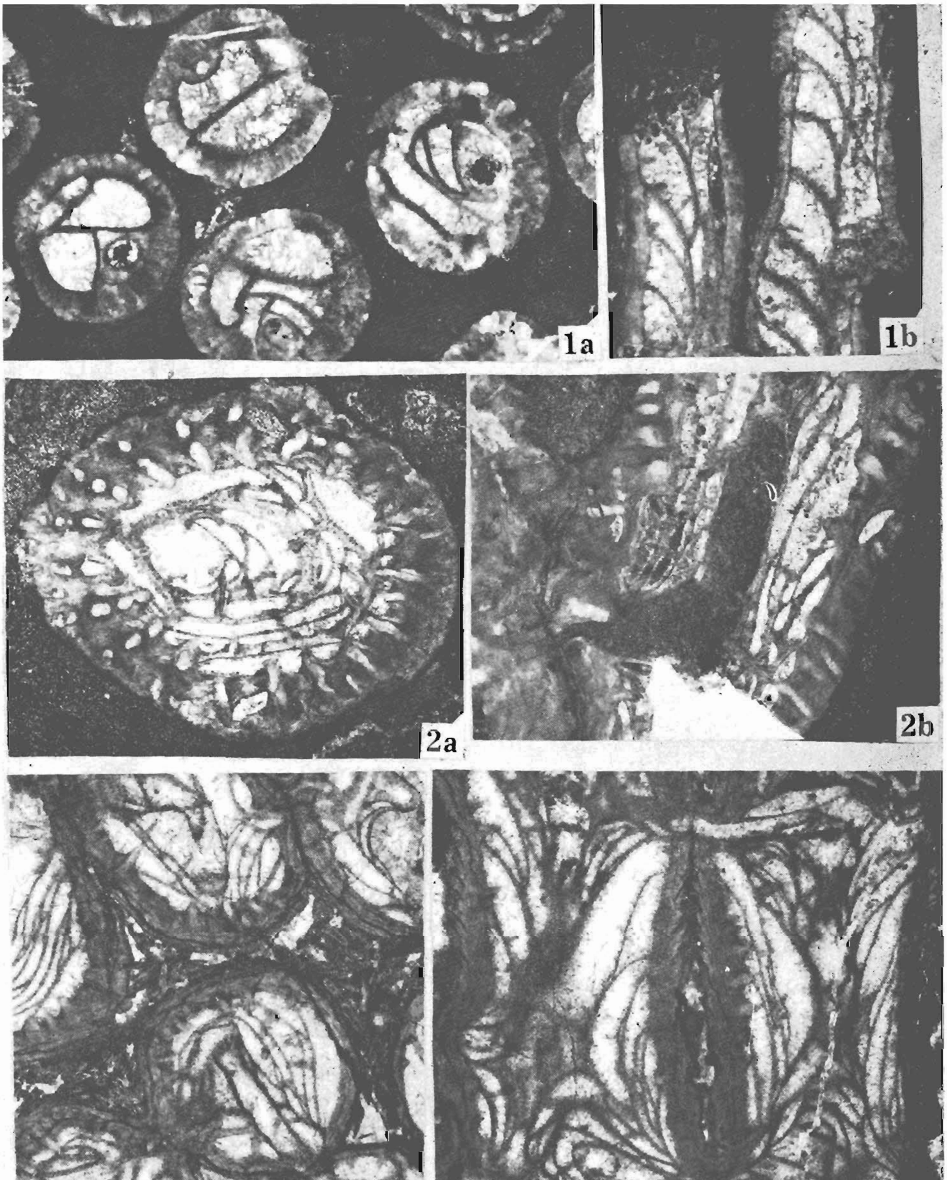
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