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FUNCTIONAL MORPHOLOGY AND SYSTEMATIC POSITION OF TABULATOMORPHS

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Tabulatomorph functional morphology being a reliable guide to locate the group among Metazoa, the authors, who were supplied with an abundant North-African material, offer evidence particularly to compare them with sponges. They provisionally conclude that most of them were allied to primitive sponges and even algae but achieved various differentiations more advanced than any of those.

K e y w o r d s: sponges, Tabulatomorpha, morphology, taxonomy, relationships.

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The recent interpretation as sponges of many multitabular fossils (classified hitherto among either Tabulatomorpha or Ectoprotca) suggests reinvestigation of the functional morphology of some questionable groups.

The tabular structure with tabulae, is also found in Chaetetida: even fossil, they sometimes display spicular rests (Termier and Termier 1977; Kaźmierczak 1979) and have been included in sclerosponges.

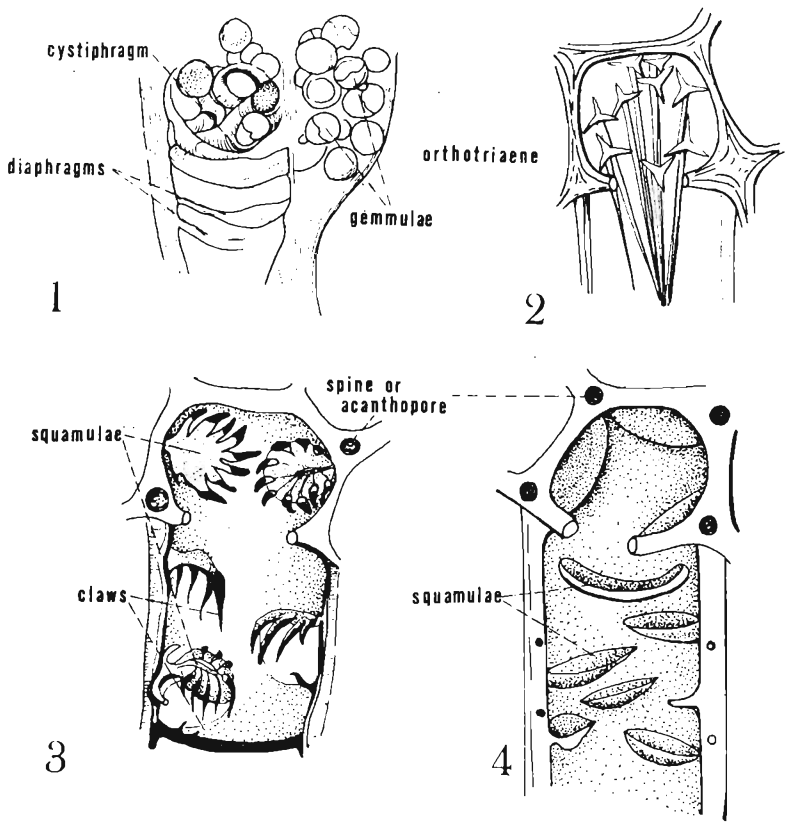
The first tabulatomorphs are Ordovician: Protaraeacea (included in Heliolitida), Tetradiacea and Lichenariida, Halysitacea. Jones and Hill (1940) believe that most of Halysitidae and *Heliolites* were close: blastogenesis, astogenesis and morphogenesis of halysitids are similar to those of Auloporacea.

Heliolitida. — *Laminoplasma* (Bondarenko 1976; Bondarenko and Stasińska 1976) displays a network in which, step by step, subcircular systems appear up to cylindrical tubes surrounding a central mesh. It is the same for *Heliolites* in which septa and spines are in continuity with the tubular system; the skeleton has a fairly labile morphology. Yet the main cylindrical tubes have 12 longitudinally continuous septa, intercalar tubes displaying the same texture. In an adult main tube concave tabulae

are found. It is possible to interpret the main tubes as oscula resulting from a partial resorption of the common meshwork; the lack of any intercalicular pores did not prevent intercommunication between the different parts if this was assumed to be through a superficial living zone, the main tubes possibly devoted to reproduction

Tetradiacea. — Tetradiacea seem to be chaetetid relatives. Yet they display a tetramerous division of the tubes by longitudinal septa; tabulae are facultative. The tubes surround a queer, whitish axial cord sinuous and tubular which is not well defined: here is a similarity with the inner tractus in radial tubes of fossil Hexactinellida. On the Sponge hypothesis, such a whitish tractus might be a manifestation of the choanosomal excurrent flow.

