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Observations on the Moving Colonies of the genus *Tethya* (Demospongia, Porifera)

I. Behaviour and Cytology

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Summary. Observations on two species of sponges, *Tethya seychellensis* from the Red Sea, and *T. aurantium* from the Mediterranean Sea revealed that young colonies are able to detach from their sites of settlement and by means of filamentous podia, to move to other sites in the vicinity. These podia are 10–16 mm long extensions of the sponge body wall that bear an adhesive knob on their distal ends. After being attached, the contracting 'podia' pull the spherical colonies of 2.0–3.0 cm in diameter, transporting them to a new site. EM observations showed that in the podia the matrix is rich in contractile myocytes, primary archaeocytes, nucleated archaeocytes and scleroblastic cells, each of which takes part in the moving ability of the podium. It was also shown that some of the archaeocytes go over a process of ripening within the podium and produce collagenic filaments deposited in the internal matrix.

Introduction

In almost all warm water seas, the sponges form a very important element of benthic sessile communities, and as such have been investigated intensively by many scientists. Recently many investigations of sponges were focused on their biology and biochemistry (Fry 1970; Harrison and Cowden 1976); ecology (Bergquist et al. 1970); and reproduction (Fell 1974; Simpson 1980). In all these publications the absolute sessile life of the adult animals is underlined. So Hyman (1940) opens the description of sponges with the statement 'no adult sponge is capable of locomotion', and Meglitsch (1972) states: 'sponges are motionless'. Observations on sponges of the genus *Tethya* reveal for the first time, as far as I know, that there are exceptions to this absolute rule and that there are sponges that know how to move. This paper describes the movements of these sponges as well as the histological and cytological base of the observed podial extension serving for this.

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Materials and Methods

Two species were investigated: *Tethya seychellensis* (Wright) from the Red Sea, and *T. aurantium* (Pallas), from the Mediterranean and also described from New Zealand (Bergquist et al. 1970). In nature, observations on living and intact colonies of sponges were performed in Eilat, Gulf of Eilat, Red Sea, as well as along some rocky habitats of the Israeli Mediterranean littoral. For observation in captivity, colonies of sponges with attached pieces of rocks, were transported to the marine section, Dept. of Zoology, and placed in glass aquaria of 0.8 m^3 sea water, provided with an internal biological filter, ozoniser and a thermoregulator that kept the temperature around 24° C ($\pm 1.5°$). Illumination was set on a 12 h day/12 h night rhythm. The individually collected colonies measured 10–25 mm in diameter and they recovered quickly after transportation. No special food was provided for the sponges, but as the same aquarium was populated by fish, crinoids, and other animals, and these were fed with a variety of food, it may be assumed that some of this formed also the food-base for the filtering sponges. Evidence for this was the observed flow of water through their oscula, the increase in diameter of the growing colonies as well as the later observed budding and formation of new small colonies, as described by Connes (1967). For histological observations parts of the colonies were fixed in Bouin's and neutral formol. The paraffin sections of 8 μ were stained with Delafield hematoxylin and Mallory Trichrom. For electronmicroscopy whole organisms or parts of them, were fixed for 2 h in 3.5% glutaraldehyde and buffered in 0.1 M cocodylate at pH 7.2. This was followed by postfixation in 2% osmium tetroxide and washing in the same buffer. Those parts were embedded in Epon 812 and sectioned with uranyl acetate and lead citrate. This material was investigated and photographed with a Jeolco B-100 EM. For Scanning electron microscope observation the fixed parts were coated with platinum and observed with a Jeolco JSM-35. The nomenclature used here to describe various cells and cell structures follow, in general, the studies of Simpson (1963, 1973), Lévi (1970) and Harrison (1974), as well as other more general texts. It is not the aim of this work to be involved in the continuous dispute and disagreements of spongiologists as to the origin and fate of all the various cell types observed.

