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Observations on the ultrastructure of the proboscis epithelia in Polycystis naegelii Kölliker (Turbellaria Eukalyptorhynchia) and some associated structures

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Abstract

SCHOCKAERT, E. R. & BEDINI, C. (Limburgs Universitair Centrum, Diepenbeek, Belgium and Istituto di Biologia Generale, Universita di Pisa): *Observations on the ultrastructure of the proboscis epithelia in Polycystis naegelii* Kölliker (Turbellaria Eukalyptorhynchia) and some associated structures. — In: T. G. KARLING & M. MEINANDER (eds.), The Alex Luther Centennial Symposium on Turbellaria, Acta Zoologica Fennica 154:175—191. 1977.

The epithelium of the anterior tip of the bodywall, of the proboscis cavity and of the proboscis cone in *Polycystis naegelii* has been studied with the electronmicroscope. These epithelia are formed by six syncytial belts separated from each other by cellular limits: one belt belongs to the epidermis, three line the cavity and two cover the cone. The posterior belt of the cavity and those of the cone are of the insunk type bringing about a peculiar relationship between the latter two. Moreover, they are associated with muscular elements under the basal cone belt but above its basement membrane. Nine different kinds of glands have been observed erupting at the surface of the epithelia in the studied area, while six different sorts of sensorial receptors are associated with them.

Our knowledge from lightmicroscopy of the proboscis of Polycystididae as well as some earlier electronmicroscopic observations on Turbellaria are commented and some conclusions for the systematics discussed.

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I. INTRODUCTION

All authors working on Polycystididae (or Kalyptorhynchia in general) under the light microscope, have paid attention to the proboscis. One of the most accurate descriptions is that of MEIXNER (1925) largely still valid today. To our knowledge electronmicroscopic data on the proboscis of Eukalyptorhynchia have only been given by RIEGER and STERRER (1975) on *Florianella bipolaris* Rieger & Sterrer, 1975, by DOE (1976) on *Gnathorhynchus* spec. and *Florianella bipolaris* and by REUTER (1975) on *Gyratrix hermaphroditus* EHRENBERG 1931. These authors restricted their attention to certain aspects with which they were concerned at the moment of their investigation.

The necessity of more detailed electronmicroscopic studies on the proboscis of Polycystididae was felt by the first author (E.R.S.) while studying this organ under the lightmicroscope, and suggested this subject for the underlying investigations. He is also responsible for the comparisons of the results with lightmicroscopic observations and for the final considerations. The major part of technical elaboration was performed by the second author (C.B.). The observations

and descriptions with EM are the result of collaboration.

In this contribution we describe the epithelial elements of the proboscis of *Polycystis naegelii* KÖLLIKER, 1845 as detailed as possible. Since these elements are often used in phylogenetic considerations (see e.g. KARLING 1963, RIEGER 1974) these data can be usefull when completed with comparable studies on the conorhynch of other Eukalypthorhynchia.

Acknowledgements

The first author acknowledges following persons and institutions: Prof. Dr. F. Papi, Director of the Institute for General Biology of the University of Pisa (Italy), as well as his scientific and technical staff for the kind reception; Prof. Dr. Tongiorgi, Director, and the staff of the "Aquario" of Livorno (Italy) for the help in collecting the material; the "Universitaire Stichting" (Belgium) for the financial support. He also wishes to thank Prof. Dr. Roeck of the Limburg Business School for linguistic correction of the text.

Abbreviations in the figures

1—6	successive syncytial belts (1 beeing the anterior belt of epidermis)
b	brain
bm	basement membrane
c	collar (of receptor)
fi	fixator muscles of bulb
g	gland (indices: explanation in text)
ic	insunk nucleiferous cellparts
kc	kinocilium
lm	longitudinal muscles (surrounding cavity and bulb)
m	mitochondrium
mc	muscles surrounding cavity
n	nucleus
pb	proboscis bulb
pc	probocis cavity
pp	proboscis pore
r	rhabdites
s	sensory element
sc	subepithelial cell strand
sd	septate desmosome
se	septum surrounding the bulb
sm	subepithelial muscle

II. MATERIAL AND METHODS

All specimens of *Polycystis naegelii* were collected from algae, at Livorno (Italy), in July 1975 and 1976. They were fixed in 1% OsO_4 in phosphate buffer 0,13 M, 0,06 M, 0,028 M with 0,7 % NaCl or in 2 % gultaraldehyde in 0,1 M phosphate buffer with 10 % sucrose for 1 h at low temperature and post fixed in OsO_4 1 % in the same buffer. The letter fixative was used after relaxation in 7 % $MgCl_2$ (40 min.). Best results were obtained with the last fixation, while results with OsO_4 in 0,06 M buffer were acceptable. Flat embedding was performed in Epon-Araldite after dehydration in alcohol series and in propyleneoxide. Sectioning was done on LKB or Porter-Bloom ultratome, staining with uranyl acetate and lead citrate and viewing under a Siemens Elmiscope 1/A.

III. OBSERVATIONS

A. The covering epithelia (Fig. 1)

The epithelium of the considered area can be called semisyncytial, though not in the sense as used by REUTER (1975: 192). We can indeed observe six zones clearly separated from each other by cellular limits perpendicular to the surface. Since they are circumferential we can call them epithelial belts, each belt being a syncytium on its own. The two by two contacts between these belts are achieved by a zonula adhaerens and deep septate desmosomes, sometimes completed by maculae adhaerentes (Figs. 3a, 4, 7, 8, 9, 10, 11, 13, 14, 15). One belt belongs

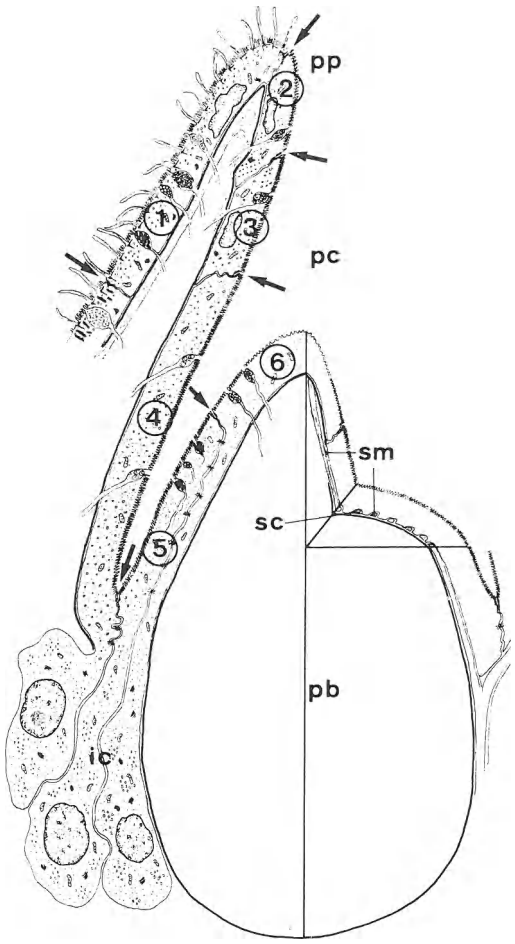

FIG. 1. Highly diagramatic reconstruction from electronmicroscopic data of the proboscis in *Polycystis naegelii*, showing epithelial elements. Successive syncytial belts indicated by encircled figures, their borders by arrows.

to the body wall (ciliated), surrounding the proboscis pore, three belts line the proboscis cavity (without cilia), one forms the basal part of the cone epithelium while the last syncytium forms the apical cap of the latter (both without cilia). As customary we shall call the zone where cavity- and cone epithelium contact each other the junction or contact zone.

