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Comparative morphology of echinoderm calcified tissues: Histology and ultrastructure of ophiuroid scales (Echinodermata, Ophiuroida)

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Summary. The calcified body wall of an ophiuroid was investigated by a new method and compared with that of other echinoderms. The previous opinion that the epidermis of ophiuroid arm shields consists of a reduced syncytium continuous with the underlying dermis is incorrect. The epidermis is distinctly separated from the dermis by a basal layer and consists of (1) supporting cells which bear the cuticle, (2) ciliated cells (hitherto unknown and probably sensory), (3) gland cells, and (4) nerve cells with the basal nerve plexus. The overall structure of the epidermis is a three-dimensional tube system (marked by the basal lamina) which penetrates the dermal tissue of the scale's pore space and continues with nerve cords situated below the scale. This arrangement is unique in echinoderms.

The dermal sclerocytes largely conform with those of the echinoid *Eucidaris*. The mineral skeleton is produced intracellularly or intrasyncytially. Moreover, dermal sclerocytes were found to release extracellular microfibrils which have nothing to do with calcite deposition. The attachment of the cuticle to the dermis is achieved by means of epidermal coupling areas. Collagen fibers fasten the scale to the underlying connective tissue sheath. The supposed fibrocytes within this sheath resemble sclerocytes. Each collagen bundle is provided with a strand of nerve fibers which, in contrast to the basal nerve plexus, are naked. They are said to influence the mechanical properties of the connective tissue.

Structures associated with cilia occur in cell types which normally lack a cilium. This finding suggests that most echinoderm cells are potentially monociliate.

A. Introduction

Descriptions of the tissues of ophiuroid dermal scales given by previous authors and summarized by Hyman (1955) and Smith (1965) put the ophiuroids in a strange contrast to other echinoderms. Although they had discovered a cuticle, neither the epithelium belonging to it nor a basal lamina nor cilia had been found. Because cell borders had not been seen, the cells of dermis and epidermis could not be distinguished, and dermis and epidermis were considered to form a common syncytium filling the pore space of the dermal scales. More recent authors have drawn ophiuroid ossicles covered with a straight epidermis. This is likewise a misrepresentation. Echinoderm skeletons consist of many porous ossicles, called stereoms, which are embedded in and filled with dermal tissue, the stroma. The calcareous nature of the ossicles is a major hindrance for studies on the underlying tissues. In contrast to vertebrate bone, echinoderm ossicles consist of a lattice of calcite trabeculae which are purely mineral, i.e. they are devoid of organic fibrils which would support their structure after decalcification.

The present study gives a necessary review of the previous descriptions. It uses a special technique developed by Märkel and Röser (1983a) for investigations on echinoderm calcified tissues. This method needs ossicles of sufficient size; thus the large and short-spined species *Ophioderma longicauda* was used. The investigation shows that ophiuroid scales have indeed a special structure in that the epidermis penetrates the whole scale. Nevertheless, they are generally in line with other echinoderms. Detailed knowledge of echinoderm calcareous tissues may also help clarify evolutionary relationships between echinoderms and vertebrates, since the presumed stem vertebrates, the calcichordata, had a calcite skeleton of echinoderm type (Jefferies 1980).

B. Materials and methods

Specimens of *Ophioderma longicauda* Linck were obtained from an aquarium supply company or collected in the Mediterranean Sea near Toulon (France) or along the coast of Sardinia (Italy). They were kept for several months in artificial sea water at room temperature or at 18° C and fed with snails and homogenized fish food.

For SEM studies of the skeleton, dried pieces of an arm were glued onto a support before KOH treatment, in order to maintain the anatomical arrangement of the ossicles.

Arm segments for histological and ultrastructural investigations were dissected and some faces quickly abraded with emery paper moistened with sea water. Due to the calcareous skeleton relatively large pieces had to be used. The process of fixation took at least 18 h at 4° C in 5% glutaraldehyde in 0.1 M Soerensen phosphate buffer (pH 7.6). The osmolarity was adjusted with sucrose to that of artificial sea water. Postfixation was carried out for 2 h with 1% osmium tetroxide in 0.1 M Soerensen buffer (pH 7.6).

Specimens used for semi-thin sections were decalcified with EDTA. The specimens were then rinsed, dehydrated,

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and embedded in araldite. The sections were stained with methylene blue-fuchsin.

For ultrathin sections, the double embedding method described by Märkel and Röser (1983a) was used. In some instances 0.05% ruthenium red was added to the fixative (Luft 1971). This staines the mucopolysaccharides and renders the borders of thin cytoplasmic laminae more distinct. Ruthenium red was used with or without later staining with uranyl acetate and lead citrate. The sections were examined with a Zeiss EM 9 S-2.

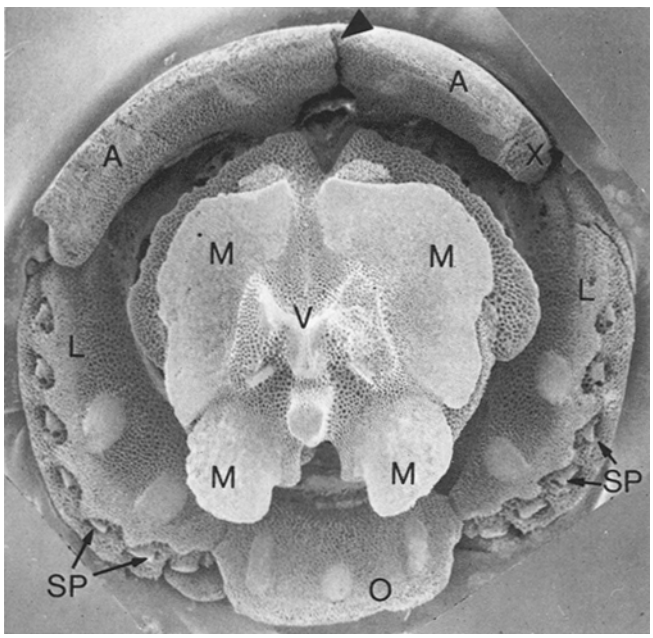


Fig. 1. Distal face of the arm skeleton with the respective ossicles in anatomical arrangement (SEM). Note that the apical scale (*A*) is secondarily subdivided (*arrow head*) and one part of it is lost (*X*). Further explanation in the text. Total diameter about 3 mm