Tethya in Nature

The palaeotropic genus *Tethya* includes several species found in the Mediterranean Sea (Riedl 1963), Japan and Australia, the Red Sea, and Indian and Pacific Oceans. Most of these species are composed of spherical or hemispherical colonies encountered from the most shallow subtidal to 100 m depth (Watanabe 1957; Fishelson 1971). Usually they are found in rocky habitats, growing attached in crevices or on the underneath of stones and corals (Fig. 1). Sometimes, *Tethya seychellensis* was found on deeper, soft bottoms, encrusting shells and pebbles. The biology of *T. aurantium* was described by Lévi (1956) and of *T. serica* from Japan was described by Watanabe (1957). In all observed instances, the attached part of the colony is flattened and almost smooth, whereas the free side is spherical and its surface tuberculate-globular, protected by a layer of protruding monaxon styles. The colonies of *T. seychellensis* (2–6 cm diam.), are orange or orange-red, whereas the Mediterranean *T. aurantium* are reddish-yellow or yellow in colour, and attain 3–4 cm diameter. Both these species usually occur in groups of 2, 3, and more together, and as observed in captivity such aggregations can be formed by budding from larger colonies (See also Lévi 1956), or, as observed by us, by active clumping of moving sponges.

Results

Tethya in Captivity

The recovery of newly transported colonies was a very quick one, and 5–6 h after being placed in the aquarium their lower part start to adhere to the substrate. Tiny extensions are observed to appear 10–18 h later over the animals bodies. In the beginning these are 1–3 mm long and resemble spinous protru-

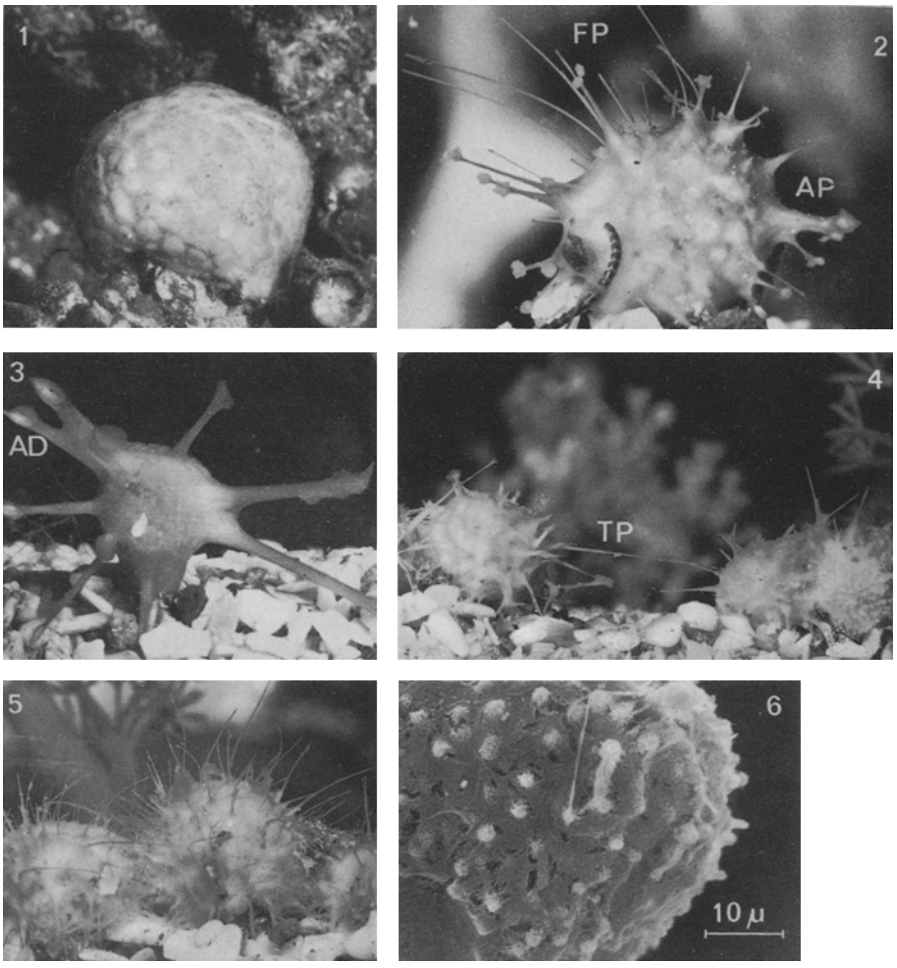

Fig. 1. *Tethya seyshelensis* colony in nature (Red Sea)

Fig. 2. The same colony as in Fig. 1, with podial extensions partly free (*FP*) and partly in stage of adhesion (*AP*)

Fig. 3. Formation of adhesive discs (*AD*) by extensions of *T. seychellensis*

Fig. 4. Touch extensions (*TP*) between settled colonies of *T. aurantium;* the right one formed by two merging colonies (dimension 15–18 mm)

