



**HAL**  
open science

**Glycogen storage and transfer in primitive invertebrates:  
Demospongea and Actiniaria. In: Lévi, C. &  
Boury-Esnault, N. (eds) Biologie des Spongiaires.  
Sponge Biology.**

Nicole Boury-Esnault, Dominique Doumenc

► **To cite this version:**

Nicole Boury-Esnault, Dominique Doumenc. Glycogen storage and transfer in primitive invertebrates: Demospongea and Actiniaria. In: Lévi, C. & Boury-Esnault, N. (eds) Biologie des Spongiaires. Sponge Biology.. Biologie des Spongiaires. Sponge Biology, Claude Lévi & Nicole Boury-Esnault, Dec 1978, Paris, France. pp.181-192. hal-04430095

**HAL Id: hal-04430095**

**<https://amu.hal.science/hal-04430095v1>**

Submitted on 7 Feb 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

GLYCOGEN STORAGE AND TRANSFER IN PRIMITIVE INVERTEBRATES:  
DEMOSPONGEA AND ACTINIARIA

Nicole Boury-Esnault et Dominique André Doumenc  
Muséum national d'Histoire naturelle,  
Laboratoire de Biologie des Invertébrés marins  
57 Rue Cuvier 75005-Paris, France.

Introduction

In the animal kingdom, glycogen is the usual energy source for metabolic and morphogenetic processes. All cells (somatic or germinal) have the capacity to synthesize it (Cage, 1917; Florkin and Scheer, 1968, 1969; de Bruijn, 1973).

In the vertebrates, glycogen storage takes place in the liver where the hepatocytes are concentrated and form an organ. The liver is directly connected to the circulatory system and may discharge glycogen into the bloodstream at any time to meet metabolic requirements or conversely, may remove and store excess glucose.

In primitive invertebrates, there is neither a special organ for glycogen storage nor a circulatory system permitting the contact of cells from one region to another. Thus there is a functional problem for glycogen storage and its transfer to regions of great demand. Glycogen was demonstrated in demosponges by Lufty (1970) and seen in electron microscopy by Lévi (1966) and Boury-Esnault (1977); however no comparative study on the amount of glycogen in the different cellular types during sponge life cycles has been attempted. No studies on glycogen in the Cnidaria have been found, with the exception of isolated cytological observations of the presence of glycogen (Lentz, 1966; Davis, 1973a et b; Chapman, 1974).

Demosponges and actinians have in common some great morphogenetic capabilities which require a large supply of energy chiefly for cellular differentiation. During gametogenesis, asexual reproduction and regeneration the energy requirement increases considerably.

In this study variations in the amount of glycogen in different cell types were analysed during morphogenesis and the cells involved in glycogen metabolism were examined. These cells in demosponges have been described as "gray cells" (Boury-Esnault, 1977) and in actinians as "cellules à aspect de macrophage" (Van Praët and Doumenc, 1975) and amoeboid cells of mesoglea (Doumenc, 1976).

Material and Methods

The following demosponges, used in this study, were collected from littoral or sublittoral zones of the Mediterranean or the French Channel:

*Polymastia mamillaris* (Müller) and *Polymastia robusta* Bowerbank (Hadromerida, Polymastiidae); *Ficulina ficus* (Linné) (Hadromerida, Suberitidae); *Cliona viridis* (Schmidt) (Hadromerida, Clionidae); *Pachymatisma johnstoni* (Bowerbank) (Tetractinellida, Geodiidae); *Hamigera hamigera* (Schmidt) (Poecilosclerida, Anchinoïdae); *Halichondria panicea* Pallas (Halichondrida, Halichondriidae); *Hymeniacidon sanguinea* (Grant), *Hemimycale columella* (Bowerbank) (Halichondrida, Hymeniacidonidae).

The actinians studied came from littoral zones of the French Channel (Dinard and Roscoff). The species studied were:

*Actinia equina*, *Bunodactis verrucosa* (Actiniaria, Actiniidae); *Cereus pedunculatus* (Actiniaria, Sagartiidae).  
*Bunodactis verrucosa* and *Cereus pedunculatus* have symbiotic algae (zooxanthellae) whereas *Actinia equina* does not.

Methods used for studying regeneration of the papilla of the sponge *Polymastia mamillaris* are given in Boury-Esnault, 1976, and methods for the regeneration of the oral disc of *Actinia equina* are in Van Praët and Doumenc, 1975. Ectosome regeneration in the sponge *Ficulina ficus* was studied after amputation of strips 2 cm long, 0,5 cm wide and 1 mm thick. Regeneration of the base of *Cereus pedunculatus* was studied during 3 weeks and regeneration of *Edwardsia* larvae cut in two was also studied. Animals were maintained in conditions of hypoxia, higher temperatures and without nutrient to control the effects of these situations on the synthesis of glycogen. Animals termed "normal sponges and normal actinians" are untraumatized adults capable of reproduction. These animals were fixed either *in situ* or immediately after collection.

Animals were fixed in 2% glutaraldehyde buffered in sodium cacodylate (0,4 M) followed by post-osmification in a 1% solution of osmium tetroxide. They were embedded in Durcupan ACM. Ultrathin sections were double-stained with uranyl acetate/lead citrate (Reynolds, 1963). Glycogen was demonstrated in thick sections by the PAS reaction with the use of dimedone (5,5 dimethyl-1,3-cyclohexanedione) for 3 h at 60° included between the oxidation reaction and the Schiff's reaction and in thin sections by the thiocarbohydrazide-silver proteinate reaction after oxidation by periodic acid (Seligman et al., 1965, modified by Thiéry, 1967) (PATAG). The presence of glycogen was evident after an hour of thiosemicarbazide action; other polysaccharide groups appeared after 18 h of action. Enzymic digestion of glycogen by salivary amylase was done for 3 h at 37° after glutaraldehyde fixation and before post osmification.

The estimation of the amount of glycogen in different cell types was done by counting the number of rosettes in electron-micrographs in each cell type. Counts were always done on sections passing through the cell nucleus. For each example, the amount of glycogen was estimated in more than thirty cells. Results are expressed in the following arbitrary amounts:

- low amount (less than 5 rosettes/cell) +
- moderate amount (5 to 50 rosettes/cell) ++
- high amount (more than 50 rosettes/cell) +++

#### Observations

##### Amount of glycogen in different cell types

A summary of glycogen contents in different cellular types of demosponges and actinians are given in tables 1 and 2 along with a comparison of results from the literature.

