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THE FIBROUS SYSTEM IN THE EXTRACELLULAR MATRIX OF HYDROMEDUSAE

Key words: Coelenterata, extracellular matrix (ECM), mesogloea, fibrous system, collagen fibres

ABSTRACT. The ultrastructure and the histochemistry of the fibrous system in the mesogloea extracellular matrix (ECM) of two hydromedusae (*Polyorchis penicillatus* and *Aglantha digitale*) has been examined. There is a fundamental difference in the architecture of the fibrous system between the two species. In *Polyorchis*, 60–150 Å thick, striated fibrils with periodicities of 60–65 Å form a three-dimensional network which fills in the entire ECM of outer and inner mesogloea. In the outer mesogloea vertical fibres (up to 1.8 µm in diameter) penetrate the three-dimensional network and branch near the exumbrellar and subumbrellar side. These branches impinge on a dense matrix covering the exumbrellar and subumbrellar surface. In *Aglantha* the branches of thick vertical fibres anchor at the subumbrellar side in a dense plexus (0.2–0.3 µm in thickness) which consists of two types of fibrils (35–40 and 80–100 nm in diameter). Towards the exumbrellar side the vertical fibres branch and intermingle with a meshwork of non-striated fibrils with uniform diameter (35–40 nm). These fibrils form a laminated structure (about 1 µm in thickness) so that fibrils of each layer course in the same direction but fibrils of adjacent layers run perpendicularly to each other. The banded pattern with periodicities of 600–640 Å observed in the electron microscope and by histochemical methods confirm the thick vertical fibres and their branches to be a collagen. There is also strong evidence that the laminated structure in *Aglantha* represents layers of collagen fibrils.

Introduction

The great bulk of the bell of hydromedusae consists of transparent extracellular matrix material (ECM, mesogloea) which is separated by the intervening subumbrellar plate endoderm into an outer and inner portion (Fig. 1).

Chemically the mesogloea of coelenterates is thought to contain mucopolysaccharides (Lowell and Haynes, 1968), collagen-like and other structural proteins (Chapman, 1953, 1959; Haynes *et al.*, 1968; for review see Adams, 1978).

The mesogloal ECM serves several distinct functions, e.g. as a base of cell attachment (Haynes *et al.*, 1968), as a substratum for cell movement (Shostak *et al.*, 1965), in control of morphogenetic processes (Schmid *et al.*, 1976), and in regulating the buoyancy

of hydromedusae (Denton, 1963; Chapman, 1966; Mackay, 1969).

Medusae differ from most other musculoskeletal systems because the muscles effecting locomotion are not arranged in antagonistic sets; instead, the subumbrellar circular muscle fibres are opposed by elastic forces generated by components of the mesogloea. Therefore the skeletal potential of the mesogloea (Chapman, 1953, 1958; Bouillon and Vandermeersche, 1956; Bargmann, 1972; Gladfelter, 1972), and its ability to act as an antagonist against muscle contraction (Chapman, 1958) is of special significance. However, information concerning the morphological structure of the mesogloea which enables it to play this mechanical role is limited (Chapman, 1953, 1959; Mackie and Mackie, 1967; Gladfelter, 1972).

The present paper describes a variety of mesogloal fibrils of two species of hydromedusae (*Polyorchis penicillatus* and *Aglantha digitale*), and the basic histochemical nature of their physical structure. All of

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these fibrils join in an elaborate network. We discuss whether they are the elements in the mesogloal ECM determining its structure as indicated by their topographical distribution and by their characteristic architecture that is strikingly related to the different locomotory systems of the above medusae.

Materials and Methods

Specimens of *Aglantha digitale* and *Polyorchis penicillatus* were collected at the Oak Bay Marina, Victoria, British Columbia, and at Pedder Bay about 30 km south of Victoria. The animals were anaesthetized in a solution of isotonic (67.5 g/l) magnesium chloride diluted 1:1 with sea water. Pieces of living and fixed tissue of the bell were pinned out with spines from the fruit of the cactus *Opuntia* in a dish containing a Sylgard layer and examined with a Zeiss microscope equipped with bright field, phase contrast, and Nomarski interference optics.

For electron microscopy (TEM) pieces of the bell were fixed in 2.5% glutaraldehyde in 0.4 M Millonig's phosphate buffer (pH 7.4) for up to several weeks, rinsed thoroughly in phosphate buffer and then post-fixed in 1% osmium tetroxide in the same buffer for 2 hr, dehydrated with acetone, embedded in epoxy resin ERL-4206 (Spurr, 1969). Sections were collected on single-hole copper

grids, stained with uranyl acetate (4 min), and lead citrate (10 min), and examined with a Zeiss electron microscope (EM-109).

For SEM, preparations were fixed and dehydrated in the same manner as for TEM, critical point dried with CO₂ and coated with gold. For internal features of the mesogloal extracellular matrix (ECM) of *Polyorchis* pieces were broken off with forceps following critical point drying.

For histochemical techniques, preparations were fixed either in 2.5% glutaraldehyde in 0.4 M Millonig's phosphate buffer (pH 7.4) or in 4% formaldehyde in cacodylate buffer. Staining procedure with Weigert's resorcin fuchsin, Fraenkel's orcein, Mollier's quadruple stain, Van Gieson trypan blue and Mallory's aniline blue collagen stain was carried out according to the methods described by Clark (1973) on hand-cut sections, which were pinned out on a coverslip containing a Sylgard layer.

Observations

A. The mesogloea of Polyorchis penicillatus
Under the light microscope, in hand-cut sections of outer mesogloea of the midbell region, two distinct layers of homogeneous transparent extracellular matrix (ECM) material can be seen. The two layers (about

Figs 1–6. Horizontal hand-cut section through an octant of *Polyorchis penicillatus* at midbell.