Fig. 5. Continuation of Fig. 4: The three colonies merge into a single large unit

Fig. 6. The knobby end of a podial extension with papule and coating layer

sions, but 10–15 h later, as they become 2–3 times longer, they become elastic and bend in various directions agitated by the water movement. At this stage these extensions resemble some kind of podia or even ambulacral tubes of echinoderms (Fig. 2). The *Tethya* sponges look like some peculiar sea-urchins 34–48 h after introduction, covered by timy extensions 10–16 mm long, sometimes longer than the diameter of the animals' body. They differ from the retractile filaments of *Donatia* (*Tethya*) *deformis* described by Edmundson (1946) from Hawaii. At this stage the distal ends of these podia swell up and become knobby, and an accumulation of cells is observed here (Fig. 2). In these elongated podia the peduncles are very tiny compared with the end parts.

As soon as a long podium touched a solid object, a stone or the glass wall of the aquarium, the terminal swelling became adhesed to the point of contact. Soon after this, modifications are observed in this knob: the adhesed part grows wider and becomes more flattened, changing from round to oval, or spoon-like. As found out, on the attached surface the epithelium extrudes some mucus substance that increases its adhesiveness. In this way adhesive discs of various forms and dimensions slowly emerge, (Fig. 3). Within a short time more podia find their anchorage on the substrate, their peduncles grow thicker and the individual is finally firmly settled on its place. As sections showed at this stage, long monaxon spicules are being deposited within the peduncle. All other non-adhered extensions are now slowly reabsorbed into the sponge body. Such a *Tethya* may remain for a long time (in some cases for 3 months) on the same spot. However, on some occasions, after a short while the settled individual starts to send out numerous new podia, attaching some of them higher or further away from those already attached and then start to move, detaching themselves from the old place. In such instances a sponge can climb up from the bottom or even pass, by bridging with the podia, from one rocky place to another. Observations on *Tethya* from the Red Sea and Meditterranean revealed that those are able to traverse 10–15 mm a day, and during 1 week some of them moved 5–8 cm. The movement is especially fast if other colonies of the same species are found in the vicinity. In such instances some kind of 'touch and approach' reflex is being activated, marked by extension of especially long podia toward the neighbouring colony (Fig. 4). Such approaching colonies can move together, and, as observed on several occasions, can merge into one larger colony (Fig. 5). Such merging of close growing sponges (*Ephydatia*) was observed by Weisenfels and Strigler (1979) and of *Halichondria sp.* by Fell and Jacob (1979). On some occasions, after being close for a while, one of the colonies starts to produce podia and extensions in opposite directions and as a result moves apart from its partners.

Microstructure of the Podia

As mentioned, 24–32 h after being placed in the aquarium, all the colonies were found bearing podia 10–16 mm long and 0.3–1.0 mm wide. The bulky ends of these extensions are covered by numerous, 90–100 μ long and 60–80 μ wide papulae, that are swollen at their distal ends (Fig. 5). Below the very delicate external pinacodermis, these papulae bear layers of euaster microscleres and because of this they look spiny. As revealed by sections, the central part

of the podium is occupied by a gelatinous core surrounded by a layer of cells varying in form and internal structures. Embedded in the gelatinous matrix are many bundles of microfibers, collagenic in nature, 0.2–0.4 μm in diameter. Most of them extend along the podium, radiating obliquely from the center toward the peripheral cell layer (Fig. 16). Also within the gelatinous core and between the fibers cells are dispersed of various form and function. The most numerous of them are primary archaeocytes or collencytes (Lévi 1970) of 15–20 μ diameter (Fig. 7a), recognized by their amoebic shapes and cytoplasma rich in inclusions and granulations. According to Hyman (1940) and many other authors these are primordial cells, progenic to other cells in the sponge body. Spindle-shape myocytes that originate from them are the second type of cells proliferating here. The long axis of these cells extends parallel to the collagenic fibers and is many times longer than the short one (Fig. 7b). In these cells the nucleus, as well as the inclusions, are small compared with those observed in the archaeocytes. Also scleroblast cells are found here, their shape is rounded and more regular, usually with primordial microscleres in their cytoplasma. The so-called 'nucleolate archaeocytes' are the largest cell types found here: they are prominent by their large nucleus, numerous globular vesicles and granulated cytoplasma (Fig. 8). Observations showed that within the podium, these cells undergo a process of ripening during which the initially prominent nucleus disintegrates and the intraplasmatic vacuoles change from granulated to delicate-fibrous (Fig. 9). At a more advanced stage of development of the intravesicular fibrous structures, the vacuole membrane and cell membrane disintegrate. As a result of this process the produced fibrous bundles, each composed of closely packed microfibrils, are now situated within the gelatinous matrix of the podium (Fig. 10). At this stage of investigation it seems that all the fibers of collagenic or sponge-like material, observed within the sponge body and outgrowths, are of this origin, produced by the special type of fibrogenous archaeocytes. This development of microfibrils seems to be in agreement with the description of spongin formation mentioned by Pompini (1976).