Demosponges: in a normal sponge, rosettes of glycogen are present in the cytoplasm of all cells except choanocytes (Tab. 1). The amount of glycogen in archaeocytes, pigmented cells, gray cells and fuschinophil cells is higher than in mecanoocytes (pinacocytes, collencytes, myocytes) and spherulous cells.

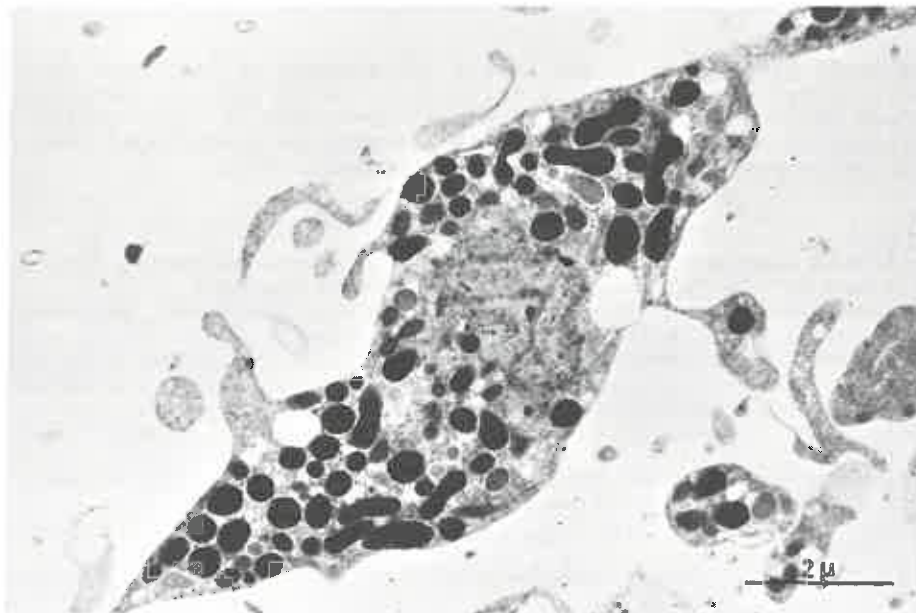


Fig. 1. Fuschinophil cell from *Ficulina ficus* (Demospongea). Normal state.  
I: osmiophilic inclusion; G: glycogen.

The amount in ovocytes and spermatozooids is also high (5 to 50 rosettes/cell). In parenchymella larva (Boury-Esnault, 1976b), the amount of glycogen is low (less than 5 rosettes/cell), but glycogen is present in all cells. In the apical part of the flagellar cells of the larva (part between the exterior of the larva and the flagellar roots) however, there is a higher concentration of rosettes (5 to 20/cell). During metamorphosis, the amount of glycogen increases in sclerocytes and pigmented cells and appears to be moderate (5 to 50 rosettes/cell) in cells which are diffe-

rennated into gray cells. Gallissian and Vacelet (1977) demonstrated an increase in the amount of glycogen in the cells during oogenesis. During regeneration, all sponge cells, including choanocytes, show an increase in their glycogen content. This increase is very strong (more than 50 rosettes/cell) in archaeocytes and particularly in gray cells and fuschinophils cells (Boury-Esnault, 1975a) (fig. 2,3). In zones where gemmules are produced during asexual reproduction, a general increase in glycogen content is observed; but it is especially important in trophocytes (De Vos, 1974) and gray cells (Garrone, 1974). During involution phenomena, glycogen increases in all cells before they lyse (Boury-Esnault, 1977).

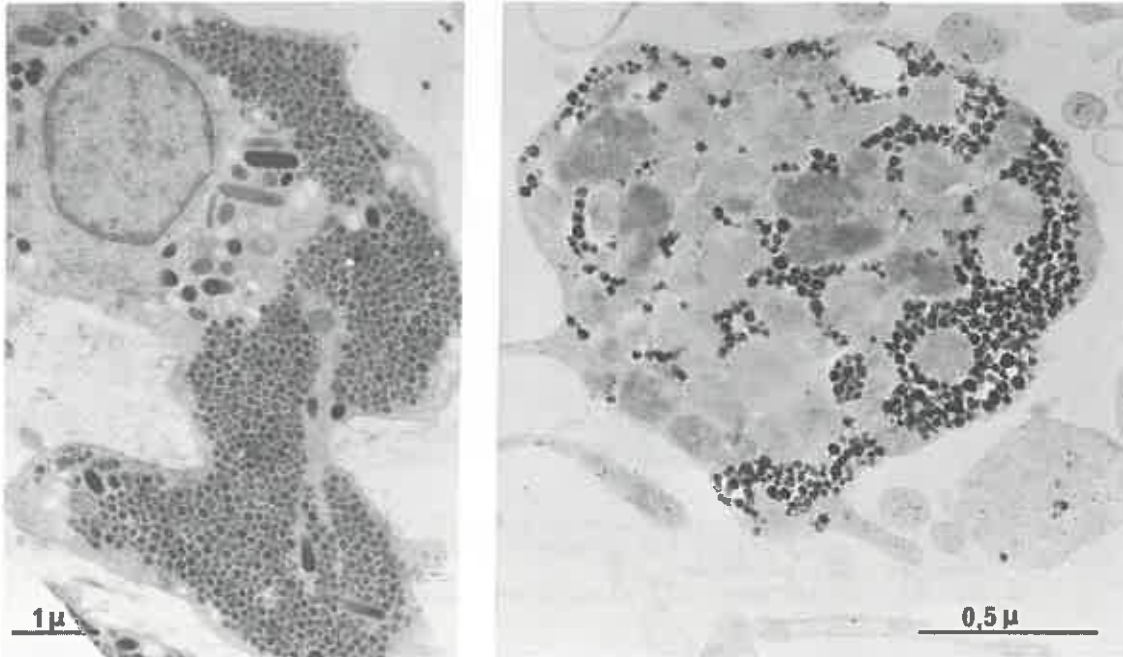


Fig. 2. Gray cell from *Polymastia mamillaris* (Demospongea) during regeneration. Note the high amount of glycogen. G: glycogen.