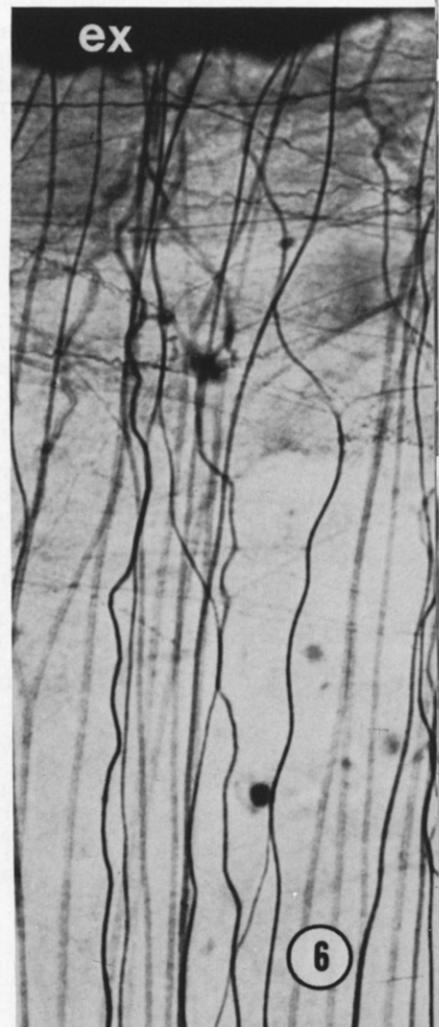
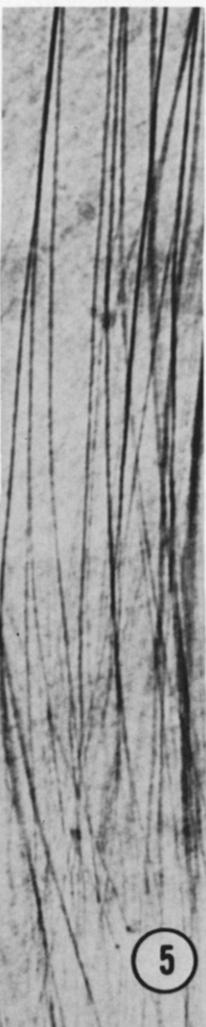
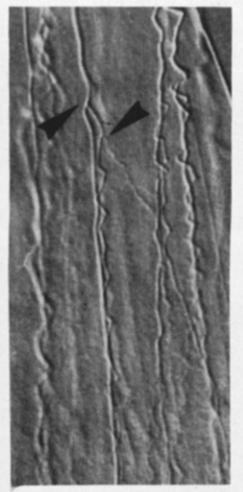
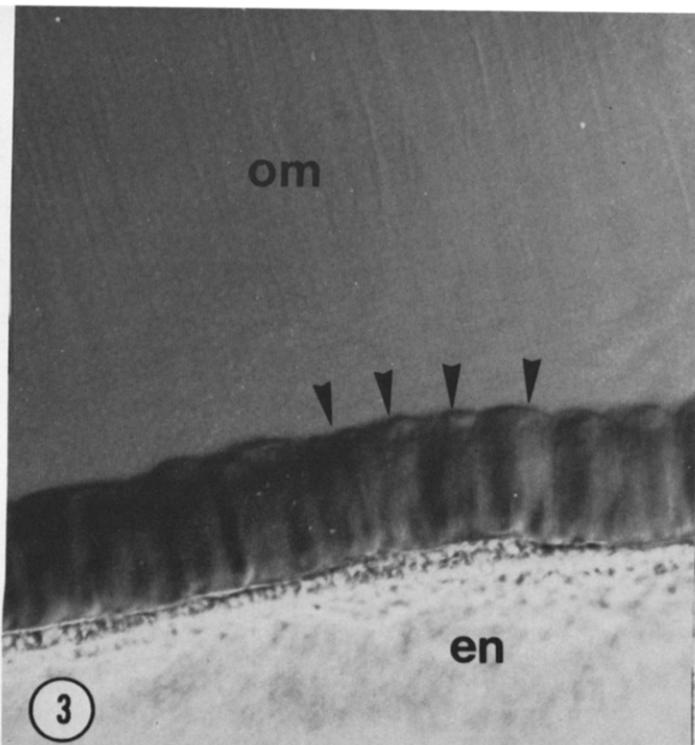
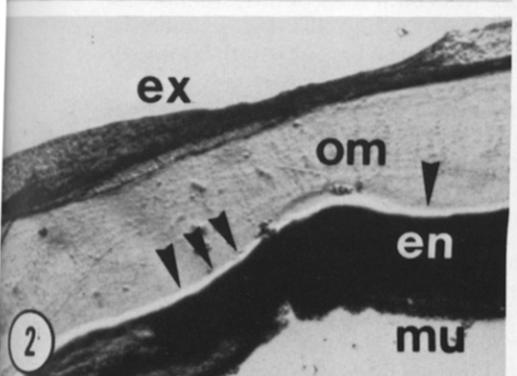
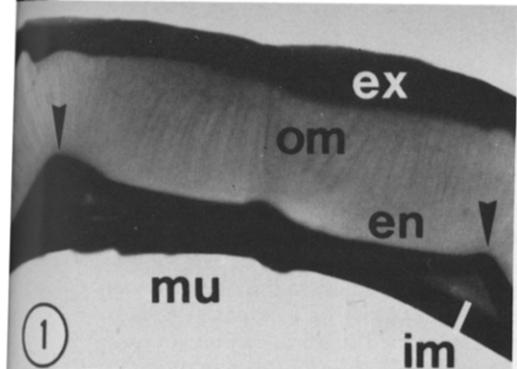
Fig. 1. The outer (om) and inner (im) mesogloea are separated by the intervening subumbrellar plate endoderm (en). Pointers indicate the apex of adradial joints. The fibres are stained with Coomassie R-250. Exumbrella (ex); swimming muscle (mu). $\times 19$.

Figs 2, 3. Two layers of outer mesogloea (om) are distinguished by a highly refractile zone at their dividing line (pointers). Exumbrella (ex); subumbrellar plate endoderm (en); swimming muscle (mu). Fig. 2, phase contrast, $\times 19$; Fig. 3, Nomarski interference optics, $\times 400$.