The cell layer that surrounds the fibrous core is formed by granulocytes or globiferous cells (Simpson 1963). In these cells the nucleus is undetectable or scarce, they almost constantly have a prominent spherical vesicle and the granulation in them is minute (Fig. 11). Bordering the fibrous core, these granulocytes are sparsely distributed, rounded, or prolonged, 10–12 μm in diameter. Toward the outside, the density of these cells increases, and the granulation within them becomes more pronounced. The most outer part of this 90–120 μ thick layer, is pseudoepithelial in form, the cells here are very dense and compressed, attaining 25–35 μ along their long axis (Fig. 12). The most outer cells, situated subpinacodermic, are bottle-shaped, with elongated neck regions, aggregating toward tubulous passages leading toward the surface. According to various authors (Hyman 1940; Simpson 1963, 1973) these are the so-called gland cells of the sponge body wall that produce a mucopolysaccharide coat over the animal. In *Tethya* as well as in other sponges (Bagby 1970) this cover is also fibrous in nature (Fig. 16).

The pinacodermis or 'epidermis' of the podium is formed by an unicellular, possibly syncytial layer of flat cells, with weakly staining nuclei (see also Junqua et al. 1974; Simpson 1973). This layer is 10–30 μm thick and most of it is

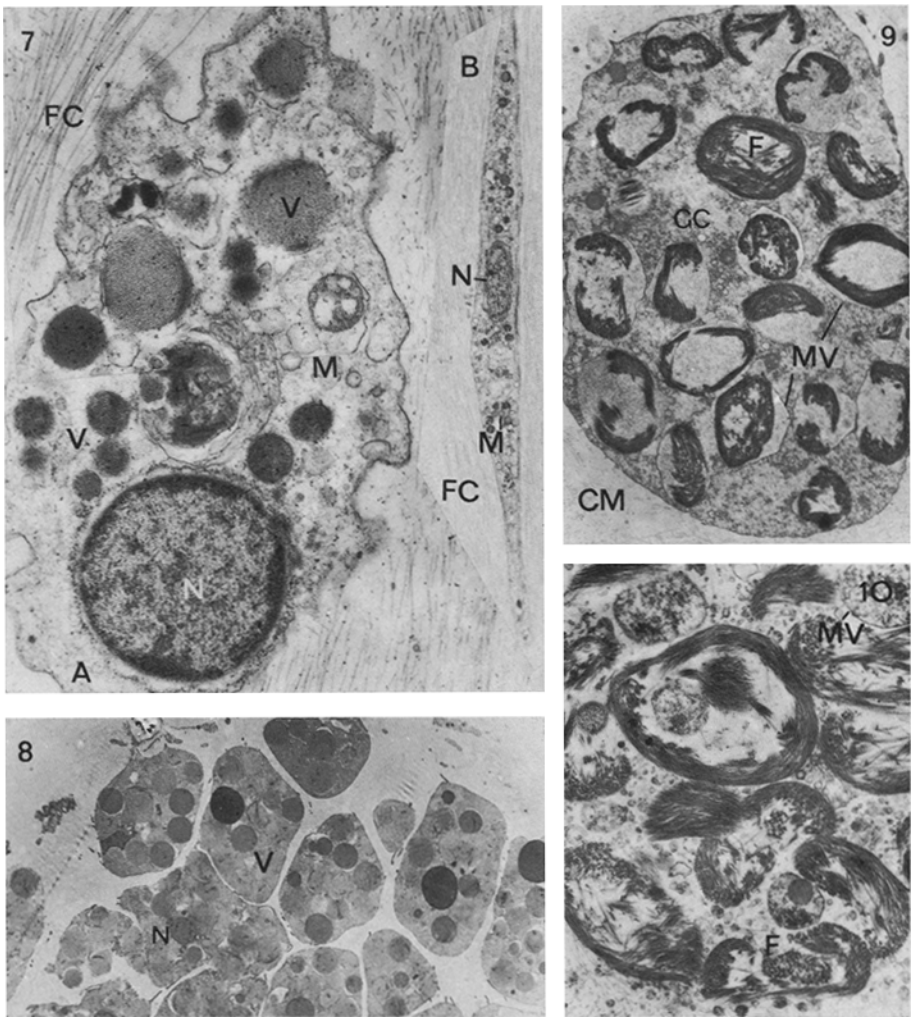

Fig. 7. **A** A primary archeaocyte (×3,000) and **B** a myocyte (×10,000) from the podial extension of T. aurantium: *N*, nucleus; *M*, mitochondria; *FC*, fibrous cortex

Fig. 8. A group of nucleolate archeaocytes: *N*, nucleus; *V*, vacuoles in various stages of ripening (×1,800)

Fig. 9. The development of fiber bundles within vacuoles of fibrinogenous cells; *F*, fibers; *MV*, membrane of vacuole; *GC*, granulated cytoplasma; *CM*, cell membrane (×20,000)

Fig. 10. Final stage of fiber development: *F*, cross and long-sections of fiber-bundles; *MV*, rudiments of vacuole-membranes (×30,000)

occupied by euaster microscleres 10–25 μm in diameter (Fig. 13). On the distal, bulky ends of the podia, these asters are situated densely, over-laying each other (Fig. 14 and 15) but along the podial peduncle they are in a single row, usually irregularly dispersed.

As the knobby end of a podial extension touches a solid object and adheres,

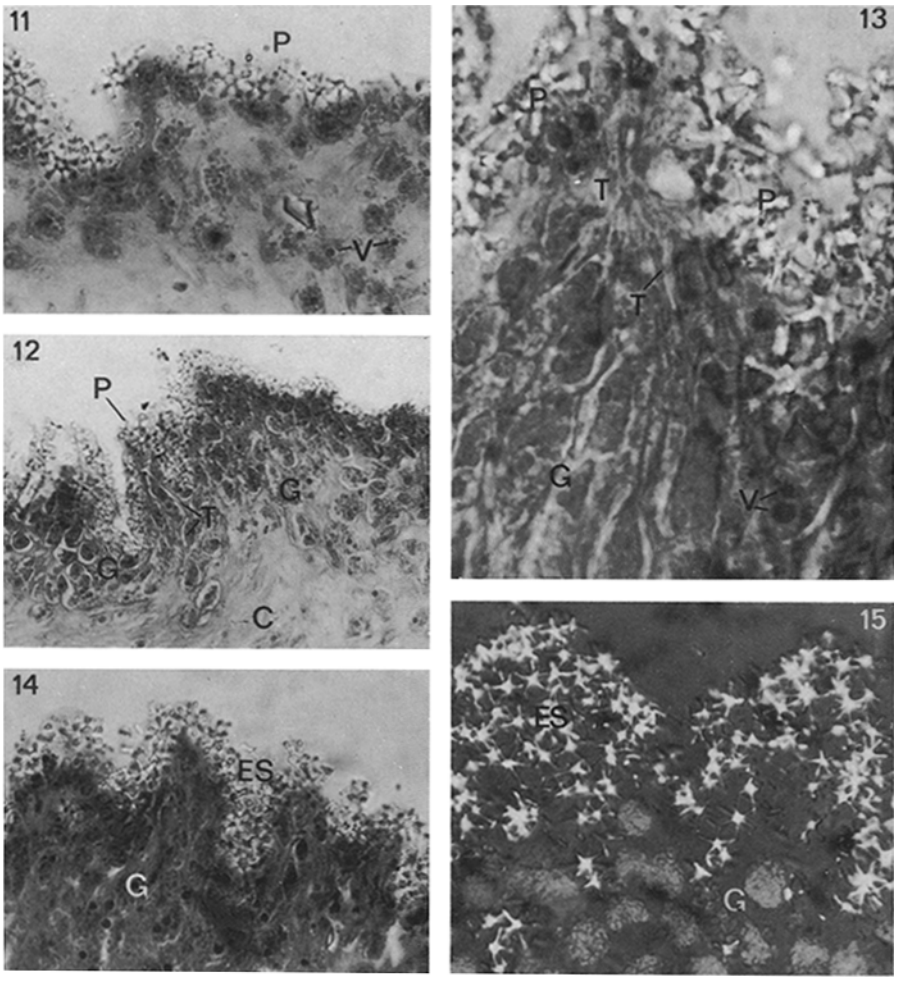

Fig. 11. Longitudinal section of a podial extension: *V*, vacuoles of globiferous cells; *P*, pinacodermis with microasters (× 800)