1. The body epithelium
(Figs. 3a and 3b)

The description of the epidermis and its basal membrane as given by BEDINI & PAPI (1974) and by REUTER (1975) with electronmicroscope for *Gyratrix hermaphroditus* is largely valid for *Polycystis naegelii*. In the latter species it is some 8—10 µm high and provided with dermal rhabdites, lacking in *Gyratrix*. These rhabdites vary in size (1,5—3 µm and more) and in appearance. They consist of a very electron dense material, packed at the irregular circumference and reticular in the centre. (With the 0,13 M-OsO_4 fixative they seem to erupt at the surface). Some of our observations suggest that this material is formed by the confluence of granule-filled vesicles, presumably originated from the numerous Golgi apparatuses. As properly noticed by REUTER (1975:192) the ciliary rootlets parallel to the epithelium surface are directed forewards.

As known from light microscopic studies, the body epithelium surrounding the proboscis opening is free from rhabdites. This region is constituted by the first syncytial epithelial belt mentioned before. It ends at the most anterior tip of the animal, its border being located around the proboscis opening and attached to the cell wall of the anterior belt lining the cavity (Fig. 4).

Ducts of five different kinds of glands (described below) pass through the whole epidermis (two in *Gyratrix* according to REUTER), but in varying relative abundance to the area considered. They are connected to the epidermis by circumferential septate desmosomes. When the slightly swollen gland ducts are empty, as in most preparations for lightmicroscopy, they leave the columnar or spongy appearance of the cytoplasm as described by MEIXNER (1925:261).

The dark staining of the surface of the epithelium in lightmicroscopic preparations is obviously due to the prescence of microvilli (described by MEIXNER as "Verfestigung des Plasmas" or "Cuticularschicht").

2. The proboscis cavity

As mentioned before, the epithelium

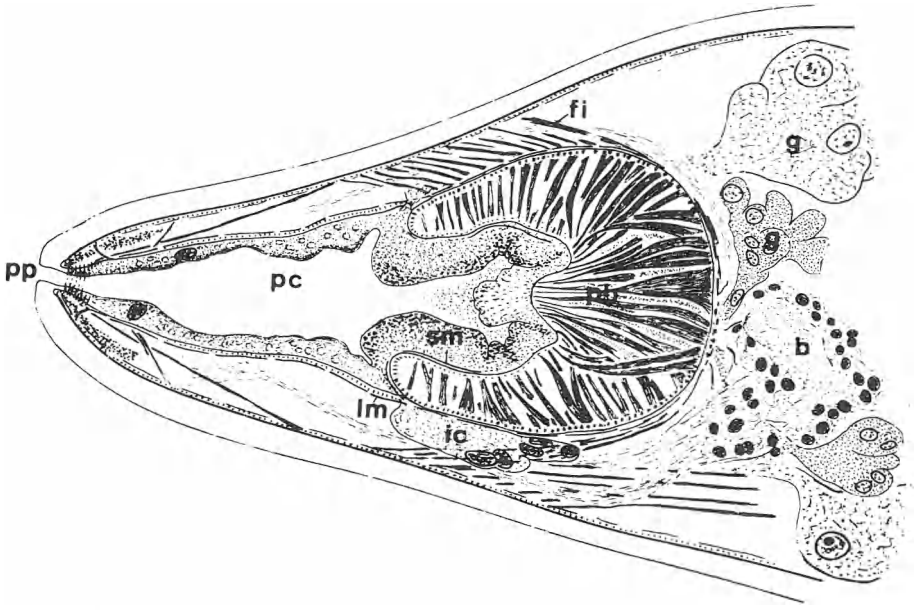

FIG. 2. Sagittal reconstruction (from the left side) of the proboscis in *Polycystis naegelii* from lightmicroscopic serial sections.

of the proboscis cavity consists of three successive syncytial belts. The anterior and median belt possess several lobate nuclei, while the posterior (proximal) belt is of the so called insunk type, i.e. with the nucleiferous cellparts lying under the basement membrane. The connection between the superficial layer and the insunk part of this syncytium is achieved through pores in the basement membrane at the juction (Figs. 8, 19, 20). The insunk cellparts, described below contribute to the formation of the cellular mass surrounding the bulb (Figs. 2, 19).

The surface of the anterior (distal) belt (Figs. 5, 6) is covered by microvilli, some 650 nm high, more or less coniform and slightly twisted. No glycocalyx is present. Near the proboscis opening the basement membrane consists of the same two layers as under the body epithelium and is continuous with them. The inner fibrous layer (here with irregular arrangement of the fibrils) gradually vanishes posteriorly. The remaining lamella that adheres to the basal epithelial plasmalemma becomes less electrondense. The cytoplasm of the distal belt has a very clear and homogenous matrix, rare Golgi's, dispersed longitudinally directed mitochondria and some multilamellar bodies. Its most conspicious feature are numerous hyaline vesicles of some 180 nm diameter in the superficial layer, while smaller vesicles (50 nm) form cheplet-like chaines in the basal 3/4 of the cytoplasm. Occasionally a gland duct with the same secretion as in the lower belts can be observed.