Fig. 3. Fuschinophil cell from *Ficulina ficus* (Demospongea) during regeneration. G: glycogen.

**Actinaria:** In a normal adult (Tab. 2), all the cells, even secretory cells, store glycogen. There is low amount (less than 5 rosettes/cell) in epithelial ectodermal cells, nemastoblasts and spiroblasts. The axonal prolongation of cells of the ectodermal nervous net and those of endodermal net have a higher amount of glycogen (5 to 50 rosettes). The spindle shaped fusiform cells or myocytes of the ectoderm and the endoderm contain 5 to 20 rosettes in the non-fibrillar region of the cell. Rosettes are clearly visible with the PATAG-reaction.

During the parenchymula stage, the epitheliocytes contain glycogen. During the actinella phase (Doumenc, 1976), the cellular differentiation in myocytes and neurocytes is linked to an increase in the amount of glycogen (to 50 rosettes/cell). Larval glycogen, essentially in the form is always associated with lipid or protein granules. During gametogenesis in *Actinia equina*, endodermal cells, which surround the zone of multiplication of oogonia and spermatogonia, are filled with so much glycogen that the cytoplasm is concealed. These cells are either epithelial or free in the base of the endoderm and the mesoglea (fig. 4a et b). In *Cereus pedunculatus*, the endodermal epithelial cells of fertile mesenteries have a large amount of glycogen (more than 50 rosettes/cell), but not as large as that in *Actinia equina*. Symbiotic algae multiply within the cells to a maximum of 5 algae per host-cell. Many of them appeared lysed.

During oral disc regeneration in *Actinia equina*, an increase of the amount of glycogen was observed in the non-ectodermal and endodermal secretory cells (spumous and granular cells) (5 to 50 rosettes/cell). In the mesoglea of the mesenteries, there are also many amoeboids cells with 5 to 50 rosettes of glycogen (Van Praët and Doumenc, 1975). The increase in the amount of glycogen which occurs during involution induced by unfavourable physiological conditions, is caused by a complete or partial autolysis of the tissue. In *Actinia equina* the appearance of glycogen in tissues is always linked to the presence of phagosomes characteristic of partial

autolysis. Thus, it is not possible to confuse this type of degeneration and the type of structure observed during morphogenesis.

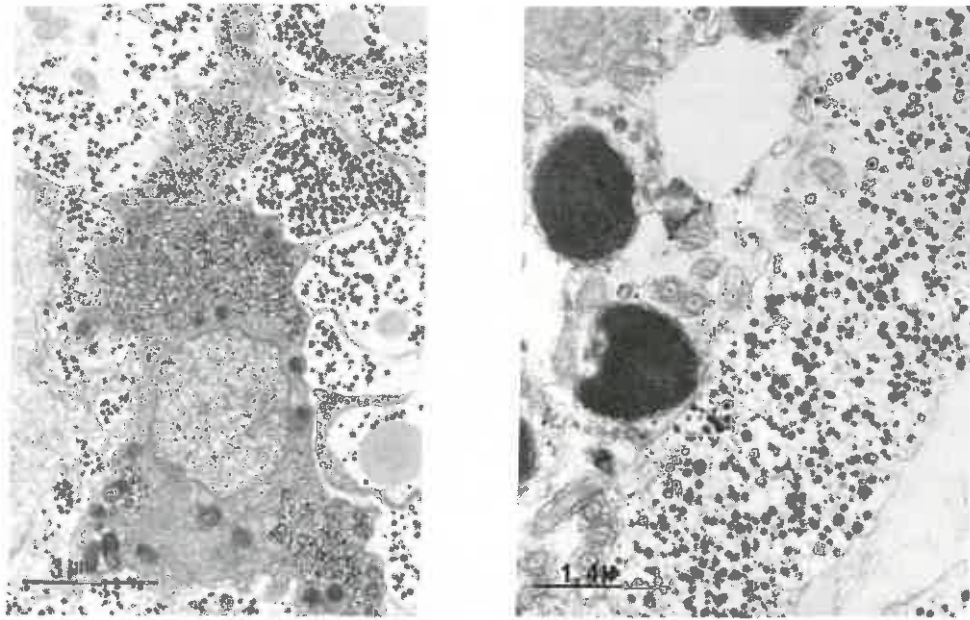


Fig. 4. Spermatogenesis in *Cereus pedunculatus* (Actiniaria).  
a. Endoderm surrounding the spermatogenesis zone. END: endoderm; GLY: glycocyte; MES: mesoglea.  
b. Spermatids (arrows) and glycocytes (GLY).

#### The Glycocyte

The analysis of the amount of glycogen in cells, during normal life and during morphogenesis shows that in Demospongia and Actiniaria, there are particular cells implicated in the metabolism of glycogen.

In demosponges, these cells are the fuschinophil cells in the Suberitidae (Fauré-Frémiet, 1932; work in progress), the trophocytes in the Spongillidae (De Vos, 1974), the gray cells in most of the other demosponges (Boury-Esnault, 1977). In actinians, these cells are some of the mesogleal amoeboid cells in the larvae (Doumenc, 1976) and in adult actinia some cells of the mesoglea with a macrophagic appearance (Van Praët and Doumenc, 1975).

To emphasize the role played by these cells in glycogenesis and without prejudging their origin or their membership to a cell line these cells are given the general name of glycocytes.

Glycocyte morphology. Glycocytes in Demospongia and Actiniaria are cells with glycogen and osmiophilic inclusions in the cytoplasm (fig. 5 et 6). In these animals, the amount of glycogen varies considerably, according to the physiological state of the animal. Glycogen is present in demosponges in the form of  $\alpha$  rosettes; it is present in the glycocytes of Actiniaria in the form of  $\beta$  particles or  $\alpha$  rosettes. Glycogen was demonstrated in thin sections by the PATAG-reaction and digestion by salivary amylase.