Fig. 12. Sub-pinacodermal layer of globiferous cells: *G*, globiferous cells; *P*, pinacodermis; *C*, cortex (× 800)

Fig. 13. Gland cells on the adhesive knob: *T*, tubules into which the neck-part of gland cells (*G*) open; *P*, pinacodermis with micrasters (× 1,200)

Fig. 14. Papulae of adhesive knob: Aggregates of gland cells and euasters

Fig. 15. Papulae of adhesive knob: Aggregates of gland cells and euasters

it goes through a histological modification: the adhesed part becomes flattened, the papula disappear on it and together with them the microscleres. In such a way the peripherial pinacodermis of the attached part becomes smooth and forms an adhesive plate, rich in mucus, but with only a few cell elements. Within a day or two, the attachment becomes stronger and needle-like styles

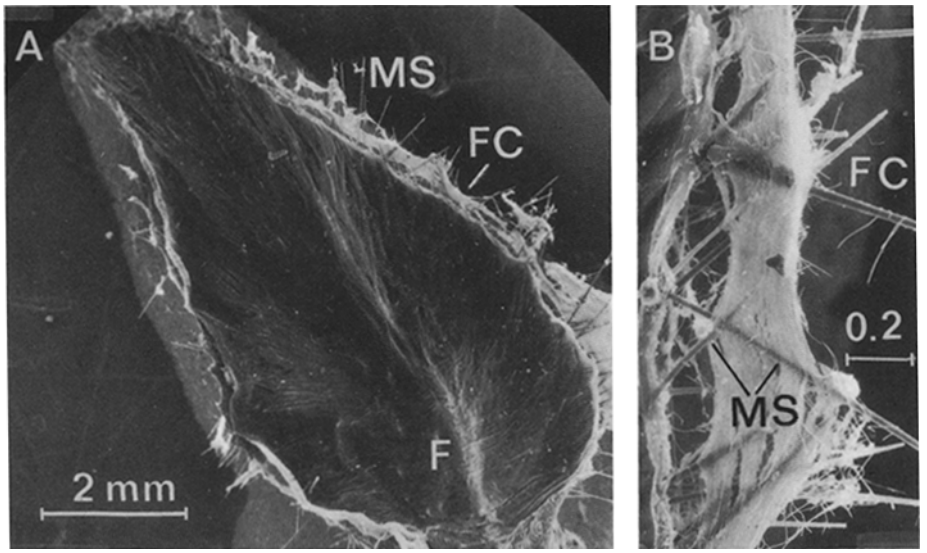

Fig. 16. An adhesive disc of *T. seychellensis: A*, Total from inner-side; *B*, enlarged portion of the marginal region; *FC*, external fibrous coating layer; *F*, fibers radiating toward the periphery; *MS*, monaxon sclerites

(monaxons) develop all along the podium, partly penetrating the pinacodermis and protruding outside (Fig. 16). Now, such an attached podium begins to contract slowly, pulling the body of the sponge toward the point of anchorage. As observed in electron microscopy sections in such contracting and thickening podia, the myocytes are much thicker and shorter than in the expanding one. It seems that these myocytes that are contractile according to Hyman (1940), are the only cytological structures of the podium able to contract and so pull the sponge body. At this stage of settlement, the development of canals lined with choanocytes starts, and in this way those peripheral outcrops become interconnected with the canal system of the sponge body.

With growth of the settled colony, the diameter of the body enlarges and proportionally to this the shortening of the podia occur. In colonies that were in aquarium for almost 1 year, settled in one place, the previous prominent extensions are detectable as small swellings on the flattened, attached side of the animal.

Induction of Movement

Only a few experiments were performed to find out what can induce the movement of a *Tethya* colony. One of these was spreading sand on a part of the colony. Such a cover very soon caused the appearance of podia and onset of detachment and movement. Changes in the intensities of light or mechanical pressure by a shell or pebble did not produce such reactions. So it seems that the resettlement of *Tethya* colonies occurs only when the danger of being buried occurs.