The microvilli at the surface of the

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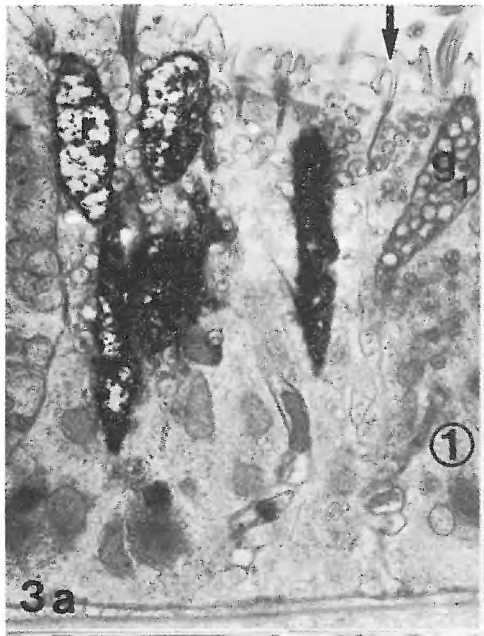
FIGS. 3—6. — 3a and 3b. Longitudinal sections of epidermis showing rhabdites and the five different glandular secretions. The anterior tip of the animals is to the right; limits between epidermis of the body and of its anterior belt (arrow) (x 8000- glut.). — 4. Borders between epidermis and anterior syncytial belt of the cavity epithelium at the proboscis opening in longitudinal section (arrow) (x 11400 — glut). — 5. Cross section trough the anterior belt of the cavity epithelium. Note the chaplet-like arrangement of the small vesicles (x 7800 OsO_4 0,13 M). — 6. Higher magnificition of the same section (x 40000).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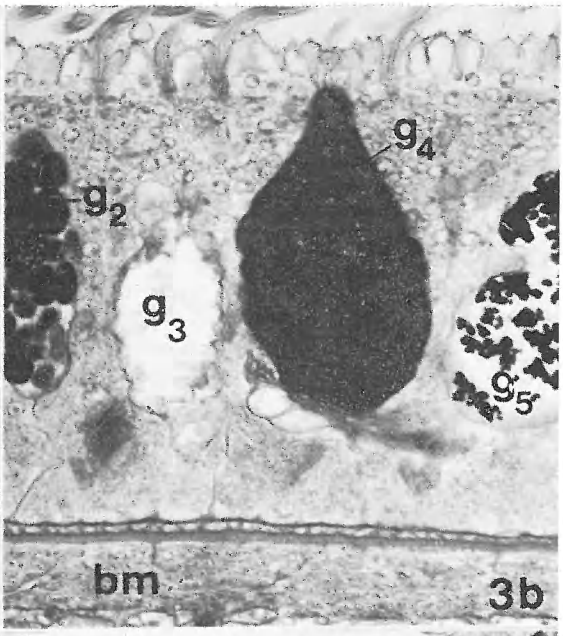
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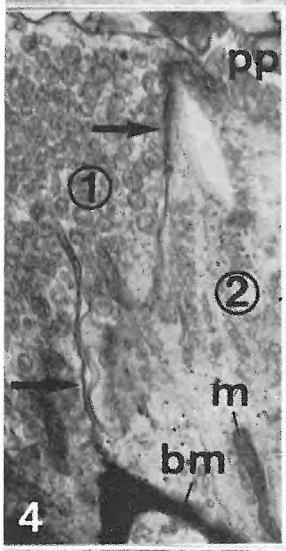
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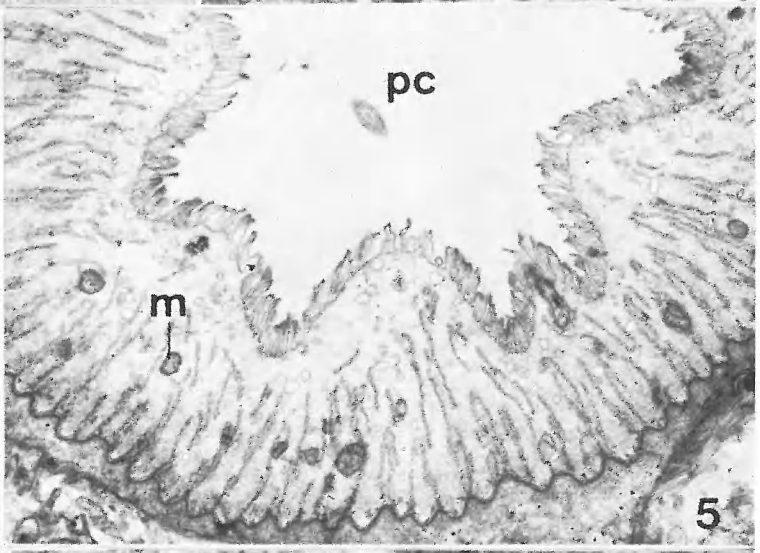
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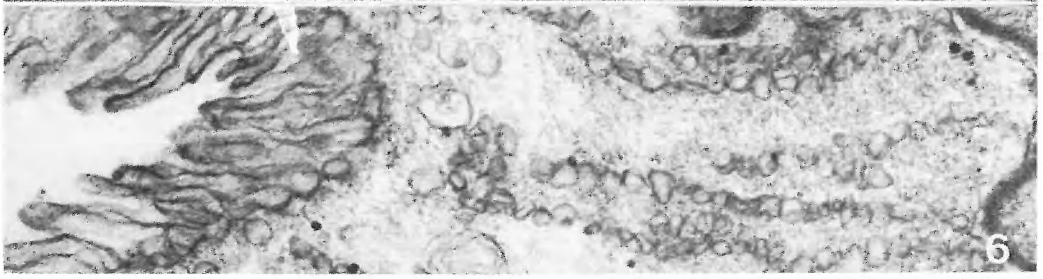
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median and proximal belts (Figs. 7 and 12) are 600 nm long, straight and cylindric. They are closely packed with some 12 microvilli per µm.

The matrix of the cytoplasm is slightly more electrondense then in the distal belt, with rather pronounced fibrous aspect, though without the formation of a real cellweb. Again numerous membrane bound vesicles can be observed, here without the striking regular arrangement as in the distal belt. Moreover, electrondense 25 nm large particles with a clear centre are spread through the cytoplasm (Figs. 10, 11, 12). Lobate nuclei and some Golgi apparatuses occur in the median belt, lacking in the proximal one where these organelles are to be found in the insunk cellparts. Glandducts, all with the same secretion content are rather abundant (Figs. 7, 12).

B. The proboscis cone

The distinct apex of the cone, well known for most Polycystididae by lightmicroscopy, is formed by a syncytium of its own, well separated from the basal syncytial belt. Both are of the insunk type, so no nuclei are found above the basement membrane, while the nucleiferous cellbodies are mixed with those of the proximal belt of the cavity. Superficial and insunk part are connected to each other through pores in the basal lamina at the junction. It is quite easily understood how this connection is accomplished for the basal cone belt, but a rather surprising state of affairs is involved for the apex. From this apical epithelial cap twelve symmetrically arranged cellular strands plunge under the basal belt but remain above the basal membrane (Fig. 14) till the junction region is reached where the basal lamina is perforated and contact with the underlaying nucleiferous cellparts is brought about.

Underneath the basal epithelial belt (but above the basement membrane) twelve muscle fibers, split off from the longitudinal muscles surrounding the cavity and the bulb, alternate with the epithelial strands (Figs. 13 and 16). These fibers pierce the basal lamina when reaching the apex, continue under the basal lamina and insert on its inner side.

At all levels, basal and apical epithelial syncytia and muscular elements are distinctly separated from each other by cellborders. Those of both epithelia are attached to each other by a zonula adherens and septate desmosomes near the surface and very numerous maculae adherentes below (Figs. 13—17). Desmosome like structures between the basal cellmembrane of the apex epithelium and inner muscles with the basement membrane in between were observed as well (Fig. 1).

The cytoplasm of the basal epithelial belt resembles that of the proximal and median belts of the cavity, except that no vesicles are present, but the electrondense particles with clear centre are (Figs. 13—16). That of the apical cap (Figs. 13, 14, 18), including the cytoplasm in the strands is extremely electronlucent, and apart from mitochondria, completely devoid of organells.

The microvilli are 450 nm long (ca 10 per µm) at the surface of the basal epithelium and 380 nm (ca 8 per µm, more apart at the very tip of the apex) and without glycoclayx.