C. Results

1. Introductory investigations

Ophiuroids are characterized by the jointed appearance of their heavily calcified arms. Each joint or segment contains a central vertebral ossicle (*V*) and a girdle of four scales or shields, apical (*A*), lateral (*L*) and oral (*O*) in position. In *O. longicauda* the apical shield is often subdivided (Fig. 1). Each lateral scale bears a row of starting points for spines (*SP*) at its distal edge. Additional appendages are not otherwise present. Adjoining vertebrae are bound together by intervertebral ligaments (*Li*, Fig. 2) and intervertebral muscles (*M*). They are surrounded by a thick connective tissue sheath (*CTS*) which bears and holds together the calcareous scales by means of collagenous bundles which pass through the basal and lateral part of the scale's pore space (Fig. 2b, arrow head). In places bundles of fibers run from the vertebral ossicle to the connective tissue sheath, but otherwise there is a well developed somatocoel (*SC*) in between. The calcite ossicles are embedded in tissue which also fills the interconnecting pore space within the ossicles. The latter contains a large amount of fluid and few cellular elements. Thus, in decalcified sections, the ossicles appear indistinct (Fig. 2).

The animal is covered with a bilayered cuticle (Fig. 3a, cu_i, cu_m). The outermost calcite trabeculae (*T*) of the scale nearly reach the surface. They are enveloped with thin cytoplasmic layers, the cell bodies belonging to these layers lying within the scale's pore space. In this manner they are largely protected from damage. The epidermis wholly penetrates the scale, and the scale's pore space contains dermal as well as epidermal tissues both strictly separated from one

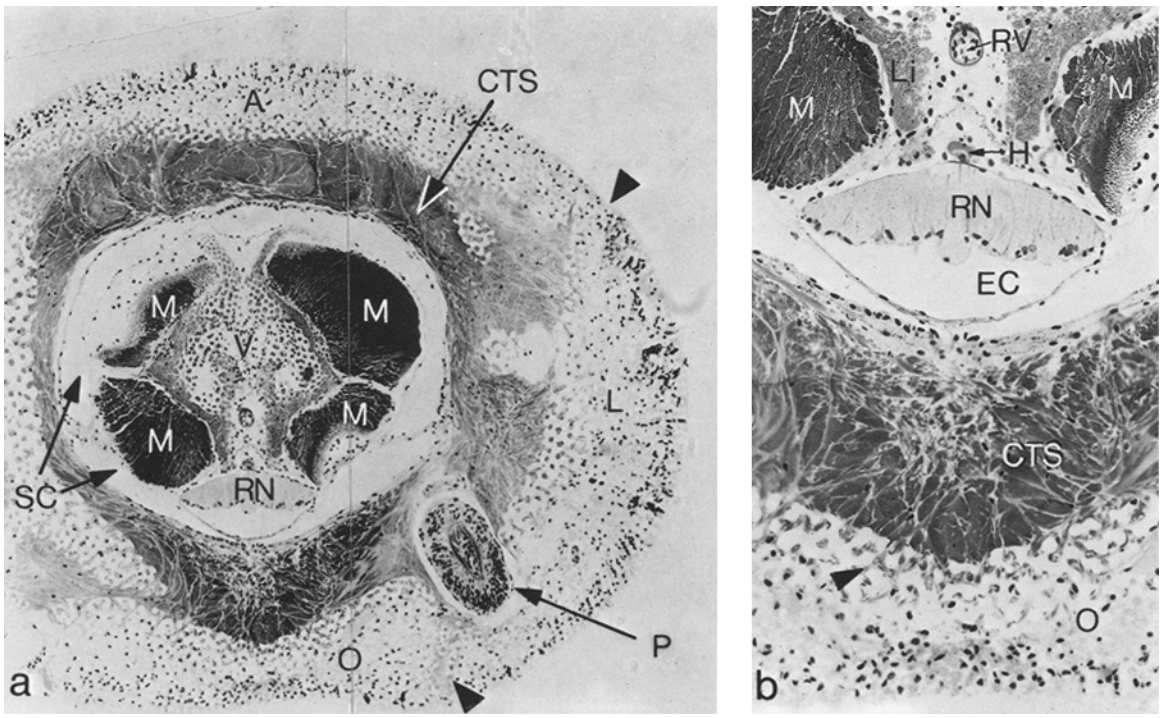


Fig. 2. a Semithin cross section through a decalcified arm (height 1.2 mm) **b** Detail of *a*. Further explanation in the text or p 10