Discussion

Until now Porifera were recognized as a phylum of organisms that after metamorphosis and attaining the adult form, settle down and from this point on, are not able to change site. Only a few of papers discussing sponge biology, show that some postmetamorphic forms are able to glide over the substrate (Levi 1956; Fell 1974) or to move slightly at least in the process of regeneration (Simpson 1963, 1980). The mobility of total sponge colonies, as described here for *Tethya aurantium* and *T. seychellensis* seems to be a unique one, however, it is possible that by looking closer at related species, we will find that this phenomenon is a more common one. That scientists did not expect such a possibility of directional movement is because these animals are lacking well defined organs that from a functional point of view, are needed for such behavior. These are levers to transport the body from one site to the next, and a drive-recognition that will enable the animal to direct the movement in a chosen way. In our *Tethya* colonies both these abilities are found as transitory systems, 'hidden' in adult sponges in a dormant stage. They are activated if the ecological situation demands it. For example, in experiments this occurred as the colony became covered by sediment. As a lever system for transportation, *Tethya* develop podial extensions histologically partly resembling extensions of gemmulae described by Watanabe (1957), filaments of *Donatia* (Edmundson 1946) or regenerative developments as mentioned by Simpson (1973). These podia of *Tethya* are provided with swollen, knobby heads, rich in mucus producing cells. As such a knot touches a hard substrate, it adheres to it, and now, as the podium starts to shorten, all the spherical sponge body is pulled toward the point (points) of attachment. During this process, the ventral sole of *Tethya's* body, lying on the substrate remains unattached, and this enables it to glide. The transporting podia protrude all over the sponge body, and many of them touch the substrate and adhere. However, as in sea urchins, the movement is directed by some external triggers, and as the contracting podia pull in one direction, other opposite directed podia hang free or become torn away from the point of attachment. One of these external attractors seemed to be other colonies of *Tethya*. As shown, in such cases the colony or colonies approach one another and in some cases, this brings them together until they merge. This shows that sponges can recognize the preferred direction of movement. These podia structurally and functionally are different from 'stolons' that form in the process of budding (Bergquist et al. 1970).

As this behavior until now was not observed in nondisturbed colonies, it seems to be some kind of escape mechanism triggered by stress. As a first sign of activation the proliferation of primary archaeocytes or nucleate cells below the external dermis (Simpson 1963) is observed. These 'totipotent' cells (Harrison 1974) form aggregations from which the podia start to develop, and also serve as primordia for several different cell types found here. Three of these cells are the most important:

1. Myocytes: spindle-like cells, resembling smooth muscle cells of other invertebrates. As these are contractile, they seem to be at least partly responsible for the podial shortening. As evidence we find that in contracted extensions the thickness of myocytes is much greater than in extended ones.

2. Fibrogenous cells: these are the cells that develop from nucleolate cells during a process of ripening within the developing podium. As seen in Fig. 6, these are of oval shape and almost totally occupied by large vacuoles. In younger cells the content of these vauoles is microgranular homogenous. At more advanced stages, the contents of the vacuoles become more opaque, and the development of fibrins commences in them. At the final stage of this process, the membranes of the numerous vacuoles and of the cell itself disintegrate, and the bundles of fibers, together with the intermediate substance, is deposited within the gelatinous cortex. So it seems that at least in *Tethya,* the production of fibers is intravacuolic occuring within the fibrogenous cells, and the deposition of them within the cortex of the sponge occurs after the producing cells disintegrate. It seems that also a part of the gelatinous matrix in which the cells and fibers are embedded, are of the same origin.

3. Globiferous or excretory cells: these are the dominant cell part of the dermal (Simpson 1973) or superficial layer of *Tethya.* Most of these cells are bottle-shaped and their necks mount onto the sponge surface, where they extrude a fibrous-adhering substance. This helps to attach the podia to the substrate, as well as covers the sponge body with a coating layer.

These three cell types, that occur in large quantities within the podial extensions form the cytological base for the movement of the colonies. It will be interesting to find out how the already settled *Tethya* colonies liberate their soles and begin to move. The ability to move, especially in smaller colonies is an important adaptation for survival, minimising the role that the larva settlement plays.

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