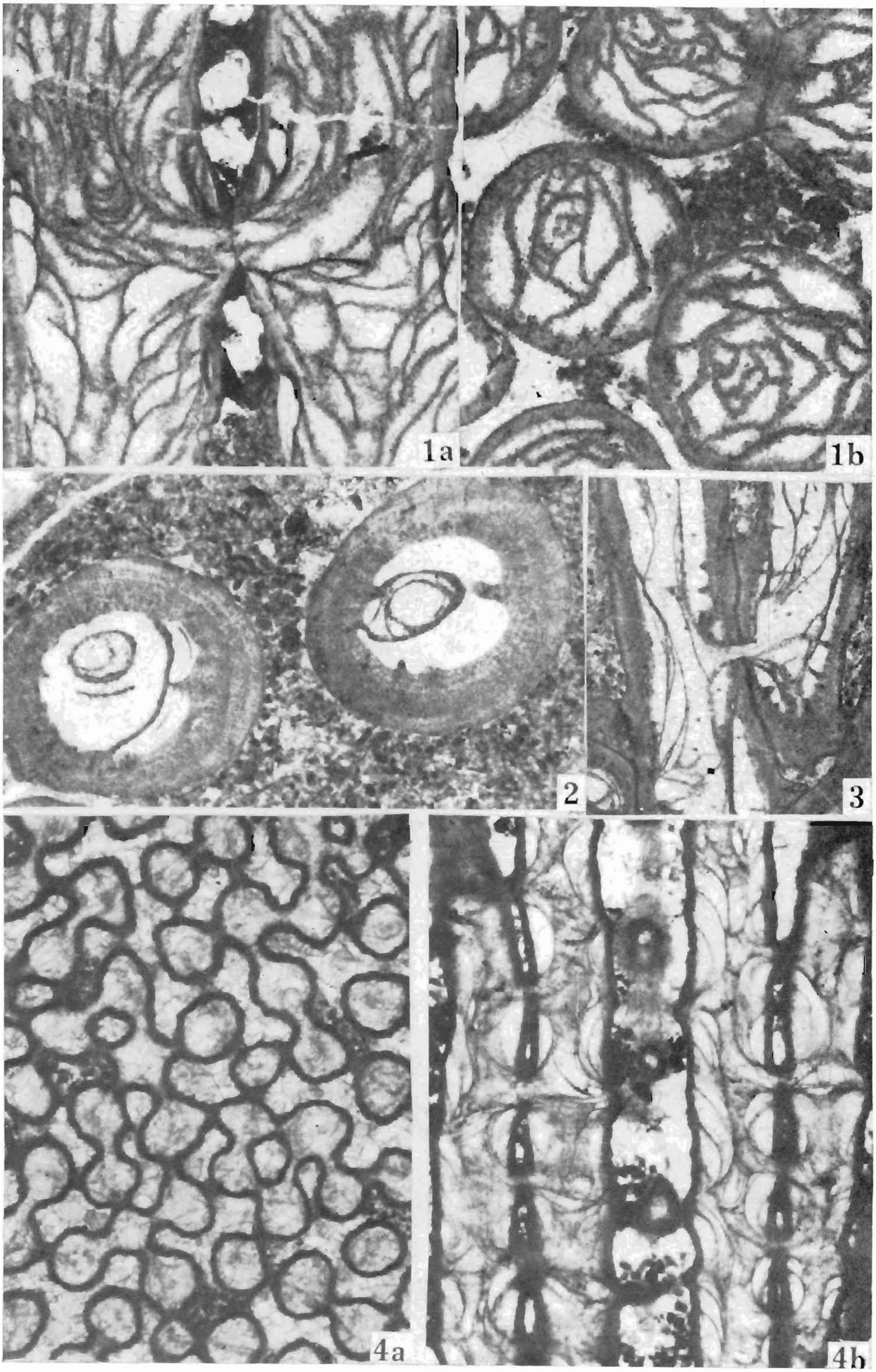
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