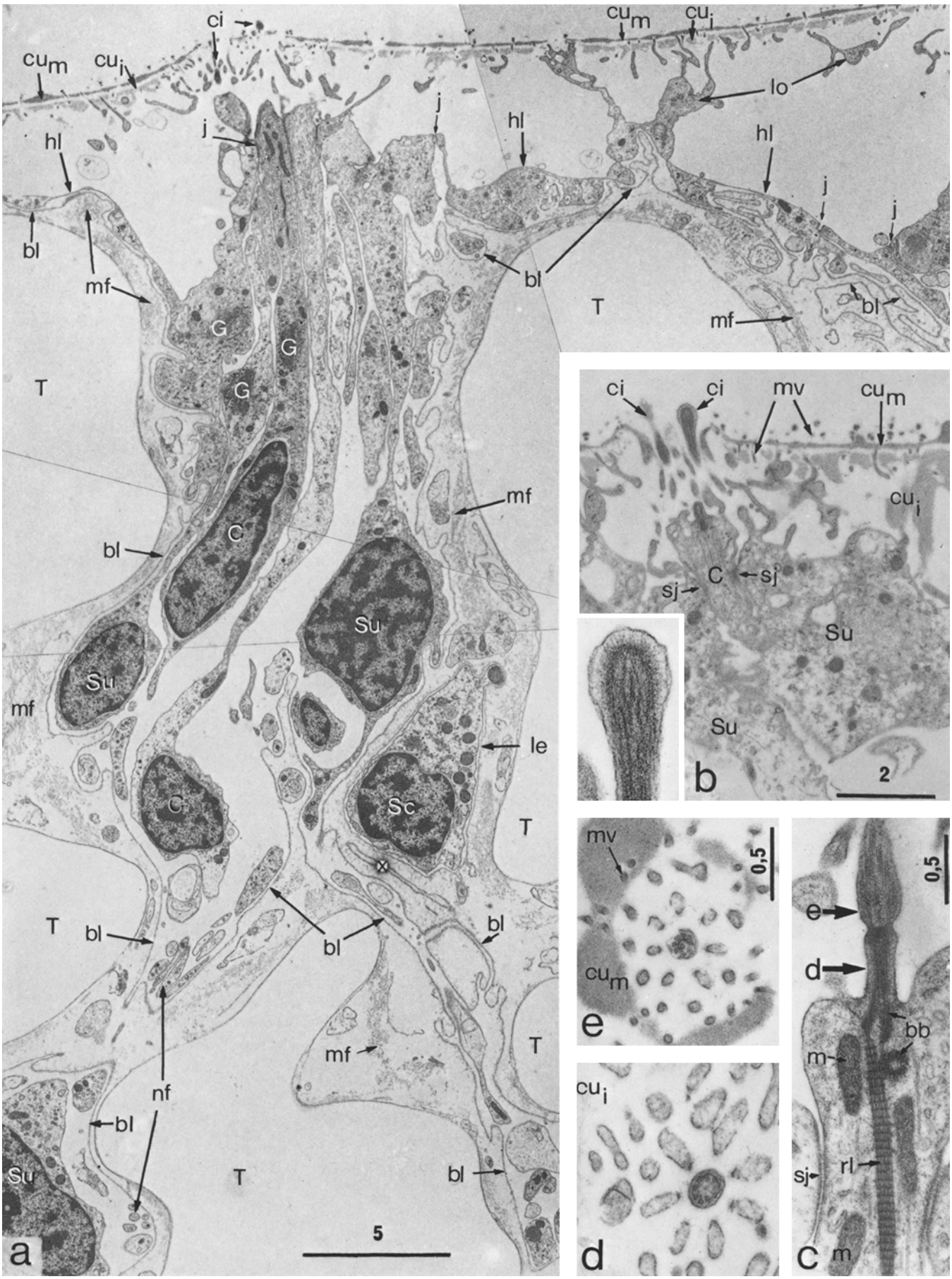


Fig. 3. **a** Low magnification photograph of a vertical pore, cut lengthwise. **b** Cilium (*ci*) with club-shaped tip (*inset*) which hardly rises above the cuticle. **c** Basal part of a cilium, cut lengthwise, showing its basal bodies (*bb*) and rootlet (*rl*). **d, e** Transversely cut cilia, the respective levels indicated in *c*. Measurements in μm

another by the basal lamina (*bl*). On the whole, the epidermis forms a tubular system of its own which is embedded in dermal tissue and never touches the calcite trabeculae. Its nerve plexus is continuous with nerve cords positioned below the scale which in their turn are continuous with the radial nerve (RN).

2. Dermis

The dermis consists of sclerocytes, phagocytes, and chromatophores. It lacks "morula cells" or granulocytes which are abundant in echinoids.

The sclerocytes (Fig. 3a, *Sc*) produce and envelop the mineral skeleton. They are similar in structure to those of the echinoid *Eucidaris* (cf. Märkel and Röser 1983a). Their mononucleate cell bodies (Fig. 4a–c) are anchored to the calcite trabeculae by stalks which spread over the young trabeculae as a continuous cytoplasmic sheath (*sh*) which is about 0.01 µm thick, too thin to contain cell organelles (Fig. 6e). In fully grown areas the sheath splits up into numerous filiform strings called distal processes (*dp*).

The sclerocytes are characterized by a boundary layer (*le*) which envelops the cell bodies and each of their branches separately (Fig. 4g). Its structure is similar to that of the basal layer, but after treatment with ruthenium red it is heavily stained, whereas the basal layer takes hardly any stain (Fig. 4f). The staining property indicates that the boundary layer contains mucopolysaccharides which occur elsewhere in calcified tissues (Kobayashi 1971) though their function is hardly understood. The function of the boundary layer itself is likewise obscure. Just as in *Eucidaris,* it terminates at the distal end of the stem (Fig. 4a, c arrow heads) and is absent in the delicate cytoplasmic sheath. The boundary layer is mentioned neither by Pilkington (1969) nor by Heatfield and Travis (1975) who described sclerocytes of several echinoids. In *Eucidaris,* specific sclerocytes, called odontoblasts, produce the tooth skeleton. These cells are also devoid of a boundary layer (Märkel unpublished).

The extracellular stroma fluid contains numerous unstriated microfibrils (*mf*) with a diameter of 10–13 nm. These fibrils are often seen to run to or from a sclerocyte. Figure 4d, e suggests the hypothesis that the sclerocyte is releasing microfibrils. In this area the cell membrane (*cs*) appears loose. Vesicles having a granular content (*gv*) and apparently coming from the Golgi apparatus (*G*) meet this area and possibly pass the cell membrane causing the boundary layer to bulge outwards. The innermost fibrils connect to granules positioned at the level of the loosened cell membrane and run to vesicles which have already passed the cell surface. The fibrils are probably polymerized in the halo between the cell membrane and the boundary layer.

Collagen fibrils are restricted to the undermost part of the scale. In this region, as well as within the connective tissue sheath (i.e. outside the skeleton), lie cells which are provided with a boundary layer (like sclerocytes) but are devoid of branches and distal processes; they are probably fibrocytes (Fig. 5d). Possibly sclerocytes and fibrocytes are of common origin and may substitute for one another. Microfibrils and striated collagen fibrils coexist in the same pore space (Fig. 7d). Microfibrils occur occasionally between collagen fibrils of the connective tissue (Fig. 5d). Similar conditions were observed in sea urchins (Hidaka and Takahashi 1983; Motokawa 1983). Crise-Benson and Benson (1979) discuss whether or not the unstriated microfibrils represent procollagen. However, at least in ophiuroids, the unstriated microfibrils are a self-supporting constituent of the stroma (see below).

Phagocytes are not numerous. However, they obviously play an important role in protection from bacterial infections. Most specimens examined showed bacteria massed together in 'islets' located within the stroma part of the pore space (Fig. 5f, g), which are enveloped with phagocytes whose cytoplasm is densely filled with SER cisternae. The infection rate was negligible in the specimens collected in Sardinia, but in specimens from the environment of Toulon the infected areas filled large parts of the pore space, and they were even found within the vertebral ossicles. It was probably because of this infection that the respective specimens largely autotomized their arms. The high infection rate in the population of Toulon may be caused by man-made pollution. Hitherto microorganismic diseases affecting echinoderms in the field are hardly known (Jangoux 1984) but they are obviously wide-spred in ophiuroids. Martínez (1977a) described obscure 'islotes' from the podia of *Ophiothrix*. His photographs reveal that they refer to enveloped groups of bacteria which are very similar in structure to those found in *Ophioderma*.