Lichenariida. — Lichenariida are even more similar to chaetetids, displaying tabulae and vesiculae. This initial group, if it is to be considered as a sponge relative, would be strictly of a coenosponge pattern, composed of tubular independent elements born through gemmation. This would explain the late appearance of pores.

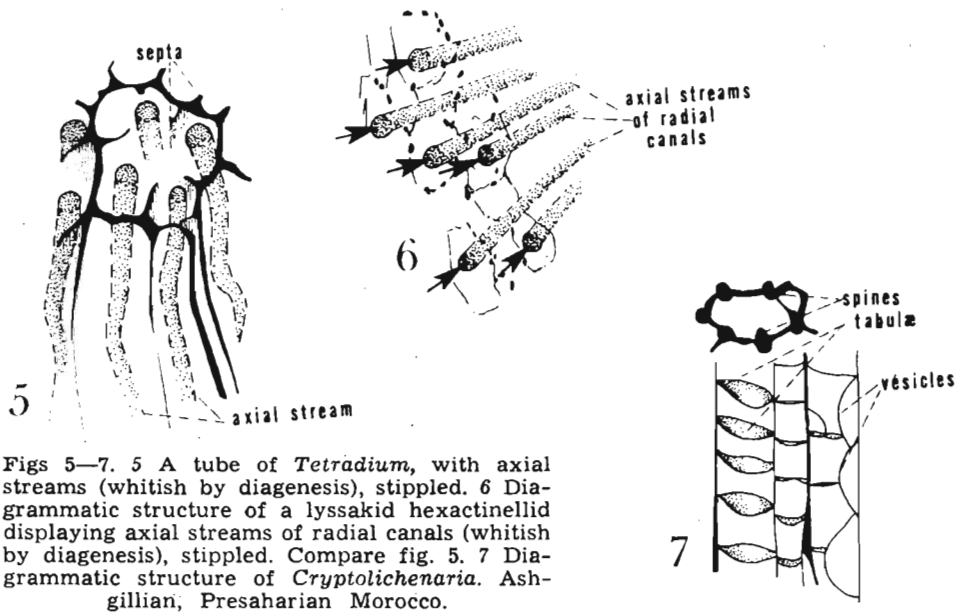


Figs 1—4. *1 Atactotoechus.* Strunian, Central Morocco. Gemmulae in tubes provided with diaphragms and cystiphragms. *2* Orthotriaene spicules in a tube of *Atactotoechus.* Upper Viséan, Libya. *3* Squamulae provided with claws in a tube of *Dekadactylus.* Pragian, Central Morocco. *4* Squamulae ("nidiform expansions") in a tube of *Caliapora,* after Schlüter 1889.

An early development is also that of Auloporacea, which includes archaic types (older and later) in which variegated trends are obvious, maybe owing to a "neotenic" evolution.

II

Trepostomata p.p. — The Trepostomata question is not yet answered. Heteroporids are stenolaemate Ectoprocta which, for Ross (1976), might be no true coelomates but yet possess differentiated tissues and organs, standing therefore for above the sponge status. Still acanthopores and cystiphragms of Trepostomata have no equivalent in heteroporids. Cystiphragms were interpreted as ovicelli by Ulrich



Figs 5—7. *5* A tube of *Tetradium*, with axial streams (whitish by diagenesis), stippled. *6* Diagrammatic structure of a lyssakid hexactinellid displaying axial streams of radial canals (whitish by diagenesis), stippled. Compare fig. 5. *7* Diagrammatic structure of *Cryptolichenaria*. Ashgillian, Presaharian Morocco.

(1900). In a representative of *Atactotoechus* (from Moroccan Strunian) we observed spherical bodies (cysts) which we believe to be survival structures: they are shaped as sponge gemmulae but also look like the cysts described in the dasyclad *Acetabularia* (Marszalek 1975).