Fig. 4. Morphology of the radial fibres of the outer mesogloea. These thick fibres run perpendicularly from the exumbrellar side (top) and impinge on the subumbrellar plate endoderm (bottom). Dark field optics. $\times 175$.

Fig. 5. A the subumbrellar side the fibres branch (*inset*, $\times 600$) into an increasingly finer network. $\times 450$.

Fig. 6. Near the exumbrellar side (ex) the branches of the vertical fibres penetrate a plexus of thinner fibres which run tangentially. $\times 450$.



750 and 50 μ in thickness, depending on the size of the bell) might differ in their consistency producing a highly refractile zone at their dividing line (Figs 2, 3). The outer mesogloea is traversed by radially arranged fibres as described in other species of jellyfish (Chapman, 1953; Bouillon and Vandermeersche, 1957; Mackie and Mackie, 1967; Gladfelter, 1972, Fig. 1). These thick fibres run perpendicularly from the exumbrellar side and impinge on the subumbrellar plate endoderm (Fig. 4). Near the exumbrellar surface the fibres branch and penetrate a plexus of fibres which run tangentially in all directions (Figs 4, 6). At the subumbrellar side the thick vertical fibres spread out into an increasingly finer network as they approach the subumbrellar plate endoderm (Fig. 5). The extent of arborization and the density of tangential fibres are more pronounced on the exumbrellar than on the subumbrellar side.

Electron microscopical observations reveal that the entire inner and outer mesogloea ECM is evenly interwoven by very fine striated fibrils which form a three-dimensional network (Figs 7–9). These fibrils are 60–150 \AA in diameter and the banded

pattern shows periodicities of 60–65 \AA . They appear to be slightly denser in zones bordering epithelia than in the mid part of the mesogloea. Additionally, a thin layer (about 100 nm in thickness) of condensed fibrous material embedded in an amorphous dense matrix covers both sides of the subumbrellar plate endoderm (Fig. 10), the exumbrellar cells (Fig. 11), and the subumbrellar muscle sheet.

In the outer mesogloea the thick vertical fibres consequently penetrate the three-dimensional network of fibrils that fills in the entire volume of the mesogloea ECM. By tearing apart the ECM material along its media longitudinal axis, in SEM preparations the thick vertical fibres are observed to stick out of the network of fine fibrils (Fig. 12). The thick fibres vary in diameter (up to 1·8 μm). They are composed of many sub-units with diameters up to 150 \AA (Fig. 13). These subunits closely resemble the fibrils arranged in the three-dimensional network. High magnification micrographs of longitudinal sections reveal the vertical fibres to be woven together by many striated fibrils, which in return seem to be a product of

Figs 7–17. TEM and SEM micrographs of mesogloea ECM of *Polyorchis penicillatus* at midbell region.

Figs 7, 8. A three-dimensional network of fine fibrils fills in the entire outer mesogloea (om). Exumbrella (ex); subumbrellar plate endoderm (en). $\times 3500$.

Fig. 9. SEM high magnification micrograph of fibrils which form the three-dimensional network. $\times 50,000$. These fibrils are banded (pointers) and TEM longitudinal sections show periodicities of 60–65 \AA (inset).

Figs 10, 11. An amorphous dense matrix covers both the subumbrellar plate endoderm (Fig. 10, pointers, $\times 5000$) and the exumbrellar side (Fig. 11, pointers, $\times 24,000$).

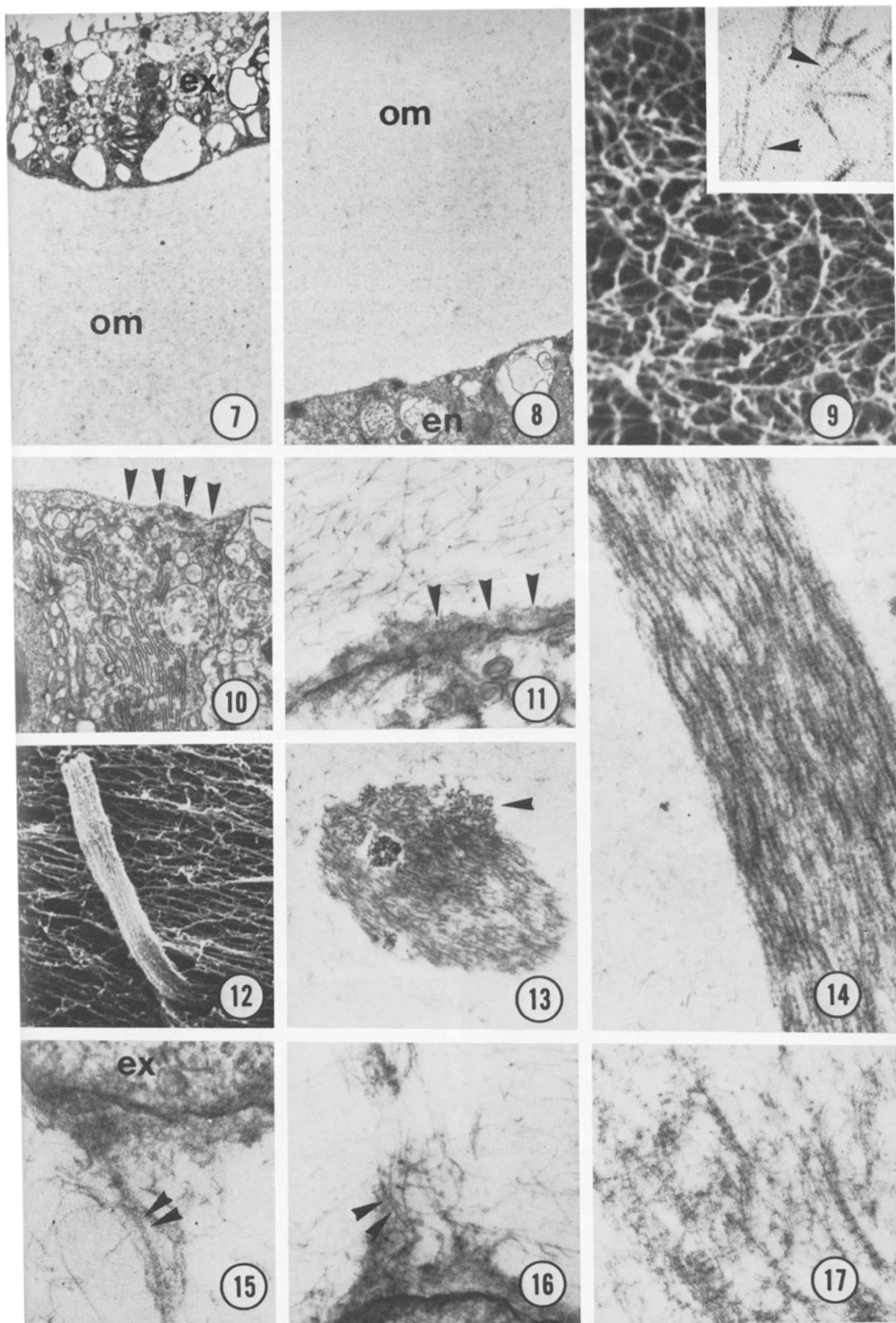
Fig. 12. SEM micrograph of thick vertical fibre which penetrates the three-dimensional network of fibrils. $\times 9000$.