Osmiophilic inclusions are ovoid or spherical granules surrounded by a membrane. De Vos (1974) in *Ephydatia fluviatilis* and Van Praët (1978) in *Actinia equina* demonstrated that these cells contain acid phosphatase. Glycolipids are found frequently in these cells (Boury-Esnault, 1977).

Glycocytes have a well developed ergastoplasm and an active Golgi apparatus. In demosponges, the differentiation of glycocytes occurs from the flagellar cells of the larva (Boury-Esnault, 1976b). But it has not been possible to determine from what adult cells they are derived, i.e. no mitosis was seen. In actinians, however, there is an affiliation between cells with a very active ergastoplasm, some rosettes and osmiophilic inclusions occurring at the extremities of the sacculae of the Golgi apparatus and cells with a large amount of  $\alpha$  rosettes, osmiophilic inclusions but without a Golgi apparatus and a visible ergastoplasm (fig. 7).

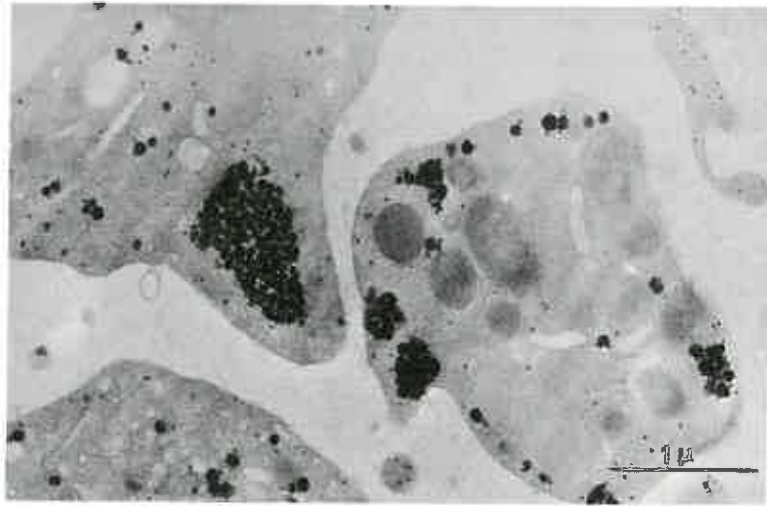


Fig. 5. *Ficulina ficus* (Demosponges): demonstration of glycogen by PATAG reaction in a glycyocyte. Note the membrane surrounding the inclusions (arrow).

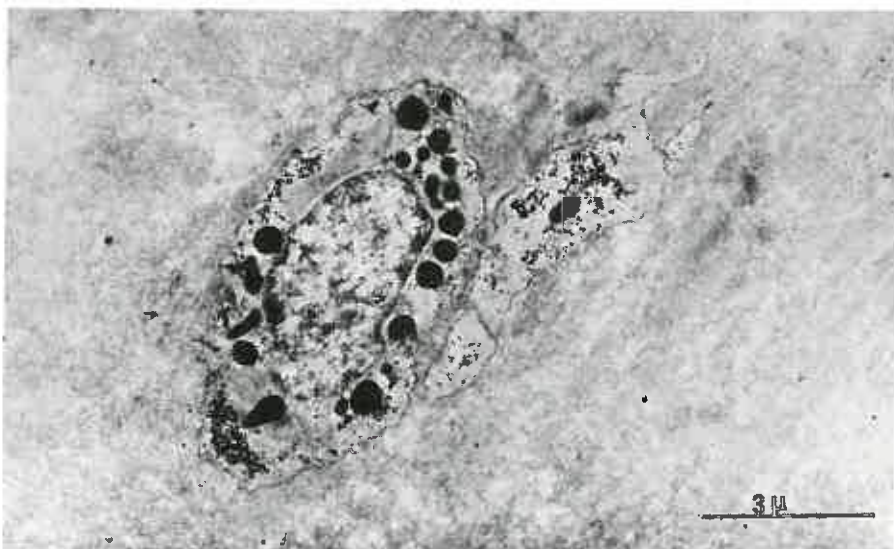


Fig. 6. Glycyocyte in the mesoglea of *Actinia equina* (Actiniaria).

DEMOSPONGES		A	B	C	D	E
PINACODERME	Pinacocytes	+		+	++	++
	Collencytes	+	+	+		++
	Sclerocytes	+	+	++	++	++
	Myocytes	+				+
	Spherulous cells	+	+	+		+
MESOHYL	Gray cells	++		++	+++	+++
	Fuscinophil	} Glycocytes	++			+++
	Trophocytes				+++	
	Archaeocytes		+	+	+	++
	Spermatozooids	++				
	Ovocytes	++				
CHOANODERME	Choanocytes				+	
	Flagellar cells of the larva		++			

Table 1. Glycogen ( $\alpha$  rosettes) contents in different cellular types of demosponges. A: normal state; B: parenchymella larva; C: metamorphosis; D: asexual reproduction; E: regeneration.

ACTINIANS		A	B	C	D
ECTODERM	Flagellar cells	+	++	++	++
	Glangular cells	+	+	+	+
	Nematoblasts, spiroblasts	+	+	+	+
	Myocytes	++	+++	+++	+++
	Neurocytes	++	++	++	++
MESOGLEA	Spermatozooids	++			
	Ovocytes (after vitellogenesis)	++			
	Glycocytes	++	+++	+++	+++
ENDODERM	Epithelial cells	+	++	++	++
	Epitheliomuscular cells	+	++	++	++
	Myocytes	++	++	++	++
	Neurocytes	++	++	++	++
	Gametogenesis zone	+++			
	Zooxantellae (pyrenoid)	+	+	+	+

Table 2. Glycogen ( $\alpha$  rosettes) contents in different cellular types of actinians. A: normal state; B: actinella phase; C: larval regeneration; D: adult regeneration.