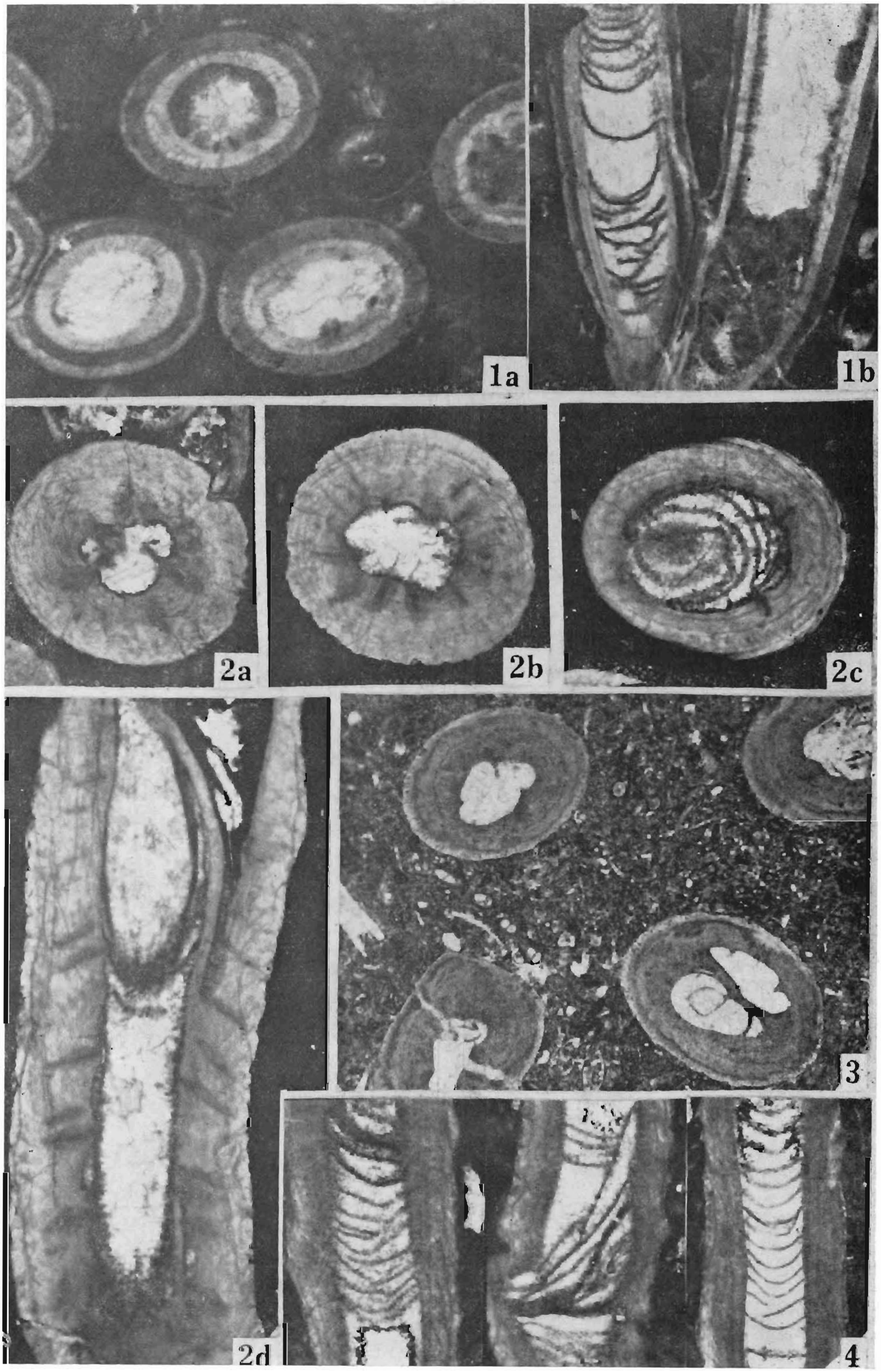
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