Fig. 13. Cross-section of vertical fibre. Each fibre is composed of many subunits (pointers). $\times 22,000$.

Fig. 14. Vertical fibre shows banded pattern in high magnification micrograph. $\times 22,000$.

Figs 15, 16. Branches of the vertical fibres anchor in the amorphous dense matrix of the exumbrellar side (Fig. 15) as well as of the subumbrellar plate endoderm (Fig. 16). Single fibrils are also banded (pointers). $\times 60,000$.

Fig. 17. Banded fibrils of the inner mesogloea. $\times 29,000$.



assembly of the subunits (Fig. 14). The periodicity of banded fibres is about 630 Å, which lies within the limits of the periodicity of collagens. The branches of the thick vertical fibres are anchored in the amorphous dense matrix of both the exumbrellar side (Fig. 15) and of the subumbrellar plate endoderm (Fig. 16).

In the inner mesogloea there are no thick vertical fibres. However, fibrils in addition to those arranged in the uniform three-dimensional network can occasionally be found. They occur singly or in small bundles and extend in various directions. These bundles of fibrils are banded with the same periodicity (about 630 Å) as the vertical fibres described above (Fig. 17).

B. The mesogloea of *Aglantha digitale*

In cross-sections, the inner mesogloea (about 0.1 µm in thickness) is a thin electron-dense matrix that separates the subumbrellar plate endoderm from the extremely well-developed striated circular muscle layer (Figs 18, 19).

The major part of the thick outer mesogloea (approximately 50 µm in thickness) consists of homogeneous electron-lucent ECM material. At the subumbrellar side a dense plexus of fibrils (about 0.2–0.3 µm in thickness) covers the elongated endodermal cells (Figs 19, 20). Two types of fibrils are mainly involved in forming this

carpet-like structure: very fine, non-striated fibrils (35–40 nm in diameter) running tangentially in all directions, and thicker striated fibrils (80–150 nm in diameter) arranged in more or less parallel order (Fig. 21).

The outer mesogloea is traversed by thick fibres which branch near the subumbrellar side where they impinge on the dense plexus (Fig. 22). These fibres, as well as their branches, are banded, and show uniform periodicity of about 610 Å (Fig. 23).

Towards the exumbrellar side the thick vertical fibres spread out into an increasingly finer meshwork as they approach the exumbrellar surface (Fig. 24). Bundles of banded fibrils and occasionally scattered granular bodies can be seen associated with the meshwork (Fig. 25). The fine non-striated fibrils forming this tight meshwork are of uniform diameter (35–40 nm; Fig. 25 inset). These fibrils are organized to each other at right angles the closer they get to the exumbrellar surface (Figs 26, 27). Finally, small groups of unidirectionally orientated fibrils join to form closely associated subunits which build up a laminated structure (Fig. 26). The subunits at the innermost region of the laminated structure are small in size (Figs 27, 28). They grow bigger within each additional layer. These bundles of fibrils are unidirectionally orientated, but fibrils of adjacent lamellae are perpendicular to each other (Figs 27–29). The outermost region of

Figs 18–23. TEM and SEM micrographs of *Aglantha digitale* at midbell region.

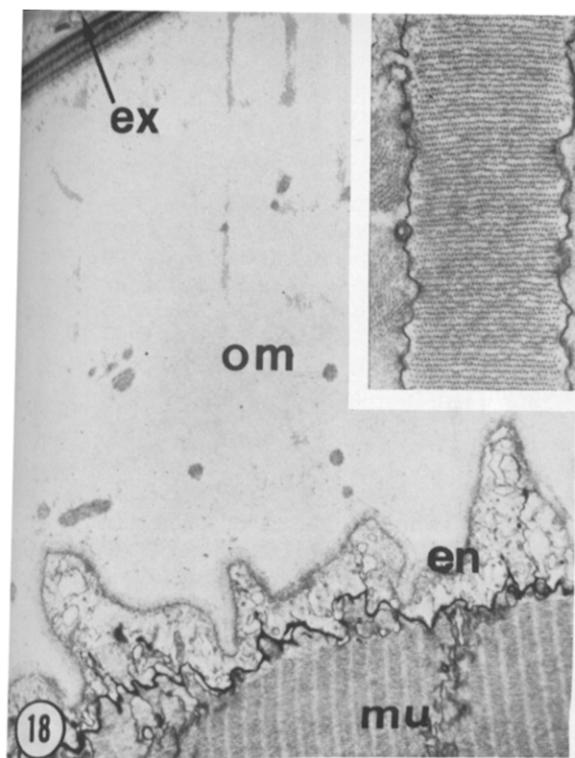
Fig. 18. Cross-section through the midbell region. Subumbrellar plate endoderm (en); exumbrellar cells (ex); swimming muscle (mu, inset, $\times 7500$); outer mesogloea (om). Parts of thick vertical fibres (arrows). $\times 5000$.