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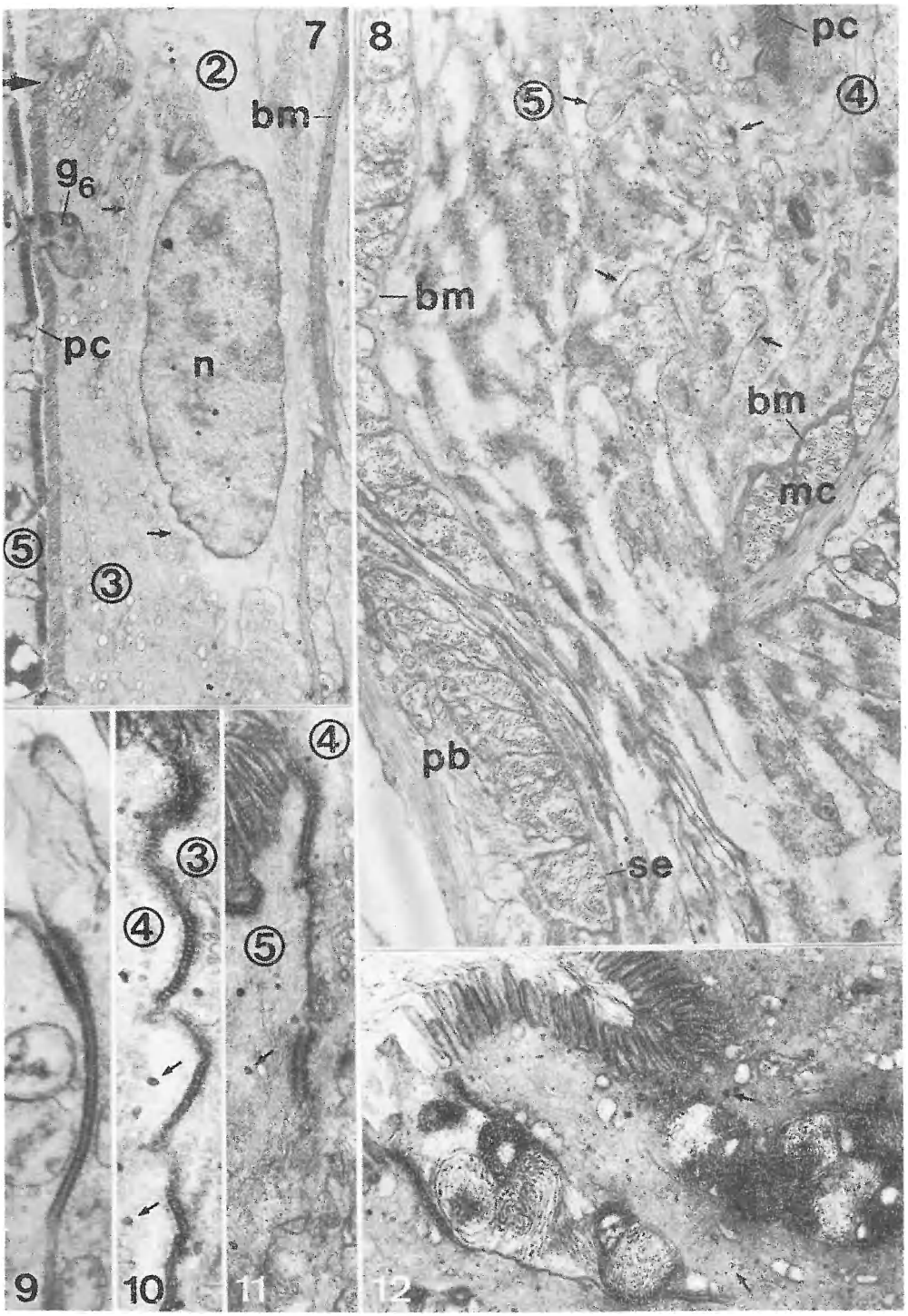
FIGS. 7—12. — 7. Longitudinal section through part of the anterior and median belts of the cavity epithelium, showing the limits between both and a nucleus in the interior belt (x 4750 — glut). — 8. Longitudinal section of the contact zone (junction) with connection of the superficial with the insunk cellparts (here of the cone epithelium). Note the strongly foiled and interdigitating cellboarders at this site and the maculae adherentes (x 2850 — glut). — 9. Cell attachment of the main part of the epidermis to its anterior belt (x 20 000 — glut). — 10. Cell attachment between proximal belt of cavity epithelium and basal belt of cone epithelium (x 47 500 — OsO_4 0,06 M). — 11. Cell attachment between median and proximal belts of the cavity epithelium. Note the electrondense particles with clear centre (x 47 500 — OsO_4 0,06 M). — 12. Terminal part of a gland-duct in the cavity epithelium (median belt). Note fibrillar material adhering to the microvilli (x 19 000 — OsO_4 0,13 M).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Through the basal belt two kinds of glands errupt at the surface, one kind through the apex (Figs. 13, 14, 18).

The subepithelial muscles and the alternating cellstrands under the basal cone epithelium were seen by MEIXNER in *P. naegelii, Polycystis crocea* (FABR. 1823) and *Progyrator mamertinus* (GRAFF, 1874) (not in the other species studied as stressed by the author) but were considered by him as differentiations of the basement membrane ("cuticulare" Differenzierungen, 1925, p. 275). They are depicted by KARLING in *Rogneda hibernica* (SOUTHERN, 1936) (1953, fig. 8), in *Danorhynchus duplostylis* KARLING, 1955 (1955: fig. 19) and in *Annulorhynchus adriaticus* KARLING, 1956 (1956: fig. 10) and also by EVDONIN (1970, fig. 2) for *Phonorhynchus helgolandicus* (METSCHNIKOFF, 1863). They were also mentioned by BRUNET (1965: 166) for *Typhlopolycystis peresi* BRUNET, 1965. In nearly all species of Polycystididae studied by us (i.e. some 65 of about 90 known species, if appropriate sections were available) these structures where without any doubt present and may safely be considered as typical polycystidid features (Fig. 33).

4. The nucleiferous cellparts

As previously mentioned, the nucleiferous cellparts of the proximal cavity belt, of the basal belt of the cone epithelium and of its apex, are found together around the bulb. The basal membrane at the junction is pierced with many pores to leave passage to the epithelial cellular connections (Figs. 8, 19, 20). All insunk cellparts are very much alike and indicating to which belt they belong is impossible. The nuclei are spherical to oviform, surrounded by several Golgi apparatuses. The granular cytoplasm contains many small vesicles and patches of mostly smooth ER. No special secretory activity can be indicated. Distinct cell borders are present between the cell sections governed by a nucleus, and though the exact number of nuclei could not be enumerated, nor in EM nor in LM preparations, it is obvious that several of these nuclei belong to only one superficial belt.

MEIXNER considered the epithelium covering the cone as anucleated. This point of view was corrected by KARLING (1931) studying *Acrohynchides robustus* (KARLING, 1931); he considered the cellmass surrounding the bulb as the insunk part of the cone epithelium (he did so in all later descriptions) and observed the perforations in the basal lamina at the junction. According to both authors this cellular mass contains nuclei of the musclefibers inside the bulb. Where these nuclei are to be found in fact can not be said at the moment.

B. The glandular elements

The excretory ducts of nine different glands perforate the epithelia considered: five go through the body epithelium, one through the cavity epithelium (the three belts), two through the basal and one through the apical syncytium of the cone.