The estimation of the amount of glycogen in different cell types was done by counting the number of  $\alpha$  rosettes in electron-micrographs in each cell type.

low amount (less than 5 rosettes/cell) +  
 moderate amount (5 to 50 rosettes/cell) ++  
 high amount (more than 50 rosettes/cell) +++

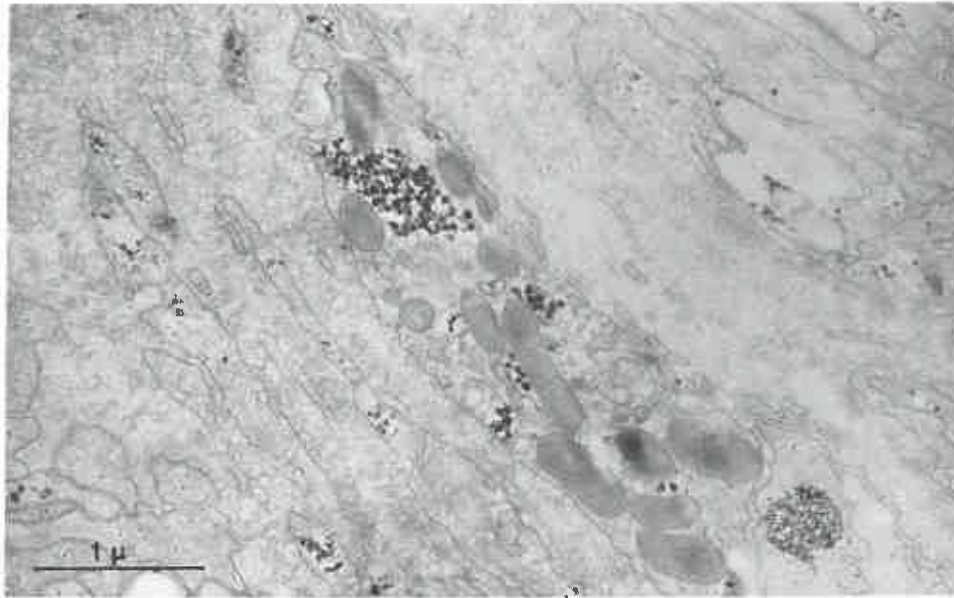


Fig. 7. Glycoocyte in the mesoglea of *Cereus pedunculatus* (Actiniaria) PATAG reaction. Note the presence of osmiophilic inclusions (arrows). MES: mesoglea.

Localisation and behavior of the glycoocyte. In normal conditions, an adult sponge requires energy for cellular turn-over and growth. The glycoocytes are, in that case, few and scattered in the ectosome and the choanosome. Though glycoocytes do not exist in sponge larvae, they are the first cellular type after the pinacocytes to differentiate during metamorphosis. During events where a great energy contribution is needed, glycoocytes always migrate and concentrate in the region concerned and there is a simultaneous increase in glycogen in the cytoplasm. During experimental morphogenesis of papillae in *Polymastia mamillaris*, sieve membranes in *Hamigera hamigera*, and ectosome in *Ficulina ficus*, the regeneration regions contain concentrations of archaeocytes and glycoocytes. Similarly, during gemmulation in *Ephydatia fluviatilis* and *Alectona millaris* the cellular clump consists of archaeocytes and glycoocytes (De Vos, 1974; Garrone, 1974). In these two examples, glycoocytes are phagocytized by archaeocytes either to differentiate or to make reserves in the case of the gemmules (fig. 8).

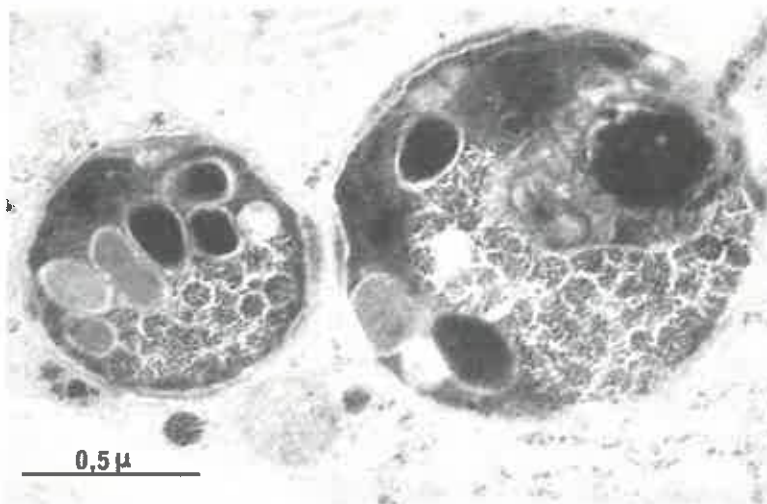


Fig. 8. Phagosomes of a glycoocyte in an archaeocyte. Glycogen and granules are always visible.

In adult actinians under normal conditions, there are few glycoocytes and they



are localized in all muscular tissue. They are present in tentacles of *Actinia equina* between ectodermal myocytes within the mesogleal extension (Van Praët and Doumenc, 1975). Glycoocytes are directly connected to spindle-shaped muscular cells but do not form characteristic connections with them. In the oral disc, glycoocytes are rare and have similar characteristics to those in the tentacle ectoderm. In mesenteries, however, they are numerous, occurring principally in the mesoglea near the muscular cells of parietal and retractor muscles. Here they have the same appearance as those in the tentacular ectoderm. In the reproductive mesenteries of *Cereus pedunculatus* and *Actinia equina*, the development of spermatogonies and their division into spermatocysts is accompanied by a migration of glycoocytes in the cysts. The localized proliferation of glycoocytes is linked with the transfer of ectodermal cells. Glycoocytes play a role in larval development as well. As in most embryonic developments, there is in *Cereus pedunculatus* a two phase metamorphosis. In the parenchymula phase before metamorphosis, no cellular type appears specialized for glycogen storage. Glycoocytes appear only during the actinella stage, after the formation of the first mesenteries, in places where ectodermal myocytes of the tentacular buds, and endodermal myocytes of the retractor muscle are differentiating (fig. 8). During regeneration, a concentration of glycoocytes was observed in the scar region. In *Actinia equina*, 24 hours after cutting off the tentacular crown, glycoocytes appeared in the mesoglea, and played an important role in tissue reorganisation until the third week (Van Praët and Doumenc, 1975). Their numbers decreased progressively to those observed in the normal animal. During experimental regeneration of the foot of *Cereus pedunculatus*, glycoocytes appeared after 48 hours and a large increase in the amount of glycogen in their cytoplasm was observed during tissue organisation.