Fig. 19. The endodermal cells (en) are separated from the circular swimming muscle (mu) by the inner mesogloea (im). $\times 21,000$.

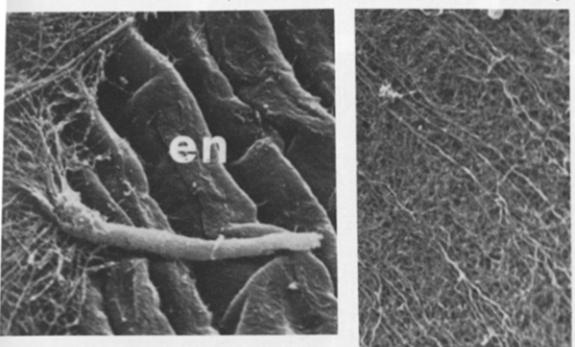
Figs 20, 21. The endodermal cells (en) are covered (inset, $\times 5500$) by a dense plexus of fibrils (Fig. 20, $\times 1200$). Two types of fibrils form this structure (Fig. 21, $\times 6000$).

Fig. 22. A thick vertical fibre runs perpendicularly from the exumbrellar (ex) side and branches (arrow) near the subumbrellar side (en). There the branches impinge (inset, $\times 1200$) on the dense plexus. $\times 780$.

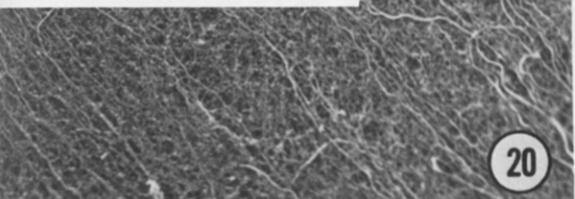
Fig. 23. The thick fibres are banded and show uniform periodicity. $\times 36,000$.



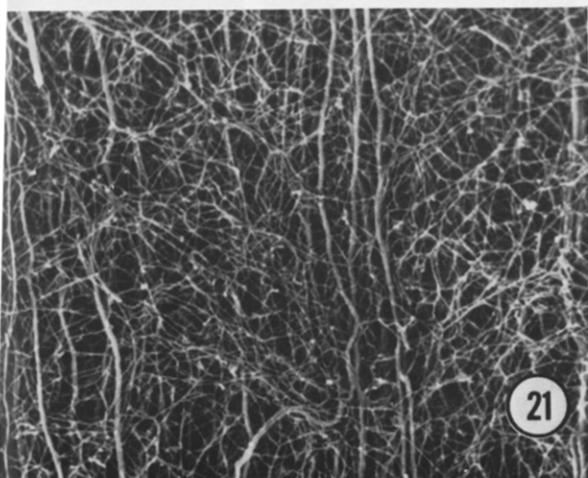
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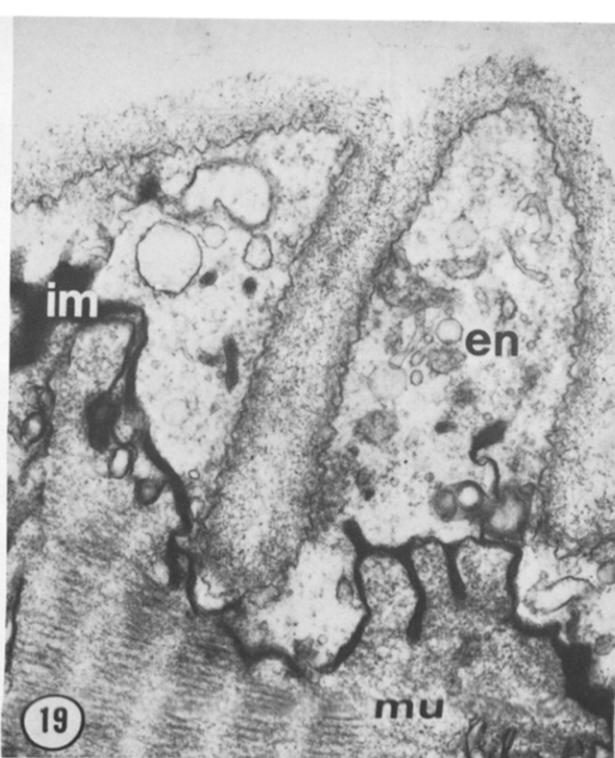
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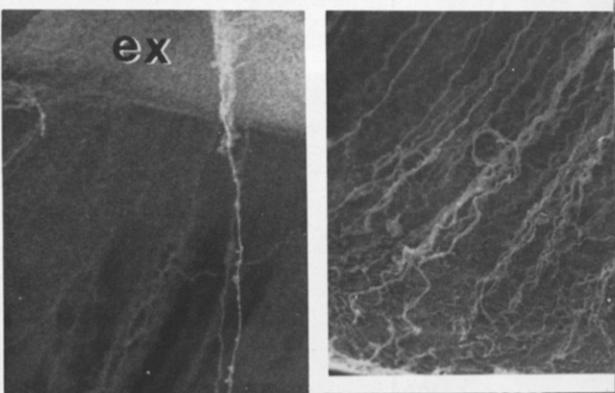
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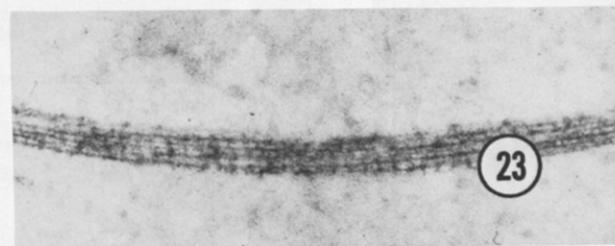


19



ex

22



23

the mesogloea exhibits two smooth layers of amorphous matrix material (Fig. 30) upon which the exumbrellar cells are situated.