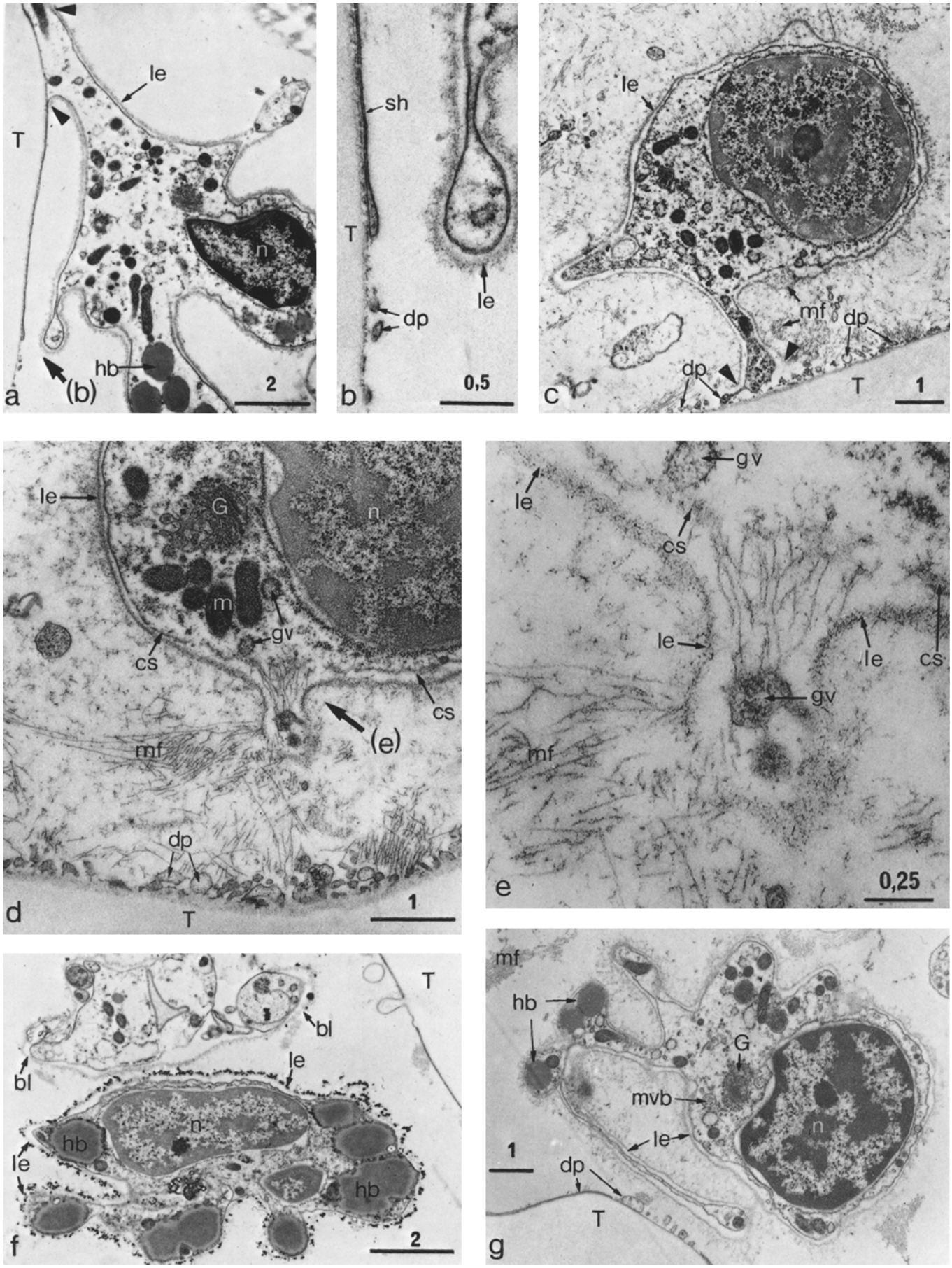
Chromatophores are present in the dark-colored apical and lateral shields. They are highly branched cells. Their branches contain the pigment granules and are more or less attached to the trabeculae, though separated from them by the distal processes of sclerocytes (Fig. 5e). Chromatophores are not restricted to the surface but are present throughout the scale. They are part of the dermis.

3. Epidermis

Near the surface the scale's pore space is largely filled with epidermal cells (Fig. 3a). Through a vertically arranged canal which has a diameter of 10–12 µm about eight cells come together and were traced up to 30 µm in length.

The supporting cells (*Su*) are the main cell type of the epidermis. Their nuclei are deeply sunken, but cytoplasmic laminae (*hl*), which are often extremely thin, spread horizontally to cover the outermost trabeculae (*T*). The laminae of neighbouring cells are connected by junctions (*j*); only in this region does the epidermis form a typical epidermal layer. Towards the interior, the cells are separated by extracellular spaces which contain a clear fluid (in contrast to those of the dermis). The sunken parts of the supporting cells protrude cytoplasmic ledges and appear star-shaped in cross-sections (Fig. 6a). The basal lamina does not run