Caliaporidae. — Caliaporidae Termier et Termier, 1979 are very close to atactotoechids and stenoporids in their wall structure and angular acanthopores. In *Caliapora* Schlüter, 1885, generally placed among tabulatomorphs between favositids and alveolitids, are observed squamulae (the so-called "nidiform processes") distributed on three columns in each tube and alternating on facing walls. In *Dekadactylus* Termier et Termier, 1979 (Pragian of Morocco), such squamulae display an upper convex part armed with 9—10 finger-like endings with acute claws and holding in the "palm" spherical bodies (interpreted by us as survival structures). *Trachyto-*

echus Duncan, 1939 (Givetian of North America) is a probable relative, in which squamulae are referred to as "fringed curved heterophragms" and, up to now, classified among stenoporid Ectoprocta.

III

Favositida. — In Favositidae, squamulae are found only in a few species. Philip (1960) has shown that these elements are more numerous when the environment undergoes major alternations, their position being controlled by the position in the animal and by the growth rate assessed by the number of tabulae: such features are often associated with the bearing of survival elements.

Striatoporidae. — The Striatoporidae are placed very near to, or even among Favositida. Ramose, they display a cortical part thickly calcified and looking like the mature/immature differentiation in ramose trepostomes. A *Striatopora* relative is *Acaciapora* Moore et Jeffords, 1945, described in Carboniferous and also present in the Middle Devonian of Morocco; lacking tabulae, it has long and numerous squamulae, regularly distributed in "calicular" tubes.

Therefore, in Caliaporidae, affiliated with Trepostomata, Favositidae and Striatoporidae, squamulae seem to hold gemmulae. Still, by their attachment to the wall, they look like "seeds" in a vegetal disposition.

The position of superficial apertures in some striatoporids also suggests a comparison between favositids and sponges. Each tube opens through the thick cortex by a lap-seamed aperture, generally subcircular as in *Striatopora* or slit-like as in *Taouzia* Termier et Termier, 1948, on which converge radial grooves. This model is quite pertinent to the sponge functional morphology, apertures being compared with oscula. Among favositids, some convergence of tabulate tubes into "rhodorhizes" is observed in *Riphaeolites* Yanet, *in* Sokolov 1955, which might be nearer the michelinids (Termier and Termier 1977).

Trachyporidae. — In cross section, *Trachypora* Milne-Edwards et Haime, 1851 is an arrangement of thick-walled tubes around an axial tube, forming ramose and delicate structures. There are neither spines nor tabulae. Some species are similar to stromatoporoids (Carpentier and Pel 1977). Superficially the funnel-shaped tubes are fairly prominent.

From the Pragian of Morocco, we wish to quote two special trachyporids: *Mejdoubia* gen.n. displays vesicular plates between the funnel-shaped tubes which walls are fibro-radiate; *Dualipora* gen.n. displays a thick stereoplasmic filling, pierced by regular tubules between the funnel-shaped tubes. These tubules, which are probably elongated pores, link up the outer surface to the axial tubes and to the interior funnel-shaped tubes; the last disposition is similar to the radial grooves converging on the apertures in striatoporids. Such a differentiation is to be compared to the incurrent and excurrent duality of sponges. Note that both trachyporids do coexist with bunches of tubes which walls are fibro-radiate, in fact more similar to an organism referred by Poncet (1956) to encrusting foraminifera without any pores.

IV

Michelinida. — Apparently favositid relatives, Michelinida might be an early offshoot of Upper Ordovician?-Lower Silurian *Paleofavosites* Twenhofel, 1914, characterized by angular pores, trabecular wall structure and trabecular-sclerodermitic spines widely distributed all over walls and tabulae. The Permian michelinid *Michelinopora indica* (Gerth, 1921) also has angular pores and frequently a sclerodermitic structure.

Pleurodictyidae and Palaeacidae. — Walls are thick and pierced by many labyrinthic canaliculi somewhat similar to a sponge network. These families contain the only examples of Tabulatomorpha displaying a definite number of "calices". Tabulae are all vesicular.

Permosomida. — Some favositids of the Hamilton group display centripetal opercula closing some parts of the tubes (Dunbar 1927). A similar opercular disposition is also known in the Permian and Triassic genera *Permosoma* Jaekel, 1918 and *Khmeria* Mansuy, 1914 which also display vesiculous tabulae and a sclerodermitic structure. Yet *Permosoma* looks very similar to a michelinid. The same structure and vesicles are observed in Permosphincta (sclerodermitic Sphinctozoa deprived of any spicules), particularly in *Cystothalamia* which is provided with the same type of columella as *Permosoma*. In the Permian *Stylonites* Gerth, 1921 such a columella is also present. Permosphinctid cupollae would therefore be permosomid opercula homologues (Termier and Termier 1977). The tubular operculate or cupollate camerae of these genera might have been some kind of silos (Termier and Termier 1979).