Since the laminated structure (about 1 μm in thickness) is tough, it can be mechanically isolated from parts underneath the outer mesogloal ECM (Figs 31, 32).

C. Histochemistry

Electron microscopical observations reveal the presence of banded fibres throughout the mesogloea in both species studied. These fibres are a major element of the ECM and they most probably represent collagen.

To investigate histochemically the nature of these fibres and their branches, five collagen specific stains were used (Clark, 1973). They are thought to designate collagen among other proteins forming fibrous structures. In hand-cut sections all of these stains (Weigert's resorcin fuchsin; Fraenkel's orcein; Van Gieson trypan blue; Mollier's

quadruple stain; Mallory's aniline blue collagen stain) show clearly positive reaction with both, the thick vertical fibres which run perpendicularly from the exumbrellar to the subumbrellar side, and their branches. In *Aglantha*, also preparations of isolated laminated structure, which lies underneath the exumbrellar sheet, show weak positive reaction with the stains.

Discussion

Since the swimming muscle of medusae is opposed to the elastic forces generated in the mesogloal ECM, the structure and property of this ECM is of special significance for the locomotory effectiveness of a jellyfish (Chapman, 1958, 1959, 1968; Gutmann, 1965, 1966; Gladfelter, 1972). Therefore we expect the mesogloea to be constructed in close functional relation to its swimming muscle system.

Figs 24–32. TEM and SEM micrographs of outer mesogloea of *Aglantha digitale* at midbell region.

Fig. 24. Branches of vertical fibres intermingle with fibrils which build up a tight meshwork at the exumbrellar side. $\times 1200$.

Fig. 25. Unidirectionally orientated fibrils are closely associated with the dense meshwork. The ends (*inset*, $\times 24,000$) of these fibrils branch (pointers) and become part of the meshwork.

Fig. 26. The peripheral fibrils of the meshwork form a laminated structure upon which the exumbrellar cells (cx) are situated. Dense body (db); nucleus (nu); outer mesogloea (om). $\times 7500$.

Figs 27–30. Morphology of the laminated structure.

Fig. 27. The fibrils of the tight meshwork run perpendicularly to each other (bottom). Groups of unidirectionally orientated fibrils join to form bundles, the subunits of the laminated structure. $\times 142,000$.

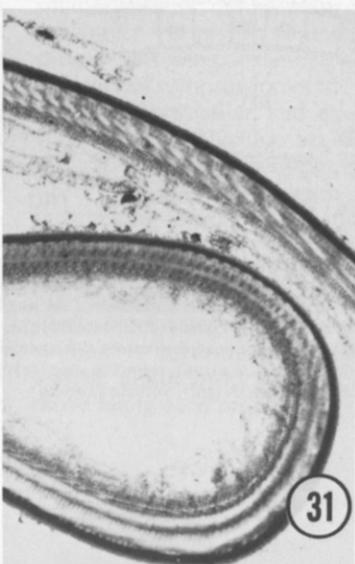
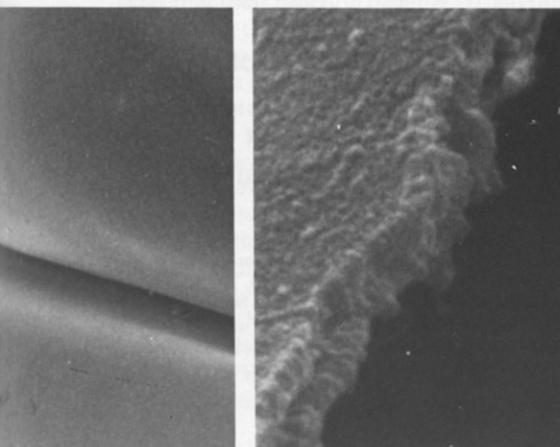
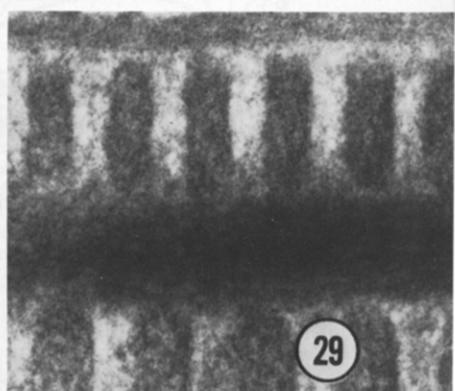
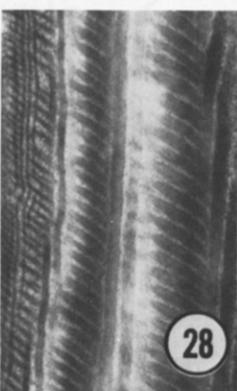
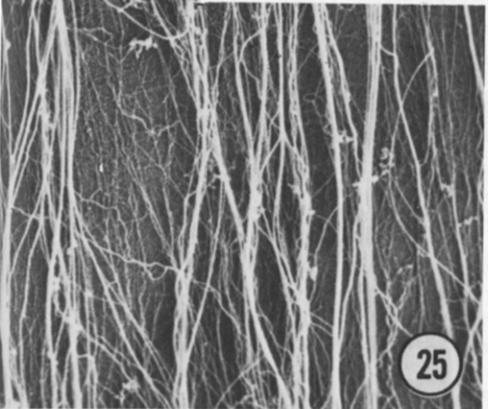
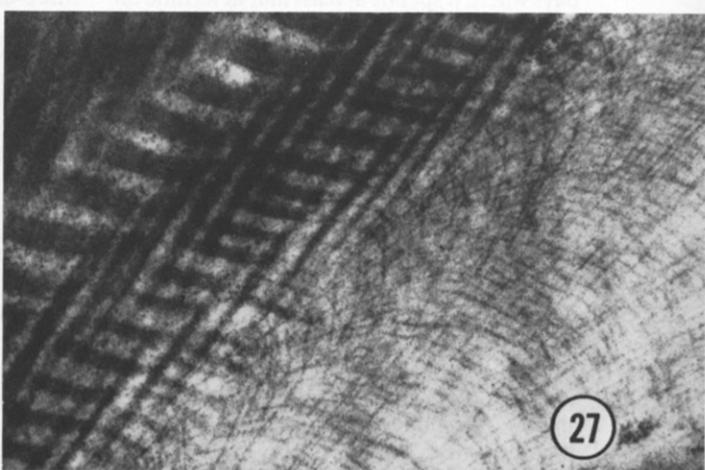
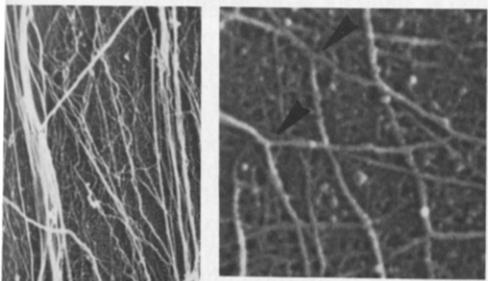
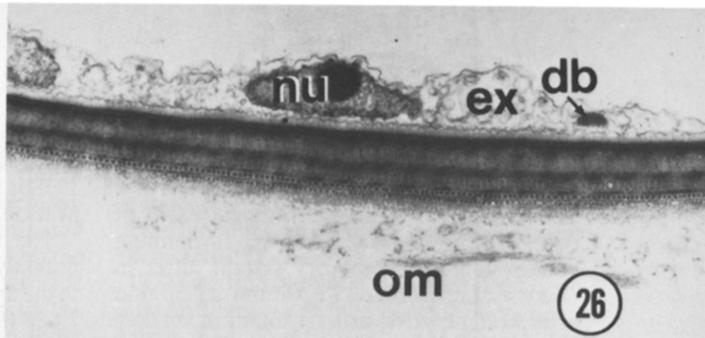
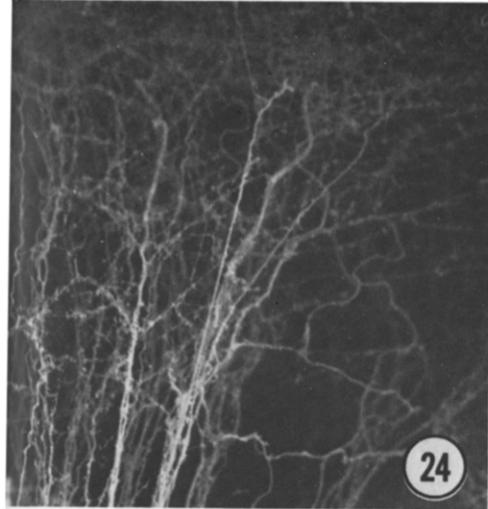
Fig. 28. Fibrils of each layer course in the same direction but fibrils of adjacent layers run perpendicularly to each other. $\times 33,000$.