Fig. 4a–g. Sclerocytes. **a** Sclerocyte cell body and its attachment to the trabecle wall. The boundary layer terminates at the arrow heads. **b** Partial view from the area indicated in **a**. **c** Sclerocyte with its stem which splits up in distal processes (*dp*) at the trabecle. In places microfibrils (*mf*) lie within the halo between cell surface (*cs*) and boundary layer (*le*). **d** Sclerocyte releasing microfibrils. **e** Detail from **d**. **f** The boundary layer stained with ruthenium red, the basal lamina (*bl*) hardly stained. **g** Characteristic shape of a branched sclerocyte. Measurements in µm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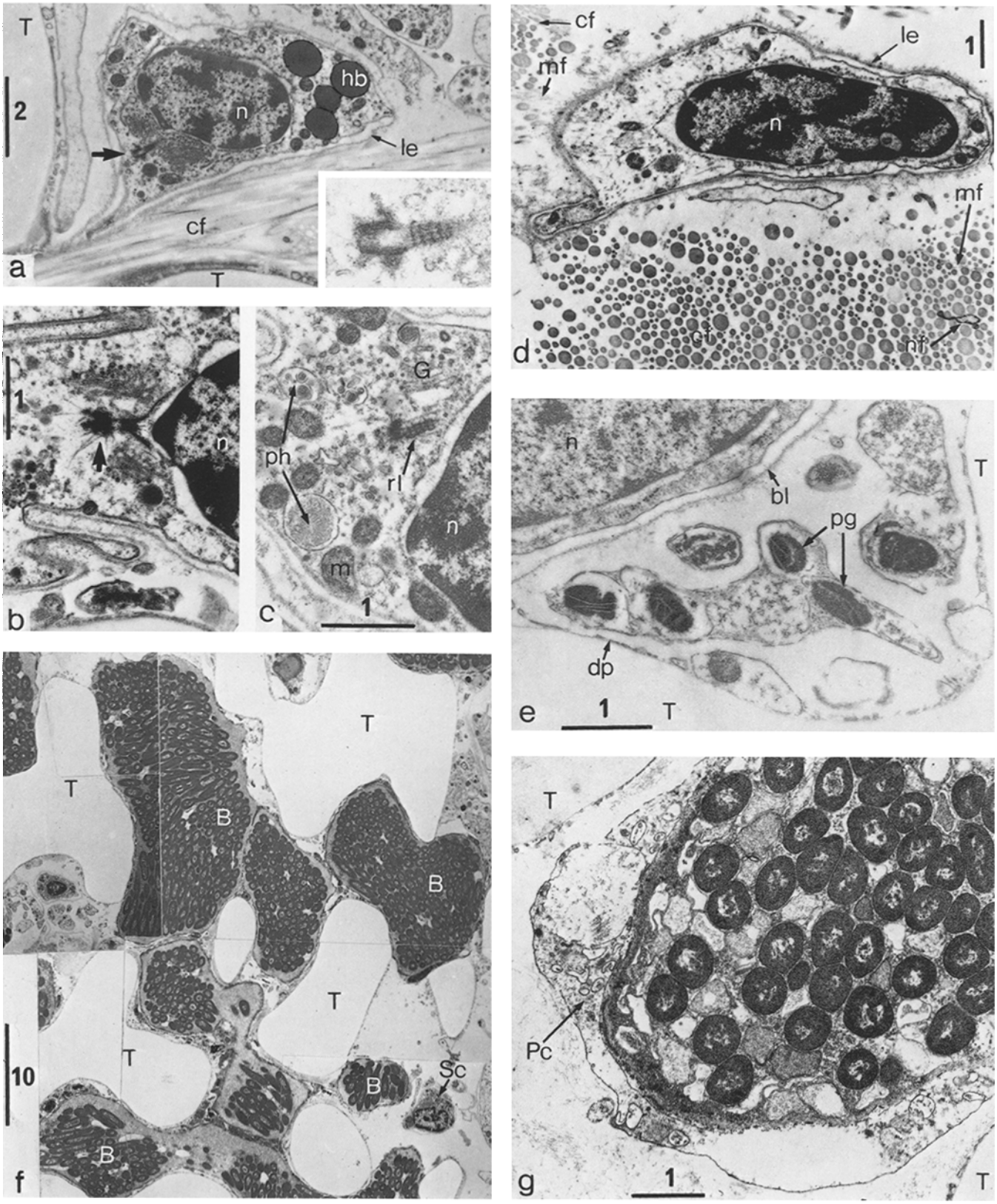

Fig. 5. **a** Sclerocyte near collagen fibers (*cf*), the arrow indicates a basal body with its rootlet (*inset*) **b** Sclerocyte with centriole and centriolar satellites (*arrow*) **c** Sclerocyte showing rootlet and phagosomes (*ph*) **d** Fibrocyte within connective tissue sheath **e** Pigment granules (*pg*) in branches of a mesodermal pigment cell **f** Small area of a scale infected with bacteria (*B*) **g** Islet of bacteria enveloped with a phagocyte. Measurements in μm