Otherwise *Permosoma* opercula look like those of *Goniophyllum* and *Calceola*, a coral group different from Rugosa (Termier and Termier 1948) and displaying some similarities with Spongia or Tabulata, with regard to the canalicules described in the rear part of the skeleton by Lafuste and Semenoff-Tian-Chansky (1968).

V

Merliida. — Similarities have been alleged to afford, on the *Merlia* pattern, a valuable reconstruction of the stromatoporoid- and the favositid-animal (Stearn 1975; Flügel 1976). Nevertheless, *Pachytheca stellimicans* Schlüter 1885 (1889) is the most comparable to *Merlia* (Termier and Termier 1979). Set into the Chaetetida (Sokolov 1955; Hill and Stumm 1956), it is built up from hexagonal complexes of three-cornered fibrous pillars surrounding an axis. And the lumen of these tube-like complexes gets narrowed to a tiny axis as in sectorized tabulae of *Merlia*. In fact *Pachytheca* is a nearer relation of stromatoporoids than chaetetids or favositids, and it is also quite close to *Merlia*.

VI

Syringoporida. — The so-called *"Caunopora"* observed in many stromatoporoids have been assigned to syringoporid symbionts. Meanwhile, in non-symbiotic syringoporids, there are extrathecal formations sometimes very similar to stromatoporids. For example, we must pay attention to the Ordovician Sarcinulacea (Sarcinulidae Sokolov, 1950 and Calapoecidae Raduguin, 1938), to Thecostegidae such as the Devonian *Thecostegites* Milne-Edwards et Haime, 1849 and *Chonostegites* Milne-Edwards et Haime, 1851 and to the Tournaisian *Groessensia* Termier et Termier (*in* Groessens *et al.* 1975). All these forms consist of subcylindrical communicating tubes in which thick walls include vertical sets of calcitic rods (so-called septal spines); otherwise, the tubes are united by external irregular tabulae.

Funnel-shaped inner tabulae of *Syringopora* are somewhat similar morphologically to the trepostomatous cystiphragms and might also assume an incubator or silo-function. Quite close to *Syringopora* in its tube morphology, with walls including calcitic rods and funnel-shaped tabulae, *Syringoalcyon* Termier et Termier, 1945 emend. 1975 displays an outer cuff of calcitic platelets similar to inner calcitic rods.

These examples indicate that syringoporids are far more complex than was initially thought. Tubes are generally apart from exothecal formations, often but not always calcified. Reasoning about caunoporid stromatopores in the symbiotic perspective, nearly all of them would be somewhat affiliated. Perhaps a sounder argument would be that syringoporid tubes were, as in favositids and in trepostomates, important organs associated with the reproductive system.

CONCLUSIONS

We made an attempt to bring together Spongia and Tabulatomorpha (table 1). A major obstacle lies in the diversified terminologies accorded to the several phyla (cnidarians, sponges or ectoprocts) to which each tabulatomorph group has been referred up to now.

Among tabulatomorphs and their relations, four groups display features suggesting some acquaintance with hypercalcified sponges: 1) Chaetetida are certainly Sclerospongia; 2) Permosomida have a few characters in common with such aspiculous sclerosponges as Permosphincta; 3) at least some Trepostomata are probably closer to Chaetetida than to Ectoprocta; otherwise the rare spicules found in them are reminiscent of the tetractinomorph spicules of *Tabulospongia japonica*, an acanthochaetetid; 4) *Pachytheca* is nearer *Merlia* than any other tabulatomorph.