Fig. 29. High magnification micrograph of three adjacent layers. $\times 250,000$.

Fig. 30. The outermost region of the laminated structure consists of two layers (*inset*, $\times 24,000$) of amorphous matrix material with a smooth surface upon which the exumbrellar cells are situated. In this SEM preparation the exumbrellar cells have been removed. $\times 120$.

Fig. 31. Cross-section through isolated laminated structure with fibrous material of the underlying tight meshwork. $\times 3300$.

Fig. 32. Tangential section through isolated laminated structure. $\times 15,000$.



In this paper we describe the pattern of a fibrous network in the mesogloea of two hydromedusae whose swimming behaviour and locomotory system differ in many aspects: *Polyorchis* (about 25–50 mm in bell diameter) is usually found in shallow bays where it spends at least half of its time on or near the bottom. Frequently the medusae hop off the bottom with a single pulsation and sometimes they swim all the way to the surface with rather slow contractions of the bell (Mills, 1981). The swimming muscle covering the subumbrellar surface forms a smooth cell layer whose basal processes contain thick and thin myofilaments (Singla, 1978a). *Aglantha*, on the other hand, is a small trachymedusan jellyfish (8–15 mm high). Its bell is twice as tall as wide and has eight radial canals. The medusae is, however, best identified by its rapid darting movement associated with the escape response. This behaviour is brought about by a nearly synchronous contraction of the well-developed thick circular muscles lining the inner surface of the bell (Singla,

1978b; Donaldson *et al.*, 1980; Roberts and Mackie, 1980; Weber *et al.*, 1982).

The mesogloea of the two species not only differ in shape and thickness but also in the architecture of the fibrous system of the ECM (Fig. 33). In *Polyorchis* a close-meshed three-dimensional network of striated fibrils fills in the entire ECM matrix of the mesogloea, there is hardly any amorphous dense matrix covering the subumbrellar and the exumbrellar side where the branches of the vertical fibres anchor. Its construction resembles a flexible foam mattress strengthened by vertical struts. Preliminary observations on the mesogloea of other hydromedusae (*Phialidium*, *Sarsia*, *Campanularia* (Schmid *et al.*, 1976)) with locomotory systems similar to the one of *Polyorchis* also have fibrous systems of the above type (results not shown). On the other hand, the thick dense plexus at the subumbrellar side, and an equally dense plexus at the exumbrellar side of the ECM of *Aglantha*, may provide better anchorage for the vertical fibres. The