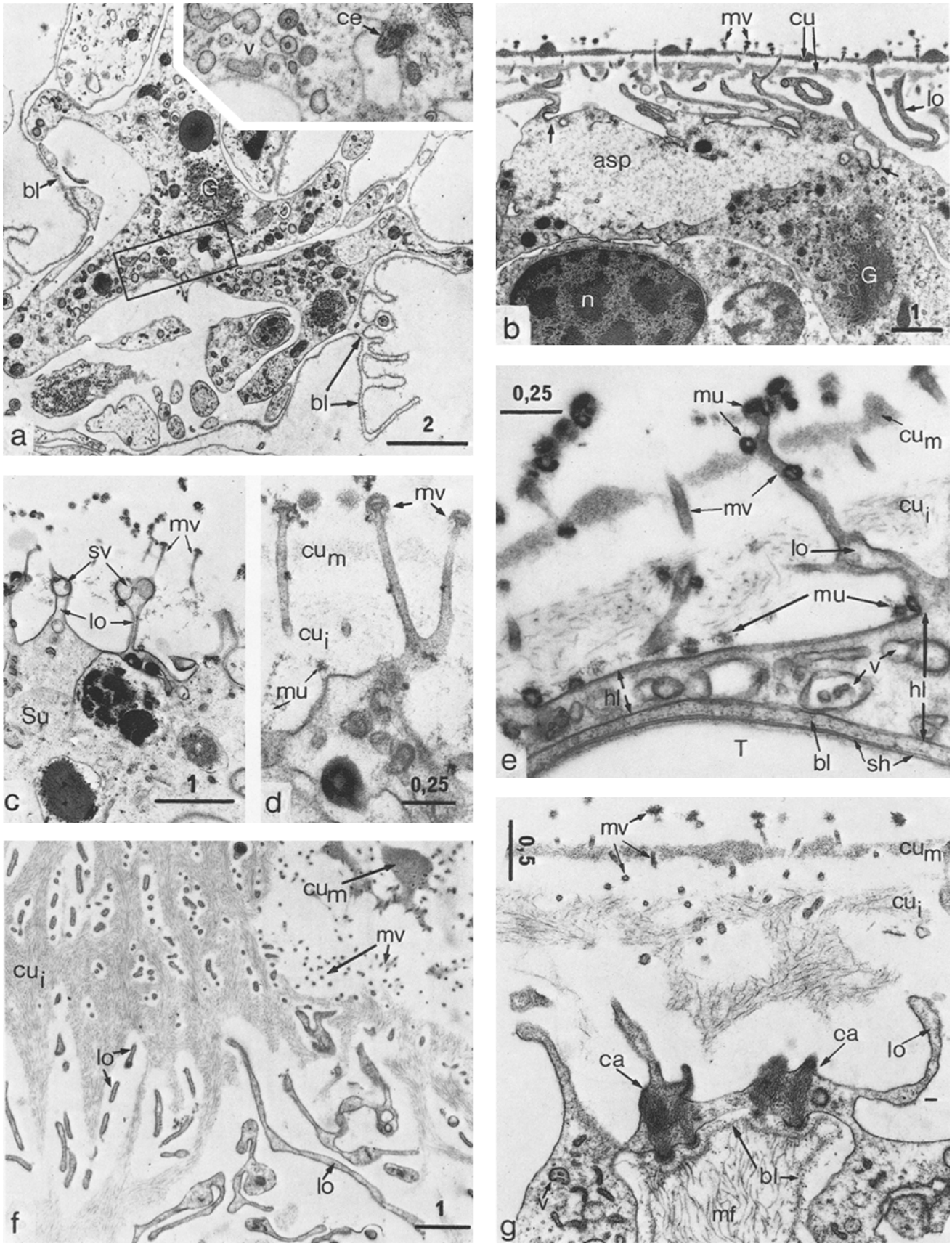

Fig. 6a–g. Supporting cells and cuticle **a** Supporting cell cut transversaly with a centriole (*ce*) and vacuoles (*v, inset*) **b** Distal part of a supporting cell filled with accumulated secretory products (*asp*) **c**, **d** Microvilli (*mv*) and cuticle stained with ruthenium red **e** Cytoplasmic sheath of a sclerocyte (*sh*) and a lamina of a supporting cell (*hl*) covering a trabecle; the specimen is stained with ruthenium red, uranyl acetate, and lead citrate **f** Cuticle, horizontally cut. Note the laminate lobes (*lo*) which split up at the level of the interior cuticular layer (cu_i) and terminate in microvilli (*mv*) which penetrate the middle layer of the cuticle (cu_m) **g** Coupling areas (*ca*) which connect the cuticle with the microfibrils of the stroma (*mf*). Vertically arranged fibrils of cu_i only partially cut. Measurements in µm

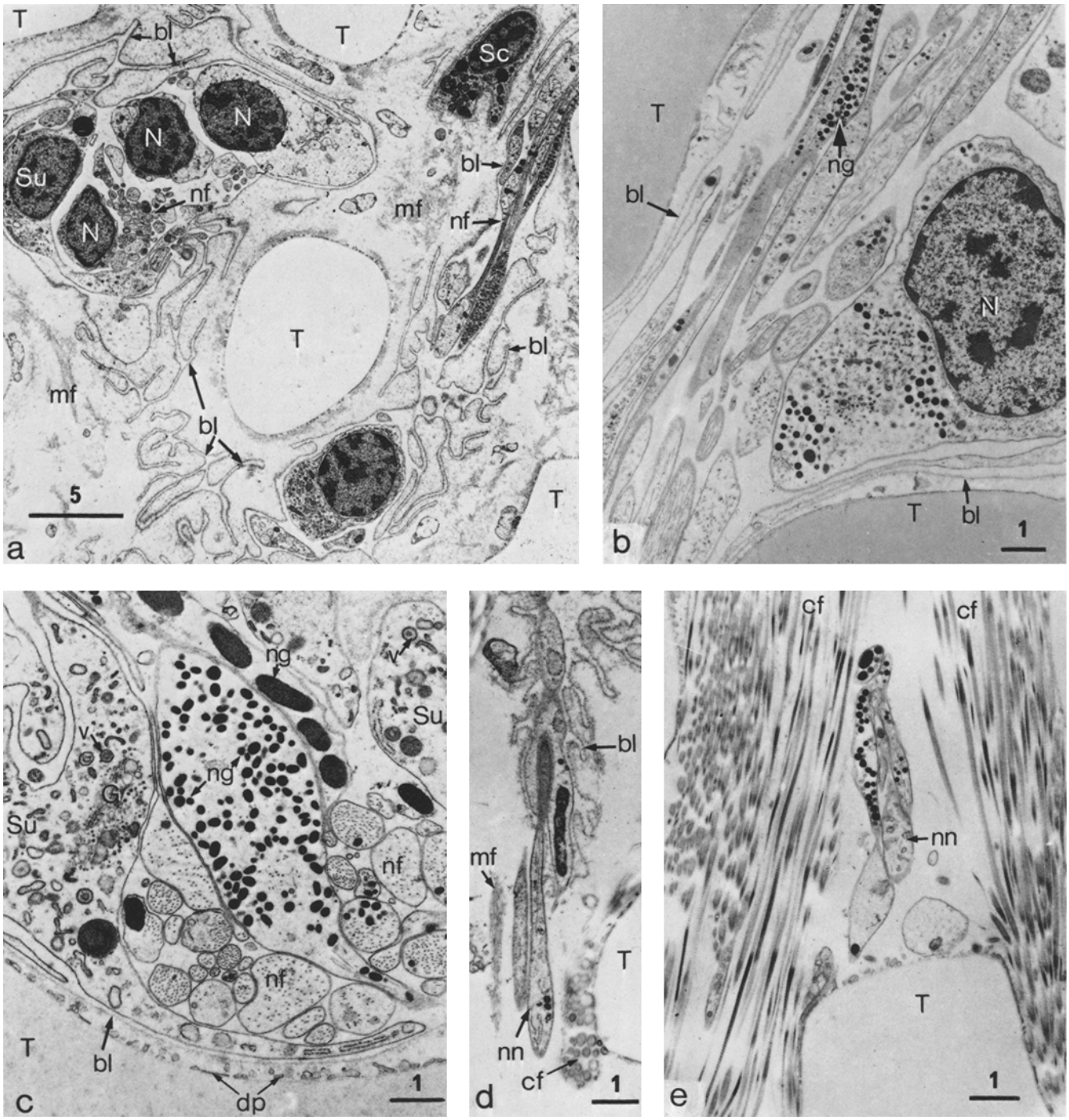

Fig. 7. **a** Scale transversaly cut at the level below the outermost epidermal cells showing the epidermal nerve plexus. **b** Supposed nerve cell (*N*) with dark granules and nerve processes partly containing granules (*ng*) **c** Part of a supporting cell (*Su*) which envelops nerve processes **d** A naked nerve process (*nn*) near a sheathed nerve bundle **e** Naked nerve processes in between collagen fibers (*cf*). Measurements in μm

parallel with the shape of the cells and forms folds which are often too narrow to contain cellular elements (Figs. 6a, 7a). The cytoplasm of the supporting cells contains peculiar vesicles (*v*, Fig. 6a inset) which have a medium dense content and exhibit partial invagination. Vesicles of this sort do not occur in other cells of the tissues investigated. Supporting cells are not restricted to the surface but occur also in the interior of the scale accompanying the epidermal nerve plexus (Fig. 7c).