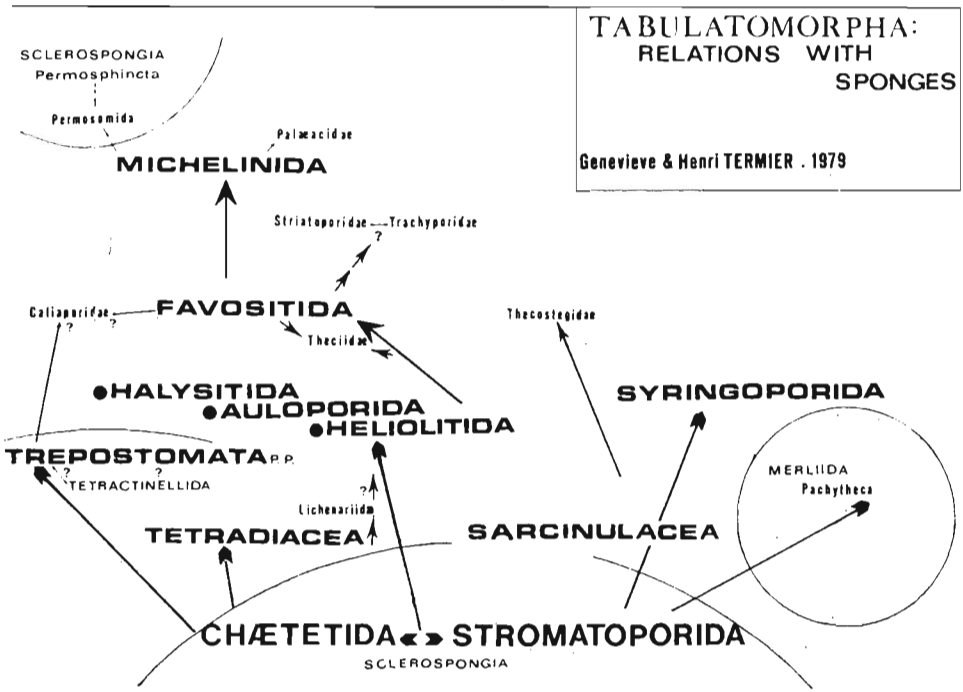
On the other hand reconstruction models based on the *Merlia* pattern have been proposed not only for stromatoporids, which are probably closer to sclerosponges, but also for favositids.

Thus nearly all Tabulatomorpha might somehow or other belong to some Spongia, the reference group being apparently not the same for each of them: this could be explained either by the tabulatomorph polyphyletism or by the fact that

the first of them were contemporaneous with the demosponge diversification. The hypercalcified tabulatomorph skeleton would be retained from an old Cambrian presponge status.

The squamular fastening of survival structures being neither of sponge type nor cnidarian, might be an original specialization from an even more primitive stock, perhaps contemporaneous with the movement of vegetal/animal parting.

Table 1



As a matter of fact many Tabulatomorpha are not mere bundles of tubes but also display some structures indicating that an important part of their life took place in intertubular space, the tubes themselves being probably devoted to the passage of excurrent currents and to breeding.

DESCRIPTIONS

Favositida

Family **Trachyporidae** Waagen et Wentzel, 1886
Genus *Mejdoubia* gen.n.

Species typica: *Mejdoubia vesiculosa* sp.n.; pl. 24: 1—3.
Derivatio nominis: *Mejdoubia* — from the locality of founding, *vesiculosa* (*Lat.*) — provided with vesiculae.

Locus typicus: Central Morocco, Sidi Mohamed Mejdoub.

Stratum typicum: Pragian, Devonian.

Diagnosis. — Branching, slender bundles of funnel-shaped non tabulate tubes, parallel in the inner part, oblique to the surface. Flattened vesiculae between the tubes. No pores.

Comparisons. — Flattened vesiculae may be degenerated crowded tubes the lumen of which is partly or completely obliterated.

Genus *Dualipora* gen. n.

Species typica: *Dualipora preciosa* sp.n.; pl. 24: 4—6, and pl. 25.

Derivatio nominis: *dualis* (*Lat.*) — double, *pora* — pore, opening (two kind of openings).

Locus typicus: Moroccan Presahara.

Stratum typicum: upper part of the Assa series: Upper Emsian. Devonian.

Diagnosis. — Branching, slender bundles of funnel-shaped non tabulate tubes, parallel in the inner part, enlarged and almost perpendicular to the surface and projecting in the outer part. Superficial stereoplasmic thick layer crossed by regularly distributed canaliculate pores, opening from the outer surface into the tubes.

Comparisons. — It differs from *Trachypora* by the presence of the canaliculate, regularly distributed pores rather easy to compare to the sponge functional duality of large oscula and tiny incurrent pores.