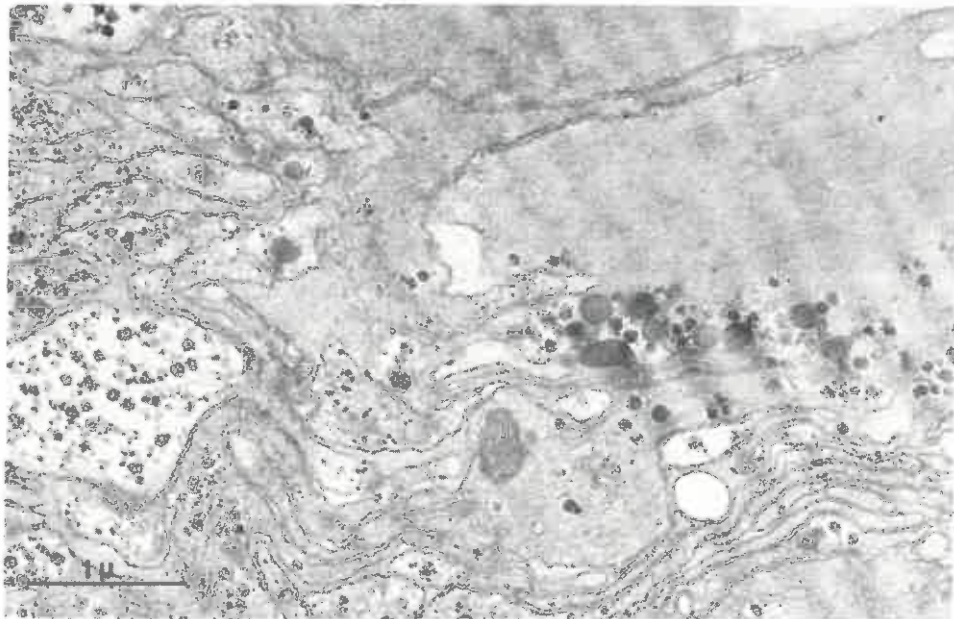


Fig. 9. Embryonic "actinella stage" of *Cereus pedunculatus* (Actiniaria).  
Note the presence of glycogen and osmiophilic inclusions inside the myocyte.  
MYO: myocyte; NC: nerve cells.

#### Discussion

##### Glycogen storage

During normal life. The cells of Demospongia and Actiniaria can store glycogen. In characteristic cellular types such as coating cells, nervous or muscular cells, the amount of glycogen is absolutely comparable with that in equivalent cells in other vertebrate and invertebrate groups. The distribution of glycogen in pinacocytes of demosponges and flagellar epithelial cells of actinians is similar to that described in epithelial tissue of nematodes (Wright and Dick, 1972), annelids (Coulon and Thouveny, 1974) and pogonophores (Southward, 1973). The amount of glycogen in endodermal epitheliocytes of actinians is also comparable with that in the gastroderm of turbellaria (Jennings, 1968) and nematodes (Wright and Dick, 1972) and in the intestine of echinoderms (Doezema, 1969) and peritoneal cells of pogonophores (Southward, 1972). Conversely, the choanocytes, functionally equivalent in demosponges to the endodermic coating cells of other invertebrates, do not have glycogen. The concentration of glycogen in muscular cells is linked to higher levels of activity.

Demosponges are not particularly active animals and the myocytes contain little glycogen (less than 5 rosettes/cell). In actinians, glycogen in the longitudinal musculature is present in larger quantities in the  $\alpha$  and  $\beta$  forms (5 to 50 rosettes/cell). The presence at the same time of  $\beta$  particles and  $\alpha$  rosettes could be linked to a double system of slow and quick contraction, as in *Stomphia coccinea* (Amerongen and Peteya, 1976).  $\beta$  particles could be used for quick contraction;  $\alpha$  rosettes, in this case, could be the storage form. Very similar phenomena have been observed in the musculature of the body wall of nematodes (Wright and Dick, 1972). Glycogen has also been observed in axonal prolongations of the neurocytes of actinians. Highly differentiated cells such as neurocytes can possess glycogen as has been described in the brain of chickens (Gage, 1917; Marmo and Castaldo, 1973) and the brain of mammals (Shimizu, 1977).

In some actinians (*Cereus pedunculatus*, *Bunodactis verrucosa*), glycogen may be provided by symbiotic algae (Zooxanthellae). In *Actinia equina* (without Zooxanthellae) the endodermal cells of mesenteries, in which the gonads develop, have more glycogen than the same cells in *Cereus pedunculatus* (with Zooxanthellae). Isotopic labelling techniques have demonstrated that symbiotic algae may transfer polysaccharides or glycerol to the cytoplasm of host cells in actinians, Zoanthids and corals (Muscatine, 1967, 1974; Trench, 1971a et b; Von Holt, 1968). In *Cereus pedunculatus*, this transfer is made either by direct transfer or by phagocytosis of Zooxanthellae. The algae accumulate polysaccharides in their pyrenoids (positive reaction with PA-TAG) resulting in considerable storage of glycogen. Similarly, the numbers of Zooxanthellae increase considerably in the host-cells of gametogenesis zones, where they often have a lytic appearance.

During morphogenesis. During morphogenesis, which involves a large energy demand, important variations in the amount of glycogen were observed. Asexual, reproduction, regeneration, gametogenesis are linked with an increase of glycogen in all cellular categories. The significance of this is that when a sponge or an actinian is faced with an event that demands greater energy production, the cell population responds by synthesizing more glycogen.

The increase of glycogen in cells during phenomena like gametogenesis (in demosponges and actinians) and gemmulogenesis (in demosponges) has been also described in genital organs of prosobranch mollusks (Chatterjee and Ghose, 1973), oogenesis in sea urchins (Tsukahara, 1971) and coelomocytes of annelids (Dales, 1969). In all cases of vitellogenesis, glycogen along with lipid is one of the forms of energy storage in the ovocyte. This energy is used during division and differentiation phases. In *Cereus pedunculatus*, the energy needed for differentiation of muscular cells during the actinella phase is provided by the large amounts of glycogen of vitelline origin accumulated in the cytoplasm; the glycogen is distributed in the different cellular categories after delamination (Dommenc, 1976). The glycogen stored in spermatozooids is the energy source used for locomotion (Tuzet *et al.*, 1970; Anderson and Personne, 1970).