The supporting cells bear the cuticle. Vertically arranged lobes (*lo*, Figs. 3a, 6f) arise from the horizontal laminae (*hl*) of the supporting cells and give rise to numerous microvilli (*mv*). Thus, in horizontal (tangential) sections, the bases of the microvilli are often arranged in lines (Fig. 6f). The ophiuroid cuticle has been described in detail by Martínez (1976) and Holland and Nealson (1978). According to these authors it consists of a thin fibrous outer layer, a granular middle layer, and a thick fibrous inner layer. In *O. longi-*

cauda the middle and inner layers (Fig. 6b–g, cu_m, cu_i) are well developed, whereas the outer layer is lacking. (The outer layer is probably not a true part of the cuticle but results from the heavily stained tips of the microvilli which in most species are all of the same length.) In sections stained with ruthenium red, flocculent precipitates (*mu*) occur between cell surface and cuticle and heavily stained bubbles adhere to the cell surface and the microvilli (Fig. 6e). Ruthenium red is said to be complexed with the acid mucopolysaccharides (Luft 1971).

The inner cuticular layer is often very thick, its fibrils running in different directions but mainly parallel to the surface. In places, however, thick bundles run vertically downwards to meet the horizontal stretched cytoplasmic lamina (*hl*) of a supporting cell within a "coupling area" (Fig. 6g, *ca*). The latter is packed with tonofilaments which traverse the lamina vertically and terminate in hemispherical half-desmosomes at its lower face. A cell-free columnar-shaped part of the stroma arises towards each coupling area. It contains unstriated microfibrils (*mf*) which vertically meet the lower face of the coupling area's basal lamina. This unique connection between cuticle and connective tissue ('fibras de union') was described for the first time by Martínez (1977b) from the podial wall of *Ophiothrix*. Aside from the tonofilaments within the coupling area, all the anchor fibers are extracellular in origin. It is probably due to these coupling areas that in ophiuroids the tonofilaments do not traverse the whole length of the supporting cells as in echinoids (Weber and Grosmann 1977; Märkel and Röser 1983a). Coupling areas are rare within the free surface of the scales. They are arranged most closely in the folds between succeeding scales and especially in the ophiuroid teeth where they fasten the highly stressed cuticle.

In contrast to the adjacent supporting cells the ciliated cells (Fig. 3a, *C*) are cylindrical in shape. They are often grouped within the same pore and united with the neighbouring cells by long septate junctions (Fig. 3c, *sj*). Numerous longitudinally arranged microtubules range from the nuclear region to the distal surface. The extremely short cilium (*ci*) is club-shaped; it measures 1.5–2 µm in length and projects at most 0.7 µm over the cuticle (Fig. 3b). Nevertheless, it is provided with a long striated rootlet (Fig. 3c, *rl*) and a second basal body (*bb*). In contrast to the opinion of Martínez (1977a), the shaft part of the cilium contains the central microtubules. However, the cilium's basis where the central microtubules are absent is long in relation to the shaft (Fig. 3d, e). Each cilium is surrounded by (normally eight) radially arranged cytoplasmic lamellae each of which bifurcates in microvilli-like processes. The latter exceed in diameter the microvilli of the supporting cells and lack their electron-dense pommels. The cuticle is interrupted in this area. Except for the shortness of the cilium, these cells reveal a striking similarity to the choanocyte-like cells described from echinoderm coelom epithelia by Nørrevang and Wingstrand (1970).

Immediately below the level of the outermost nuclei, strands of axonal processes run in different directions (Figs. 3a, 7a, *nf*) and penetrate the whole scale. Without exeption they are sheathed with basal lamina or, in other words, they run within the epidermis. These strands eventually unite to form large nerve cords which are continuous with the radial nerve cord. They contain lengthwise-stretched microtubules and vesicles of different shapes and diameters (Fig. 7g, *ng*) which often crowd together at one side allowing the microtubules to pass without hindrance (Fig. 7b). Bodies of nerve cells (*N*) which likewise contain dark granules lie in this region. Sunken supporting cells (Fig. 7c, *Su*), recognizable from their characteristic vesicles, occasionally attend the nerve bundles.

At the level of the collagen bundles, strands of thin nerve fibers occur which are naked (not ensheathed by basal lamina) but provided with the same neurogranula mentioned (Fig. 7e). Within the scale they only occur in the collagen-containing part. Scattered naked fibers lie also within the connective tissue sheath, and each bundle of collagen fibers which runs through the pores of the vertebrae in order to connect arm joints is likewise provided with naked fibers. Naked nerve fibers have been figured by Wilkie (1979) from the intervertebral ligament of *Ophiocomina*. He fully described the granules that they contain and suggests that they control the ligament's tensile stress. However, these granules are also present in sheathed nerve fibers and far from the collagen bundles.

D. Discussion

1. Sclerocytes

The main function of the sclerocytes is the formation of the calcite skeleton. Moreover, they obviously produce extracellular microfibrils which in some places may combine to form striated fibrils. Neither microfibrils nor collagen fibrils have anything to do with calcite deposition itself, although they are often abundant in the regions of calcite deposition. Echinoderm ossicles are connected with one another by collagen fibers which pass through their outermost pore spaces, and the ossicles grow peripherally. However, these two facts are independent of each other. Unaware of these details, several authors have called the fibrils the skeleton's organic matrix (Travis et al. 1967; Pucci-Minafra et al. 1980). However, very young trabeculae are wholly encircled by a continuous cytoplasmic sheath of sclerocytes and calcite deposition occurs within an intracellular or intrasyncytial space. This has also been seen in ultrastructural investigations on larval skeletons (Gibbins et al. 1969) and echinoid teeth (Kniprath 1974; Märkel unpublished). Calcite deposition takes place in the space between sheath and calcite which is filled with a clear fluid. The sclerocytes are the only syncytial cells within the scale tissues. Heatfield and Travis (1975) emphatically disagree with the opinion that the skeletal elements are intracellular with respect to the sclerocytes. Indeed, fully grown calcite trabeculae are covered with filamentous cytoplasmic processes (*dp*) in place of a continuous sheath. Thus, they become partly uncovered and the question whether they are intra- or extracellular in position becomes invalid. Incidentally, it is impossible to decide whether or not the sclerocytes are still syncytial. In half-grown ossicles the fully grown trabeculae are covered with distal processes, whereas the growth face is still covered with a continuous sheath which seals this face, as well as a space between sheath and calcite, off from the environment (Märkel and Röser 1983b). The enclosed space is obviously necessary for calcite deposition, and it fully corresponds to the intrasyncytial space of young stages.