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EXPLANATION OF PLATES 24 AND 25

Plate 24

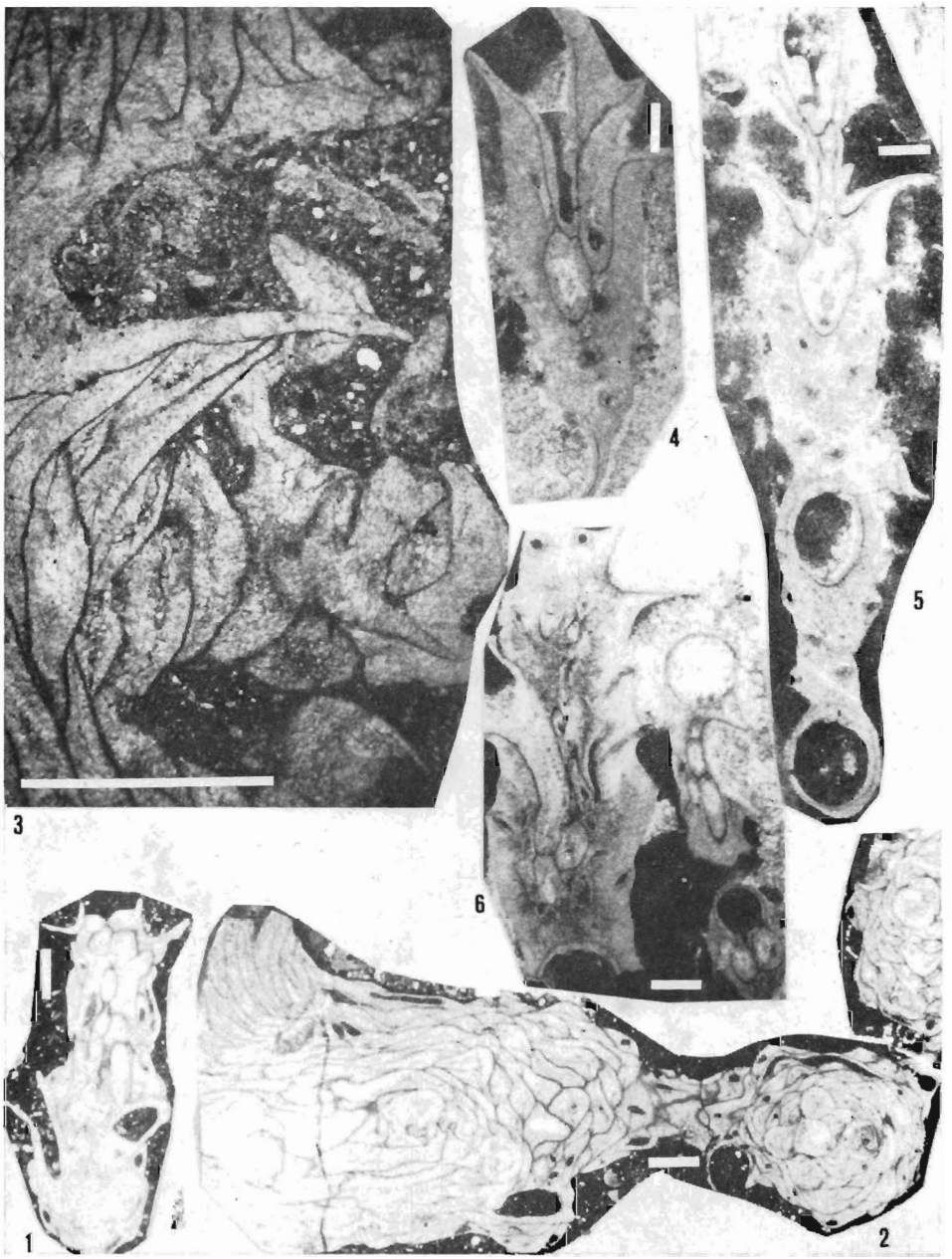
1—3. *Mejdoubia vesiculosa* gen. et sp.n.: *1* longitudinal section showing the funnel--shaped tubes and, between them the vesiculae; *2* transverse section of a branch ing piece; *3* enlarged section of two large funnel-shaped tubes and the vesiculae between them. Holotype: *2*