The secretory cellparts are all situated under de basal membrane, highly intermingled and remote from the outlet. Only at the surface the secretory products can be identified, but they are seldom present in the deeper parts of the ducts which are evidently branched. The secretory products found at the body surface are: membrane bound vesicles with con-

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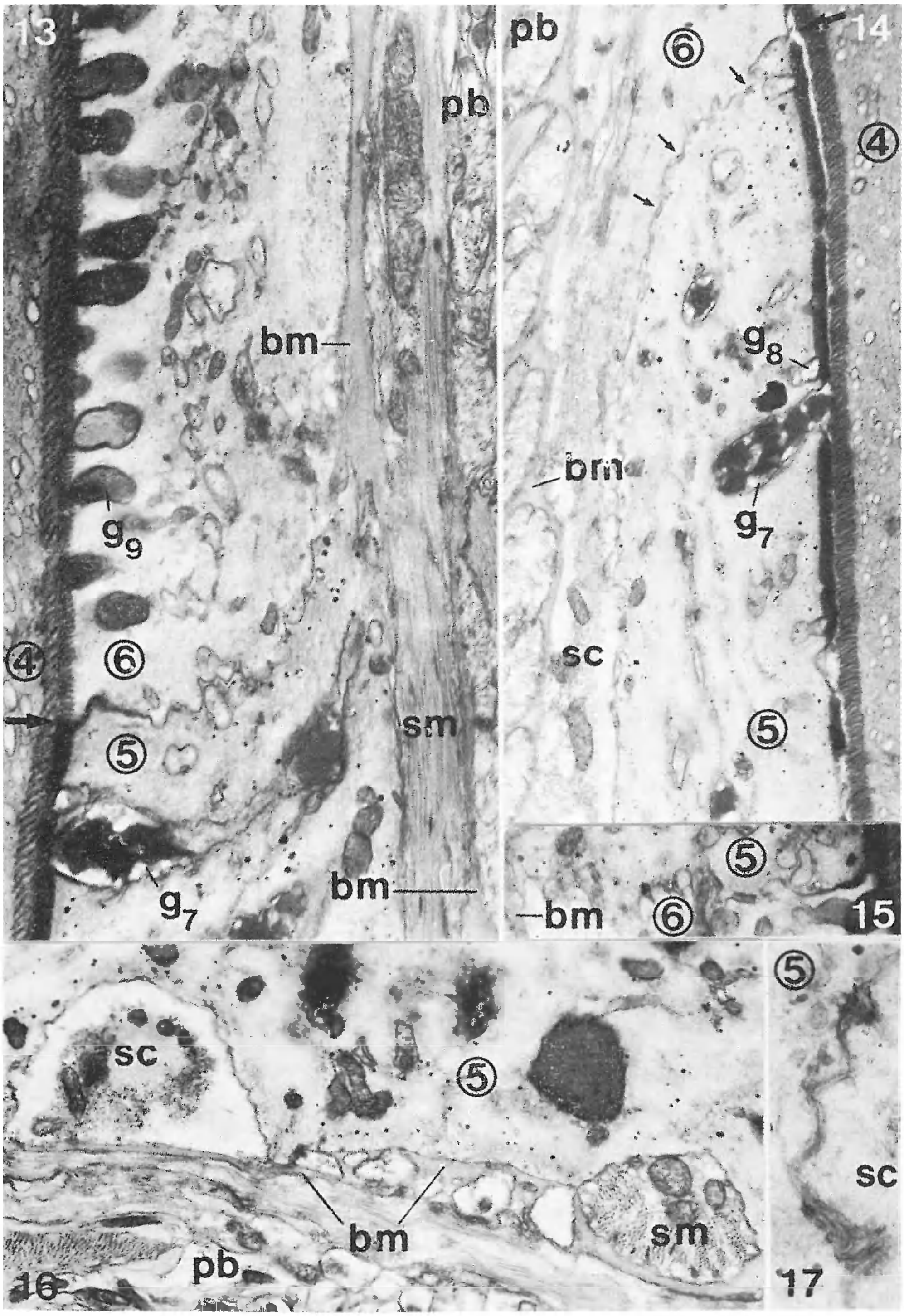
FIGS. 13—17. — 13. Longitudinal section through part of the basal and apical belts of the cone epithelium with the subepithelial muscle perforating the basal lamina. Note different relative length and density of the microvilli of cavity (left) and cone epithelium. (x 5700 — glut). — 14. Longitudinal section through parts of the basal and apical belts of cone epithelium, showing a cell strand from the apical cap running under the basal belt. Note the numerous maculae adherentes (x 5700 — glut). — 15. Limit between apical and basal cone belts, where no subepithelial nucleus nor cellstrand occur (x 7600 — glut). — 16. Cross section through the basal belt of the cone epithelium showing alternating cell strands and subepithelial muscles (x 7600 — glut). — 17. Maculae adherentes between the basal cone belt and a cell strand (appr. 40 000 — glut). —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tent of low electron density (Fig. 3, g_1), highly electrondense spherules (Fig. 3, g_2), a fibrous mass (Fig. 3, g_3) membrane bound balls with granular content of moderate electron density (Fig. 3, g_4) and fine granules of very high electron density (Fig. 3, g_5). Only two glandular secretions have been reported by REUTER in *Gyratrix hermaphroditus* (with "dark granules" and "light granules", l.c.: p. 194). The content of the gland ducts in the cavity epithelium consists of clews of fibrillar material (Figs. 7 and 12 g_6) that often can be found in the cavity itself, adhering to the microvilli. The outlets are less abundant in the anterior belt, increasing in number backwards. The most numerous and most conspicious glandular elements of the basal cone epithelium are ducts filled with large membrane bound spheres with electron opaque content (Figs. 13, 14 g_7). The irregular outline of these spherules is to be considered as an artifact in the material of *Polycystis naegelii.*

The second type of secretion found in gland necks in the basal cone belt are empty membrane-bound vesicles in *Polycystis naegelii* (Fig. 14. g_8), while they bear an highly electrondense core in *Gyratrix* (according to REUTER's picture, fig. 6). The ducts of both these glands penetrate the epithelium at the junction. As far as can be concluded from our observations, they do not go through the muscular bulb. On the contrary, those running to the apex, enter the bulb at its posterior side and pierce the basal lamina under the apical cap itself. They are filled with elongated, membrane-bound rods with finely punctuated content (Figs. 13 and 18, g_9), also in *Gyratrix.*

The proboscis of Polycystididae is usually considered as an adhesive organ. We would therefore expect a kind of duo-gland system as described by TYLER (1976 and 1977) in the adhesive organs of other Turbellaria. Now three different kinds of secretions are present here, the function of which can only be guessed, though a "viscid" and a "releasing" element must be involved. Nor an elaborated cellweb nor specialised microvilli can be indicated which are the usual structures associated with the viscid glands.

As mentioned before, the glandducts in and to the epidermis are mostly empty in lightmicroscopic preparations. In well preserved material eosinophilous and/or basophilous secretions can be observed. The cellbodies of these glands are to be found at the level of the brain and even more backwards. Almost no cellular material (and *a fortiori* no glands) is present between the proboscis cavity and the body wall, nor in light-, nor in electronmicroscopic preparations, except some nerves and of course the glandducts.