In the vertebrate bone, on the contrary, the osteoblasts provide collagen fibrils as well as apatite crystals both

firmly combined. According to Jefferies (1980) echinoderms and vertebrates are sister groups, and the stem vertebrates still had a calcite skeleton of the echinoderm type. Assuming that this hypothesis is true, the sclerocyte represents the more primitive type compared with the vertebrate osteoblast. This suggest that a stem vertebrate sclerocyte, the very first osteocyte, had the ability to combine both its products to form a composite material, the bone. Composite materials are also produced by echinoderms (sea urchin teeth) but in a totally different manner (Märkel et al. 1977).

2. *Epidermis*

Unlike previous studies the present ultrastructural investigation shows that (i) ophiuroid scales are provided with an epithelium composed of individual cells and (ii) sensory cilia over the areas of the arm scales are present.

The cuticle is obviously produced by the supporting cells. Although the synthesis of the cuticular substances and their release was not observed, the secretory droplets of medium density within their distal lobes (Fig. 6c, *sv*) and the heavily stained ones within the microvilli (not figured) probably contain the precursor substances of the cuticle. The thickness of the cuticle and the shortness of the epidermal cilia may be interpreted as an adaptation to the peculiar mode of ophiuroid movement, which is performed by snake-like motions of the arms kept in contact with the bottom. The ambulacral tentacles are rarely involved. The cuticle is, therefore, more stressed than in other echinoderms and it seems likely that its unusual linkage with the dermis by means of coupling areas is developed in order to withstand this stress. Moreover, cilia of normal length seem unsuitable under these conditions and are replaced by shorter ones. Ophiuroids are known to lack highly developed sense organs. The club-shaped cilia are numerous and obviously play the most important sensory role, which Smith (1965) took to be held by free nerve endings.

The ophiuroid nerve system has been studied mainly with respect to its main cords (Cobb and Stubbs 1981; Stubbs and Cobb 1981) and its role in autotomy (Wilkie 1978a–c; 1979), whereas the epithelial nerve plexus is known from the tube feet (Martínez 1977c). We only incidentally studied the unique structure of the epidermal nerve plexus within the scale. It seems likely that the sheathed and the naked nerve strands differ in function, although both contain granules of the same structure. It is noteworthy that the naked strands are restricted to areas which contain collagen bundles and that each bundle contains few fibers of this sort. These findings suggest that the nervously mediated changes in mechanical properties of the ophiuroid connective tissue (Wilkie 1978a) are due to naked fibers.

The structure of the ophiuroid nerve plexus is unique among echinoderms. Echinoderms have a well developed basiepithelial nerve plexus containing strands of nerve fibers and ganglion cells (Weber and Grosmann 1977). Normally, for instance in echinoid spines, the epithelium occupies at most the outermost pores (Pilkington 1969; Märkel and Röser 1983a), whereas in the spines of the echinoid *Diadema* it is more sunken (Burkhardt et al. 1983). Nevertheless, even in *Diadema* the epidermis and its basal nerve plexus are clearly restricted to the surface and not intermingled with stroma tissue.

3. *Cilia and related structures*

Monociliated cells are a common feature of all echinoderm epithelia. Rudimentary cilia have previously been observed in muscle cells lining the tube feet of *Ophioderma brevispinum* (Gardiner and Rieger 1980). The present investigation shows that a cilium or rootlet-like structures normally associated with a cilium may occur even in cells which are normally devoid of a cilium (e.g. supporting cells, sclerocytes, phagocytes). This striking finding suggests that nearly all echinoderm cells are potentially monociliate and have the *anlage* of a cilium at least early in their life cycle. This hypothesis is strengthened by most recent investigations on the teeth of the echinoid *Eucidaris* (Märkel unpublished). Sea urchin teeth grow continually and their basal growth region contains an aggregate of proliferating cells which is the site of odontoblast production and shows a considerable amount of mitotic activity. The cells of this aggregate have a free cilium and two basal bodies and rootlets. The differentiated odontoblasts, however, no longer possess cilia. This finding suggests that the above mentioned ciliated cells or cells with remnants of cilia structures are cells in an early stage of differentiation.

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Abbreviations

A	apical shield	*m*	mitochondrium
asp	secretory products	*mf*	microfibrils
B	bacteria	*mu*	mucus
bb	basal body	*mv*	microvilli
bl	basal lamina	*mvb*	multivesicular body
C	ciliated cell	*N*	nerve cell
ca	coupling area	*n*	nucleus
ci	cilium,	*nf*	neurofibrils
cf	collagen fibrils	*ng*	neurogranules
cs	cell surface	*nn*	naked neurofibrils
CTS	connective tissue sheath	*O*	oral shield
cu_i	inner cuticular layer	*P*	tube foot
cu_m	middle cuticular layer	*Pc*	phagocyte
dp	distal processes (Sc)	*pg*	pigment granules
EC	epineural canal	*rl*	rootlet
G	Golgi complex	*RN*	radial nerve
gv	granular vesicle	*RV*	radial vessel
H	haemal vessel	*Sc*	sclerocyte
hb	homogeneous body	*sh*	cytoplasmic sheath (Sc)
hl	horizontal lamina (Su)	*sj*	septate junction
j	cell junction	*Su*	supporting cell
L	lateral shield	*sv*	secretory vesicle
le	boundary layer (Sc)	*T*	calcite trabeculum
lo	distal lobe (Su)	*V*	vertebral ossicle
M	intervertebral muscle or its attachment	*v*	vesicle (Su)

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