4—6. *Dualipora preciosa* gen. et sp.n. The sections showing the funnel-shaped tubes and canaliculate pores piercing the stereoplasm and the outer rim of the large tubes. Holotype: *5*

Scale bars 1 mm

Plate 25

Reconstruction of *Dualipora preciosa* gen. et sp.n.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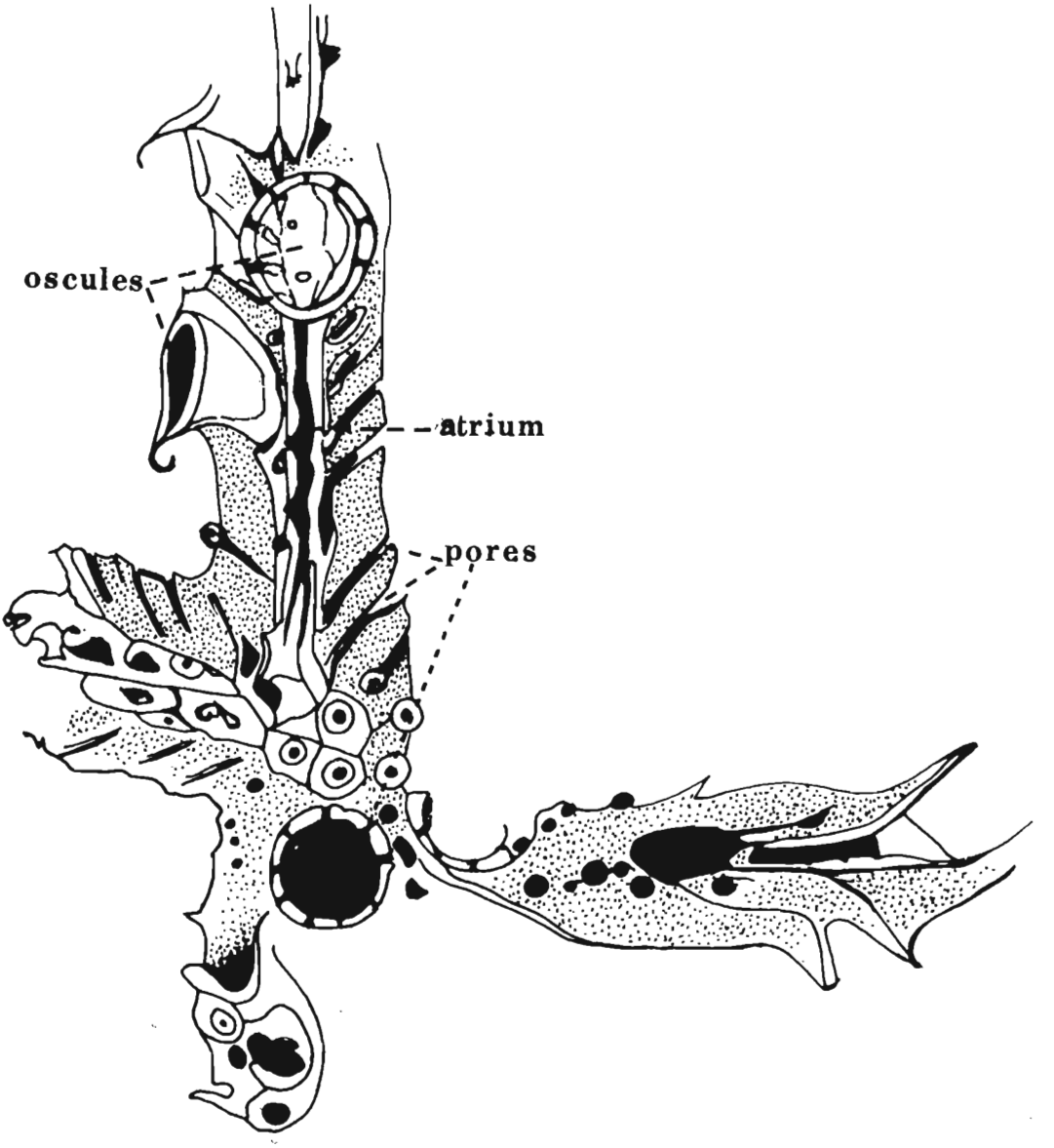

Reconstruction of *Dualipora preciosa* gen. et sp.n.