No glands have ever been reported in the cavity-epithelium by lightmicroscopists. In *P. naegelii* (and some other large species) we have seen clear vacuoles (Fig. 2) probably the empty terminal parts of the glandducts. Only MEIXNER has given an extensive description of the glandular elements of the proboscis cone. KARLING (div. loc.) sometimes mentions there existence. The secretion in the apex is very fine and eosinophilous under the lightmicroscope; if it is expulsed, the cytoplasm of the epithelium gets a striated aspect. The cellbodies form two pairs of groups, one pair above, the other one under the brain (Fig. 2, g). Their faint ducts converge to the posterior pole of the proboscis bulb, go though several pores of

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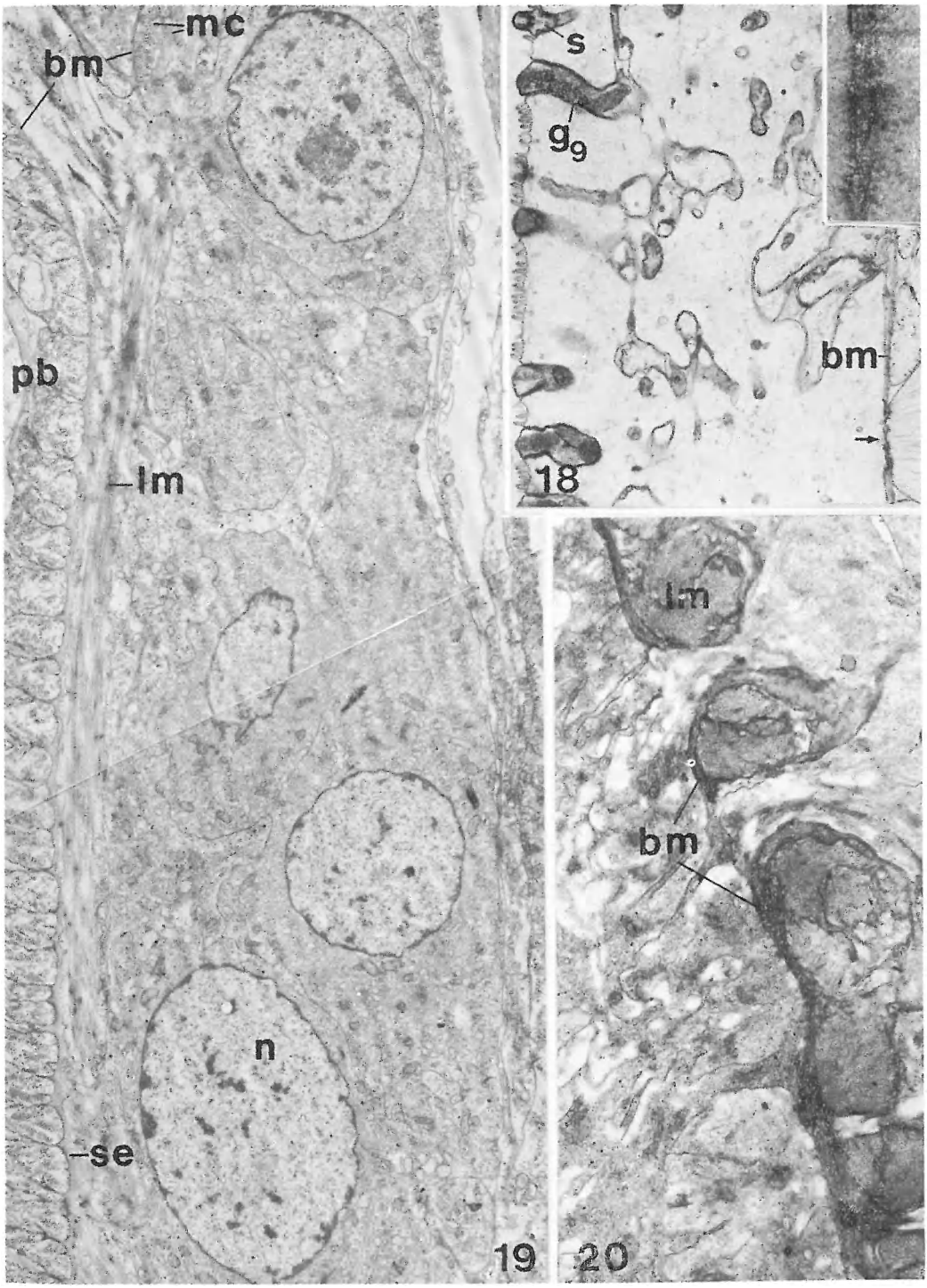
FIGS. 18—20. — 18. Part of the apical cap with glandular and sensorial elements. Note desmosome like structures between epithelium and muscles (x 8000 — glut). Inset: High magnification of the desmosome-like structures, with muscles to the right (x 50 000). — 19. Nucleiferous cellparts in longitudinal sections (bulb at left side). Cellparts governed by a nucleus are clearly boardered, while the connection with the superficial syncytial layer can be seen top left (to be compared with Fig. 18) (x 3000 — glut). — 20. Cross section at the junction with perforations through the basal lamina, leaving passage to epithelial cellular elements (superficial part to the left). Note the strongly foiled and interdigitating membranes (x 3000 — glut).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the septum (also according to EM observations) and straight to the apex [MEIXNER 1925:267, 271, 275 for *Gyratrix hermaphroditus, Opisthocystis goettei* (BRESSLAU, 1905) and *Progyrator mamertinus;* KARLING 1931:15 for *Acrorhynchides robustus;* own observations]. The secretions in the basal epithelial belt of the cone have the appearance of eosinophilous rods, strongly stained by Fe-hematoxyline and are homologized with dermal rhabdites by MEIXNER (1925:267). These rods are evidently the ducts filled with the large electrondense spherules. Two pairs of large glands are situated just behind those which supply the apex and were considered by MEIXNER (1925: 271) as the sites of synthesis for the secretion in the basal cone epithelium. However, according to our own observations the very fine secretion they contain, is actually eosinophilous, but do not take the Fe-hematoxyline. Moreover ducts apparently coming from these glands were seen running to the anterior tip of the animal. Further studies are required.

C. The sensory elements

REUTER (1975) has reported four different types of receptors in the epithelia of *Gyratrix hermaphroditus.* They have all been observed in *Polycystis naegelii,* though slight differences are to be noted for three of them, and two other receptors were found as well. It would be beyond the scope of this paper to treat these receptors to full extent; we give a concise description of the new ones and indicate the differences of the known ones in reference to REUTER's description, using her classification.

1. The receptor type II
(Figs. 21—24)

The cell-attachment of this receptor to the epidermis in *P. naegelii* is achieved by a short zonula adherens and septate desmosomes. The collar of the 8 stereocilia do not exceed the epidermis surface and are some 50 nm apart from the ciliary shaft. The space left in between is filled with an amorph material of moderat electrondensity. In the electronmicrograph reproduced in Fig. 24 there is a faint indication that "accessory" (annular) rootlets may be present as in comparable receptors of some Proseriata (EHLERS & EHLERS 1977). As mentioned by REUTER, this type of receptor occurs in groups. In *P. naegelii* 8 symmetrically arranged such groups, each of them with about 17 receptors form a girdle around the anterior tip of the animal, just behind the posterior limit of the anterior syncytial belt of the epidermis.

2. The receptor type III
(Figs. 25 and 26)

The balloon-like transformed cilium of this receptor exhibits a cytoplasmatic condensation in its centre, but vesicular elements were never observed. Its narrow neck in which the basal body is situated is always surrounded by a funnel-like protuberance of the dendrite. The ciliary rootless is much longer in *P. naegelii* than in *Gyratrix* (nearly 2 µm long), i.e. about twice as long as the balloon, while in *Gyratrix* it is shorter than the balloon is high.