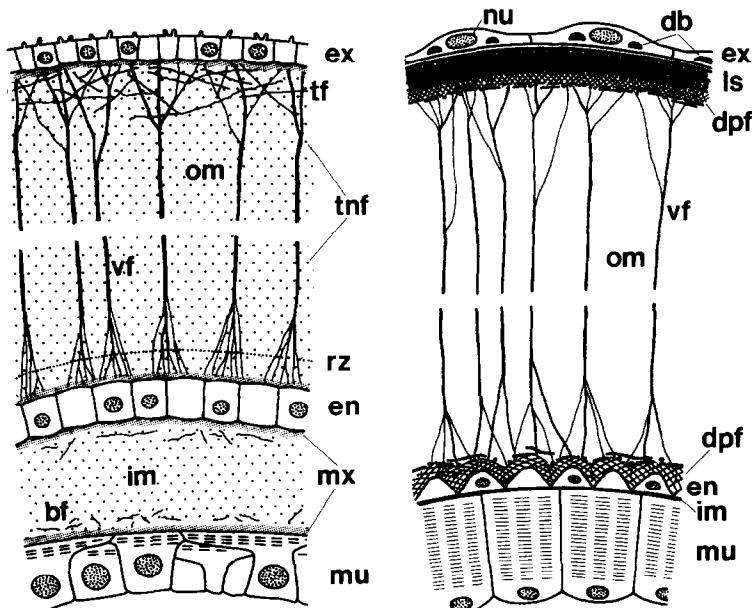


Fig. 33. Schematic representation of elements involved in the architecture of the fibrous system in the mesogloea ECM of *Polyorchis penicillatus* (left) and *Aglantha digitale* (right). The diagram does not show the actual size of the single elements. Bundles of fibrils (bf); dense body (db); dense plexus of fibrils (dpf); subumbrellar plate endoderm (en); exumbrella (ex); inner mesogloea (im); laminated structure (ls); swimming muscle (mu); dense matrix (mx); nucleus (nu); outer mesogloea (om); refractile zone (rz); plexus of tangential fibres (tf); three-dimensional network of fibrils (tnf); verticila fibre (vf).

impression of a solid 'ladder-like' architecture is emphasized by both the laminated structure at the exumbrellar side, and by the tight framework at the subumbrellar side where the muscle sheet is attached to the subumbrellar plate endoderm by the inner mesogloea.

Although pattern differs significantly in the two species studied, there is general resemblance of the constituent fibres. The banded pattern with periodicities of about 620 Å observed with the electron microscope and histochemical methods in both species confirm the thick vertical fibres and their branches to be a collagen. Furthermore, we suggest that the laminated structure at the exumbrellar side of *Aglantha digitale* represents layers of collagen fibrils. There the fibrils in each layer course in the same direction and those of adjacent layers in a perpendicular direction, comparable to the organization, e.g. in the stroma of all submammalian corneas or in the dorsal skin of tadpole (Hay, 1981). Even though the presence of collagen has been demonstrated in all investigated cnidaria (for reviews see Gladfelter, 1972; Adams, 1978) its relationship either to the matrix material or to the visible fibres of the ECM was still controversial (Chapman, 1953a, 1959, 1966; Bouillon and Vandermeerssche, 1956; Bouillon *et al.*, 1958; Alexander, 1964; Mackie and Mackie, 1967). Both biochemical analysis to determine types of collagen and other ECM components of the mesogloea, as well as immunochemistry to describe its spatial distribution, are objects of current research in our group.

The distribution of thick vertical fibres suggests that their function in general is not only to maintain the radial integrity of portions of the ECM that thicken during contraction, but may also be important in effecting recovery of the contracted state (Chapman, 1966; Gladfelter, 1972). In any case, the authors think the thick vertical fibres essentially act as springs. However, collagenous fibres are inelastic in nature (Hay, 1982) and the contorted, roughly helical conformation of vertical fibres that would allow elasticity is probably due to shrinkage of the matrix during fixation (Mackie and Mackie, 1967; Gladfelter, 1972). The following aspects may explain this apparent contradiction: first, the topographical distribution, second, the

architecture of the fibres and, third, the characteristic ultrastructure of the thick fibres themselves. (1) In agreement with Gladfelter (1972) we find an increasing fibre density on adradial joints in *Polyorchis* and along radial canals in *Aglantha* (results not shown). On the basis of the inverse relationship between fibre density and deformability of the mesogloea (Gladfelter, 1972) it is likely that one function of these fibres is to provide radially orientated tensile strength to the bell. It also implies very limited elasticity of the fibres since the adradial joints of the subumbrellar plate endoderm where the fibres anchor are lifted up during contraction (Fig. 34). Therefore, the actual difference in

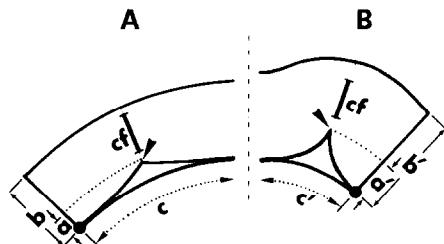


Fig. 34. Cross-sectional diagram of one quadrant at midbell of *Polyorchis* (after Gladfelter, 1972). The diagram illustrates the dimensions of the bell in relaxed condition (A) and in contracted condition (B). a, ah height of adradial joints; b, bh thickness of bell; c, ch length of subumbrellar arc. Arrowheads indicate the apex of adradial joints. cf, central portion of thick vertical fibre (without branches), equal length in relaxed and contracted condition.

length of the fibres during contraction compared with the relaxed state of the bell is smaller than the deformation of the bell suggests. (2) However, contraction not only causes thickening of the bell but also significant lateral compression of the fibrous plexus at the subumbrellar and exumbrellar side (Gladfelter, 1972; Fig. 34). For this reason the anchorages of the branches of vertical fibres move closer to each other which causes lengthening of the fibre complex. (3) A limited elastic property of the thick vertical fibres can be explained by the fact that they are composed of many subunits of collagen fibrils woven together. Even though each subunit is inelastic in nature, the fibres assume elastic properties when these fibrils move along each other.

Although the mesogloeaal ECM of coelenterates contains mucopolysaccharides (Lowell and Haynes, 1968) the question to what extent these mucopolysaccharides, particularly the glycosaminoglycans, are involved in maintaining the structure of the ECM and so might influence their functional properties, is beyond the aim of this paper.

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