The increase of glycogen that appears in whole cells of blastema (during regeneration of the papilla of *Polymastia mamillaris*, the sieve of *Hamigera hamigera*, the ectosome of *Ficulina ficus*, the oral disc of *Actinia equina* and the foot of *Cereus pedunculatus*) is very similar to that observed during regeneration of tentacles in Arionidae and Lunacidae (Chetail, 1963). As early as the first hours after excision an intense glycogenesis supplements the energy requirement of the differentiation phase.

#### Glycogen transfer

In demosponges and actinians, glycogen transfer is realized by a cellular type, which is essential during morphogenesis. The name glycocyte is proposed for this cell type.

A morphological analogy was observed between glycocytes from Demospongia and Actiniaria. In these two cases, these cells were characterized by a large amount of glycogen and the presence of osmiophilic inclusions in their cytoplasm. These inclusions are similar ultrastructurally as well as histochemically and they contain acid phosphatases and glycolipids. Their Golgian origine was observed in two cases. But their significance remains unknown.

These cells react similarly during morphogenesis. They can migrate from all tissue to the morphogenesis zones where glycogen is needed. The problem of the absence of a specialized organ (as the liver of vertebrates, the hepato-pancreas of mollusks (Bennet and Nakada, 1968), the posterior intestine of echinoderms (Doezema, 1969) and the pyloric gland of ascidians (Ermak, 1977; Gaill in press) ) and the absence of a circulatory system, have been solved by demosponges and actinians in a similar way: the glycogenic function is performed by cells able to react at any

moment to a demand by increasing their capacity for glycogen synthesis and by migrating to the zones of demand. Thus glycocytes are found near the longitudinal musculature, in vitellogenesis zones during sexual or asexual reproduction and in regenerative blastema.

The passage of glycogen, from glycocytes to recipient cells is either direct, by intermembranary diffusion as probably in the case of the differentiation of muscle in actinians, or by phagocytosis of glycocytes by archaeocytes in demosponges which may use this energy to differentiate.

#### Conclusion

During the normal life of a sponge or an actinian, the metabolism is weak and each cellular category supplies its own needs. During events requiring particularly large energy contribution, however, there is in these two cases a new cell system: the glycocyte. These cells are not only able to synthesize glycogen in large amounts but also can carry it by migration to the zones of demand.

The second ability is quite original and it is considered that these cells represent a scattered organ able to respond to the same stimulus. In more evolved phyla these cells are grouped in an organ and are in contact by means of a circulatory system. The scattered organ represented by the glycocytes in sponges and actinians show the importance of glycogenesis in the more primitive phyla of the animal kingdom.

#### Acknowledgements

We gratefully acknowledge Dr. C. Wilkinson for his assistance in revising the manuscript.

#### References

- Amerongen, H.M., Peteya, D.J. 1976. The ultrastructure of the muscle system *Stomphia coccinea* in Coelenterate ecology and behavior". edited by G.O. Mackie. Plenum Press. New York and London, 541-547.
- Anderson, W.A., Personne, P. 1970. The localization of glycogen in the spermatozoa of various invertebrate and vertebrate species. J. Cell. Biol., 44, 29-51.
- Bennet, R., Nakada, H.I. 1968. Comparative carbohydrate metabolism of marine molluscs. I. The intermediary metabolism of *Mytilus californianus* and *Haliotis rufescens*. Comp. Biochem. Physiol., 24, 787-797.
- Boury-Esnault, N. 1975. Les cellules de l'ectosome des Démonesponges: distribution, morphologie, origine, fonction. Thèse Doctorat Etat Université Paris VI. n° CNRS - AO 11524.
- Boury-Esnault, N. 1976a. Morphogénèse expérimentale des papilles inhalantes de l'éponge *Polymastia mamillaris* (Müller). Archs Zool. exp. gén., 117 (2), 181-196.
- Boury-Esnault, N. 1976b. Ultrastructure de la larve parenchymella d'*Hamigera hamigera* (Schmidt) (Démonesponge, Poecilosclerida). Origine des cellules grises. Cah. Biol. mar. 17, 9-20.
- Boury-Esnault, N. 1977. A cell type in Sponges involved in the metabolism of glycogen: the gray cells. Cell Tiss. Res., 175, 523-539.
- De Bruijn, W.C. 1973. Glycogen, its chemistry and morphologic appearance in the electron microscope, I. A modified  $O_8O_4$  fixative which selectivity contrasts glycogen. J. Ultrastruct. Res., U.S.A., 42 (1-2-, 29-50.
- Chapman, D.M. 1974. Cnidarian histology in Coelenterate biology Reviews and New perspectives Ed. Muscatine L., Lenhoff H.M., 1-36.
- Chatterjee, B., Ghose, K.C. 1973. Seasonal variation in stored glycogen and lipid in the digestive gland and genital organs of two freshwater prosobranchs. Proc. Mal. Soc., London, 40 (5), 407-412.
- Chétail, M. 1963. Etude de la régénération du tentacule oculaire chez un Arionidae (*Arion rufus* L.) et un Limacidae (*Agriolimax agrestis* L.). Arch. Anat. microsc. morph. exp., 52, 129-203.
- Coulon, J., Thouveny, Y. 1974. Etude ultrastructurale de la différenciation cellulaire dans la régénération antérieure de l'Annélide: *Owenia fusiformis* (Delle Chiaje). I.