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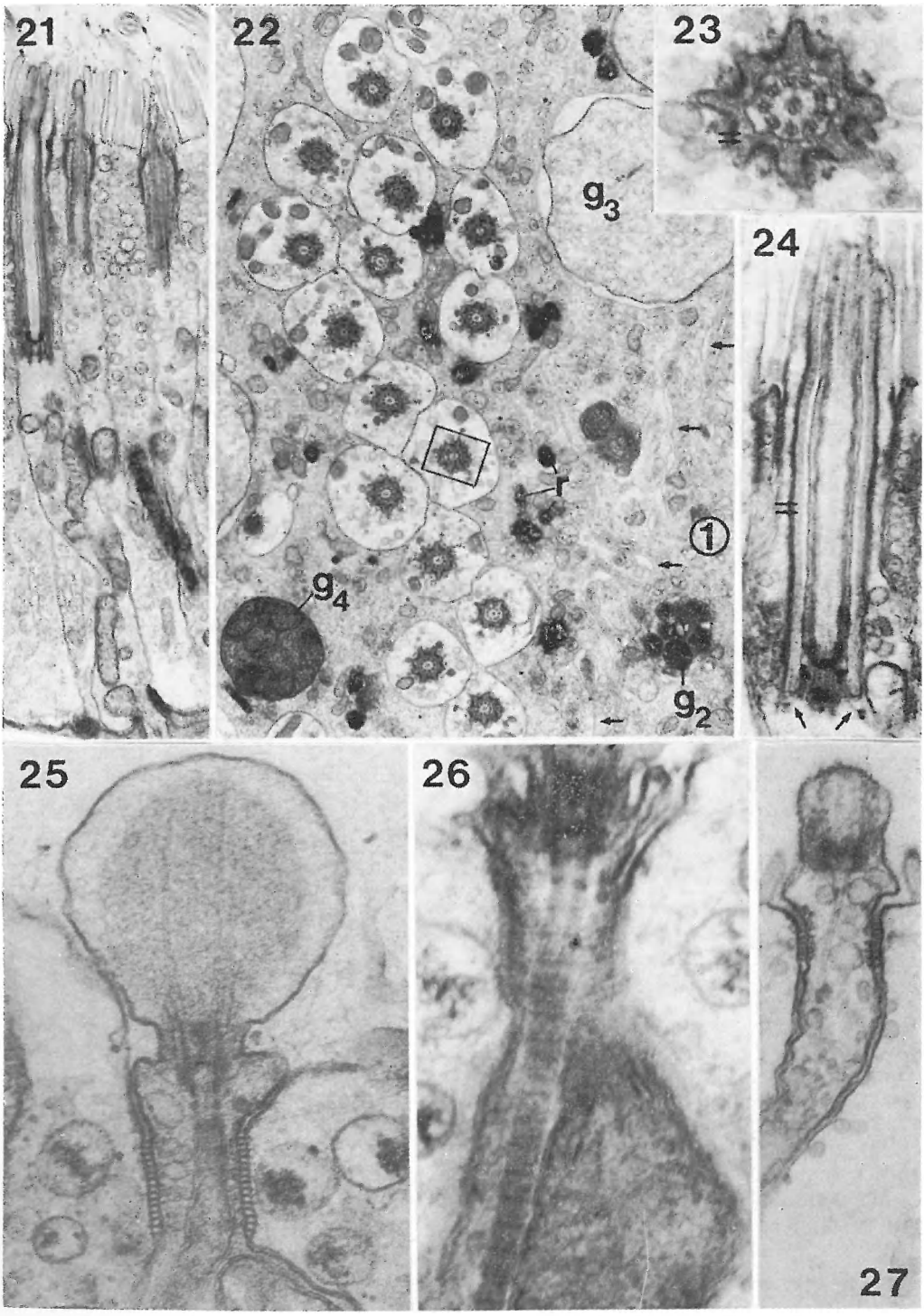
FIGS. 21—27. — 21. Three longitudinally sectioned receptors of type II (appr. x 14 000 — glut). — 22. A group of receptors type II in a tangential section through epidermis. Arrows indicate limit between epidermis and its anterior belt (appr. x 10 000 — glut). — 23. High magnification of the cilium and stereocilia of the receptors indicated in Fig. 22. Note the material between stereocilia and ciliary shaft (appr. x 35 000). — 24. Longitudinally sectioned terminal part of a receptor type II. Note cell attachment, the material between stereocilia and ciliary shaft (double arrow) and indication of "circular rootlet") (x 28 000 — OsO_3 0,06). — 25. Terminal part of the balloonlike receptor type III (x 47 500 — glut). — 26. Basal part of receptor III with rootlet (x 56 00 — glut). — 27. Terminal part of receptor type IV in the apex of the cone epithelium (x 44 000 — glut).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3. The receptor type IV (Fig. 27)

Type IV is the receptor in the cavity and cone epithelium, extremely abundant in the apex (Fig. 18). The great variation due to the "instability of its membrane" (REUTER:201) was not observed. All receptors of type IV had a short blunt ciliary process, often hardly exceeding the microvilli.

4. The receptor type V (Fig. 28)

This peculiar receptor consists of a short cilium and a bulging vesicle. Favourable sections through this receptor were encountered only two or three times; sections through the vesicle alone were seen more often and initially taken for receptors of type III. This receptor is in any way poorly represented, easily overlooked, and more investigations are required. The cilium with moderately long (?) rootlet is pushed aside by the vesicle; whether it is really short as in our electronmicrographs can not be said at this moment. At the side opposite to the vesicle a finger-like protuberance is seen near the cilium and it is not excluded that the base of the cilium is in reality surrounded by a collar with asymmetric swelling filled with vesicular and tubular elements. A zonula adherens and septate desmosomes connect the receptor to the epidermis.

5. The receptor type VI (Figs. 29—32)

Receptors of this type form a girdle (number of receptors not stated) in the bodywall some distance behind the posterior limit of the anterior epidermal belt. The apical border of the dendrite lies some 2 μm lower than the epidermis surface. Around this oval pit (4×5 μm) the neurolemma forms a collarlike fold with which the attachment to the epidermis is performed by septate desmosomes.