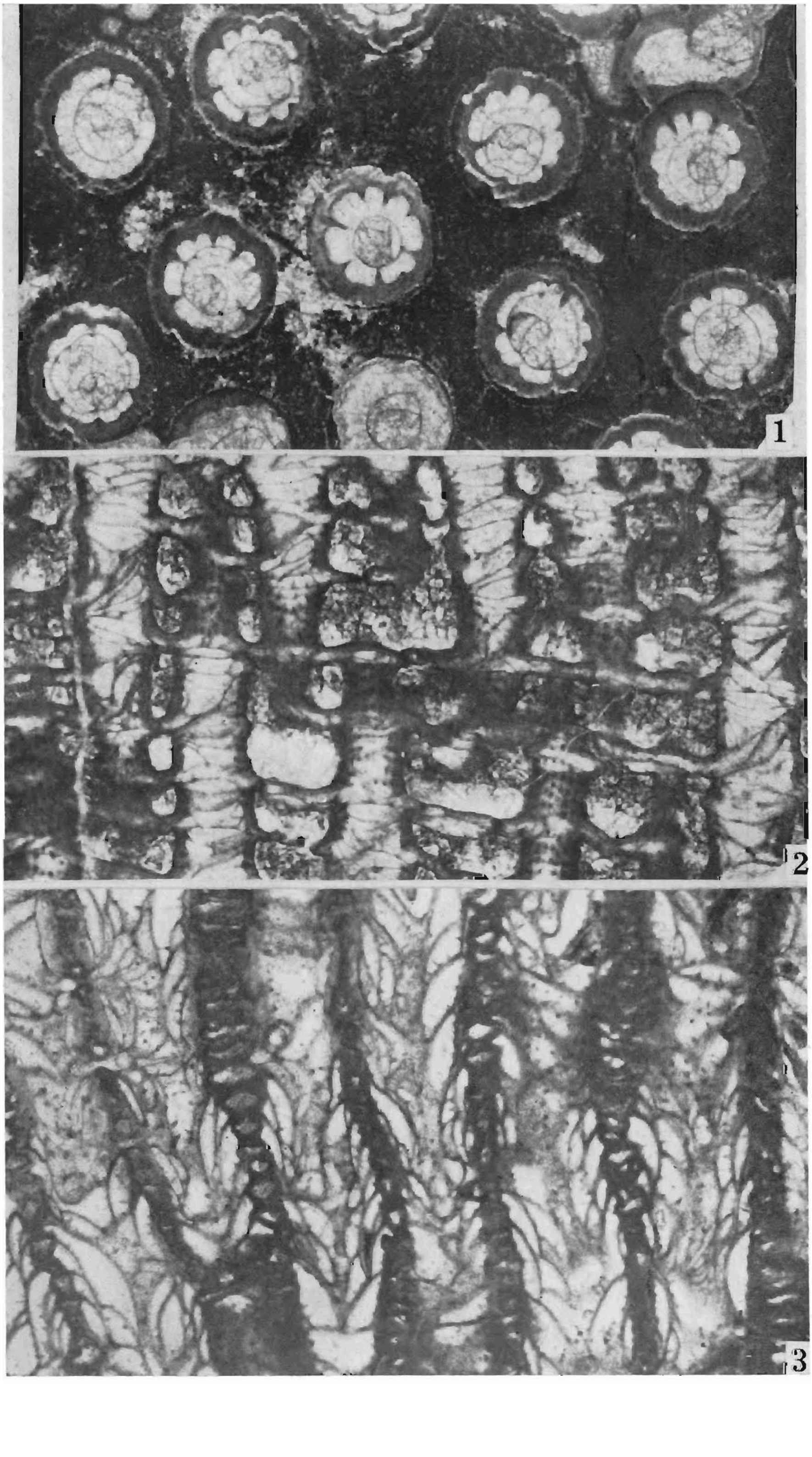
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