- L'épiderme (phénomène d'autophagie). Ann. Emb. Morphogen., 7, 61-79.
- Dales, R.P. 1969. Respiration and energy metabolism. Chemical Zoology, 4, 93-107. Ed. Florkin and Scheer. Academic Press.
- Davis, L.E. 1973a. Histological and ultrastructural Studies of the basal disk of *Hydra* I. The Glandulomuscular cell. Z. Zellforsch., 139, 1-27
- Davis, L.E. 1973b. Histological and ultrastructural studies of the basal disk of *Hydra* II. Nerve Cells and other epithelial Cells. Z. Zellforsch., 139, 29-45.
- Doezema, P. 1969. Carbohydrates and carbohydrates metabolism of Echinoderms. Chemical Zoology, 3, 101-119. Ed. Florkin and Sheer. Academic Press.
- Doumenc, D.A. 1976. Etude ultrastructurale des stades parenchymula et actinella de l'actinie *Cereus pedunculatus* Pennant. Archs Zool. exp. gén., 117 (3), 295-324.
- Ermak, T.H. 1977. Glycogen deposits in the pyloric gland of the Ascidian *Styela clava* (Urochordata). Cell Tiss. Res., 176, 47-55.
- Fauré-Frémiet, M.E. 1932. Morphogénèse expérimentale (reconstitution) chez *Ficulina ficus* L. Archs Anat. microsc., 28 (I), 1-80.
- Florkin, M., Scheer, B.T. 1968. Chemical Zoology. II. Porifera, Coelenterata and Plathelminthes. Academic Press.
- Florkin, M., Scheer, B.T. 1969. Chemical Zoology. III. Echinodermata, Nematoda and Acanthocephala. Academic Press.
- Gage, S.H. 1917. Glycogen in the nervous system of vertebrates. J. Comp. Neurol., 27, 451-463.
- Gaill, F. Glycogène et dégénérescence dans la glande polyrique de *Dendrodoa grossularia* (sous presse).
- Gallisian, M.F., Vacelet, J. 1976. Ultrastructure de quelques stades de l'ovogenèse de Spongiaires du genre *Verongia* (Dictyoceratida). Annls Sc. nat., 18 (4), 381-404.
- Garrone, R. 1974. Ultrastructure d'une "gemmule armée" planctonique d'éponge Clonidae. Inclusions fibrillaires et genèse du collagène. Archs Anat. microsc. Morph. exp., 63, 163-182.
- Jennings, J.B. 1968. Platyhelminthes, Mesozoa. II. Nutrition and Digestion in Chemical Zoology, 2, 305-323. Ed. Florkin and Scheer. Academic Press.
- Lentz, Th.L. 1966. The cell biology of Hydra. Ed. North-Holland Publishing Company. Amsterdam.
- Lévi, C. 1966. Le glycogène chez les Spongiaires. C. R. Soc. Biol., Paris, 160, 651-652.
- Lufty, R.G. 1960. Histochemical studies on glycogen in the cells of the fresh water sponge *Ephydatia fluviatilis*. La Cellule, 61, 145-149.
- Marmo, F., Castaldo, L. 1973. On the presence of glycogen in the rhombencephalon of chick embryos during development. Experientia, 29, 854-856.
- Muscatine, L. 1961. Symbiosis in marine and freshwater coelenterates. In the biology of *Hydra*. Ed. Lenhoff and Loomis. 255-268.
- Muscatine, L. 1965. Symbiosis of *Hydra* and Algae. III. Extracellular products of the algae. Comp. Biochem. Physiol., 16, 77-92.
- Muscatine, L. 1967. Glycerol excretion by symbiotic algae from corals and *Tridacna* and its control by the host. Science, 156, 516-519.
- Muscatine, L. 1974. Endosymbiosis of Cnidarians and algae in "Coelenterate Biology, Reviews and new Perspectives". edited by Muscatine L. et H. Lenhoff, IX, 359-395.
- Seligman, A.M., Hanker, J.S., Wasserkrug, H., Dmochowski, H., Katzoff, L. 1965. Histochemical demonstration of some oxidized macromolecules with thiocarbohydrazide (TCH) or thiosemicarbazide (TSC) and osmium tetroxide. J. Histochem. Cytochem., 13, 629-639.

- Shimizu, N. 1955. Histochemical studies of glycogen of the area postrema and the allied structures of the mammalian brain. J. Comp. Neurol., 102, 323-339.
- Southward, E.C. 1973. The distribution of glycogen in the tissues of *Siboglinum atlanticum* (Pogonophora). J. mar. biol. Ass. U.K., 53, 665-671.
- Thierry, J.P. 1967. Mise en évidence des polysaccharides sur coupes fines en microscopie électronique. J. Microscopie, 6, 987-1018.
- Trench, R.K. 1971a. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. I. The assimilation of photosynthetic products of zooxanthellae by two marine coelenterates. Proc. Roy. Soc., ser. B, 177, 225-235.
- Trench, J.P. 1971b. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. II. Liberation of fixed  $^{14}\text{C}$  by zooxanthellae in vitro. Proc. Roy. Soc., ser. B, 177, 237-250.
- Tsukahara, J. 1971. Electron microscopic studies on the behavior of glycogen particles during oogenesis in the sea urchin. Develop. Growth Differ., 13 (4), 367-378.
- Tuzet, O., Garrone, R., Pavans de Ceccaty, M. 1970. Observations ultrastructurales sur la spermatogenèse chez la Démosponge *Aplysilla rosea* Schulze (Dendrocératide): une métaplasie exemplaire. Annls. Sc. Nat., 12 (1), 27-50.
- Vacelet, J. 1971. Etude en microscopie électronique de l'association entre une cyanophycée chroococcale et une éponge du genre *Verongia*. J. Microscopie, 12 (3), 363-380.
- Von Holt, C., Von Holt, M. 1968. Transfer of photosynthetic products from zooxanthellae hosts. Comp. Biochem. Physiol., 24, 73-81.
- Van Praët, M. 1978. Etude histochimique et ultrastructurale des régions digestives d'*Actinia equina* L. (Cnidaria, Actinaria). Cah. Biol. mar., 19, 4, 415-432.
- Van Praët, M., Doumenc, D.A. 1975. Morphologie et morphogenèse expérimentale du tentacule chez *Actinia equina* L. J. Microscopie, 23 (1), 29-38.
- De Vos, L. 1974. Etude ultrastructurale de la formation et de l'éclosion des gemmules d'*Ephydatia fluviatilis* L. Thèse Doctorat en Sciences (Zoologie). Université Libre de Bruxelles.
- Wright, K.A., Dick, T.A. 1972. Glycogen: its ultrastructural staining characteristics and distribution in some Nematodes. Z. Parasitenk., 40, 75-86.