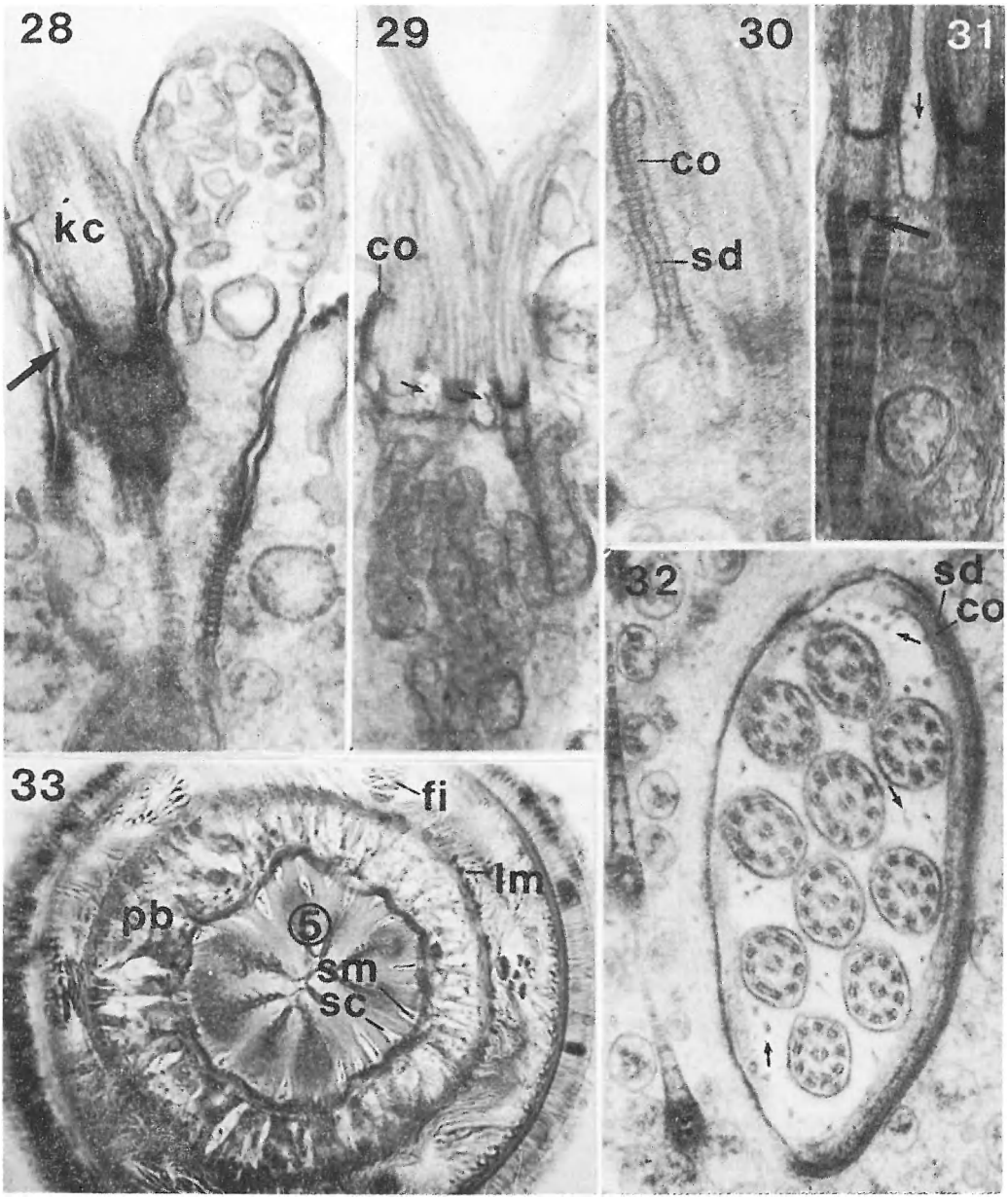
This collar does not exceed the epidermis surface. The 10 cilia originating from the bottom of the pit differ from those of the epidermis by the presence of an electrondense granule at the bottom of the basal body. Some material, resembling the glycocalyx occurs between them. To the best of our knowledge, multiciliary receptors have only been reported for Proseriata (BEDINI et al. 1975). Lightmicroscopic data on receptors are not available for Polycystididae, apart from those of REUTER on the balloonlike receptor of type III (1975:200).

IV. FINAL CONSIDERATIONS

The proboscis within the Polycystididae is a very stable structure with minor variations on a basic theme and therefore not very appropriate for intrafamiliar phylogenetic consideration. One of those minor variations is the different position of the nuclei in the cavity epithelium and it might become interesting for the systematics in the future. Four possible situations with respect to the position of these nuclei are found in the family:

1. several nuclei present in the distal half *(Polycystis, Acrorhynchides . . .);*
2. no nuclei present at all above the basal membrane (Duplacrorhynchinae, *Paracrorhynchus, Progyrator . . .);*
3. nuclei present only at the junction, above the basal membrane *(Phonorhynchus, Cincturorhynchus, Gyratrix, Danorhynchus, Gallorhynchus, Neopolycystis . . .);*
4. nuclei present in the distal half and at the junction *(Rogneda, Annulorhynchus . . .).*

On the other hand MEIXNER (1925: 274) indicates that the number of nuclei diminishes in older individuals, also ob-



FIGS. 28—33. — 28. Longitudinally sectioned terminal end of a receptor type V. Note the finger-like protuberance at the left of the cilium (x 50 000 — glut). — 29. Longitudinally sectioned receptor of type VI (x 20 000 — glut). — 30. High magnification through the collar of a receptor type VI (appr. x 50 000 — glut). — 31. Rootlet and basal body of two cilia of a receptor type VI. Note the electron dense granule at the bottom of the basal body (x 44 000 — glut). — 32. Receptor of type VI in a tangential section through the epidermis, showing circumferential septate desmosomes and the collar. Note glycocalyx-like material between cilia (also indicated in Fig. 29) (x 36 000 — glut). — 33. Cross section through anterior body end in light microscope with basal cone epithelium in the centre, showing subepithelial muscles and cell strands.

served by KARLING (1931:12) in *Achrorhynchides robustus* where often no nuclei are present at all in fully mature individuals.

Different suppositions can be made to explain this state of affairs with our present knowledge of the situation in *P. naegelii:*

For situation 2 mentioned above: only one syncytial belt lines the cavity, with the nuclei in insunk cellparts or, more belts line the cavity, all with insunk nuclei (this would implicate a system of interlacing strands as described in the cone epithelium).

For situation 3: the cavity epithelium consists of only one syncytial belt with incomplete insunk nuclei; or it consists of two belts, the proximal with insunk nuclei, the distal one with incompletely insunk nuclei; or it consists of these belts with different degrees of migration of the nuclei.

For situation 4: the nuclei at the junction are those of the most proximal of three belts, not yet insunk; or they are nuclei of the median belt which initiated their migration.

Other combinations for the four situations can be imagined, but they are all the result of one or both of the following processes: more cellular borders are eliminated at the surface i.e. an increased "simplification in horizontal direction" in REUTER's terminology (1975 201) or the nuclei of more syncytial belt migrate under the basement membrane i.e. an increassed "vertical functiona polarisation" (REUTER 1975). As it ha been discussed by REUTER we can say that, the less this horizontal simplification and/or the vertical polarisation is elaborated, the more apomorph the condition and v.v. In terms of lightmicroscopy this could provisionally be translated as: the more nuclei present in the cavity epithelium, the more apomorph the condition may be, but this characteristic should be used with caution at the moment and the use of E.M. is compulsary.

In our opinion, the underlying electron microscopic observation do not bring any arguments for theories about the evolution of the proboscis in Eukalyptorhynchia (as it was expected by RIEGER 1974). The septum around the bulb has indeed the same morphology as the basal lamina of the epithelium but can also be a product of the muscles (KARLING in RIEGER 1974), since muscle cells are indeed mostly surrounded by a similar coat, even in vertebrates. We have no doubt the main function of the proboscis is an adhesive one, the sensorial function evidently secundary with only one kind of receptors.

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