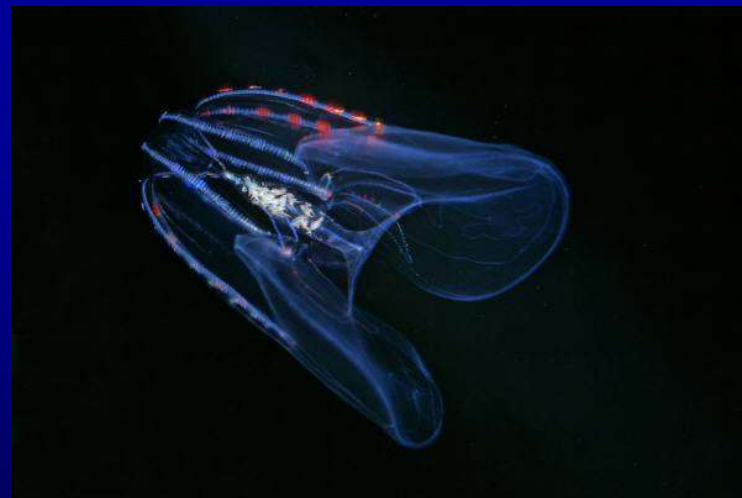
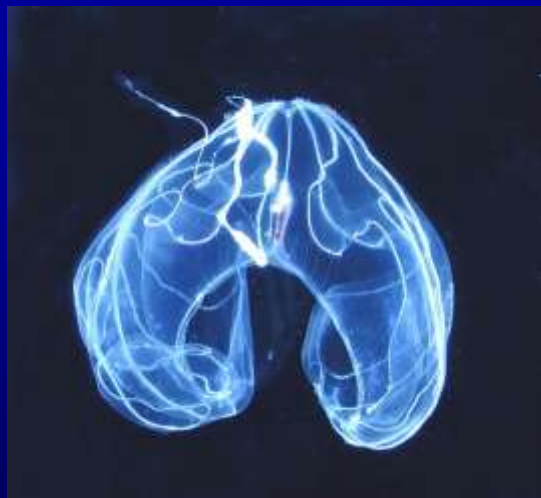




Stenophora = Гребневики



Karl Heinrich Mertens

*Beobachtungen und Untersuchungen  
über die Beroeartigen Acalephen*

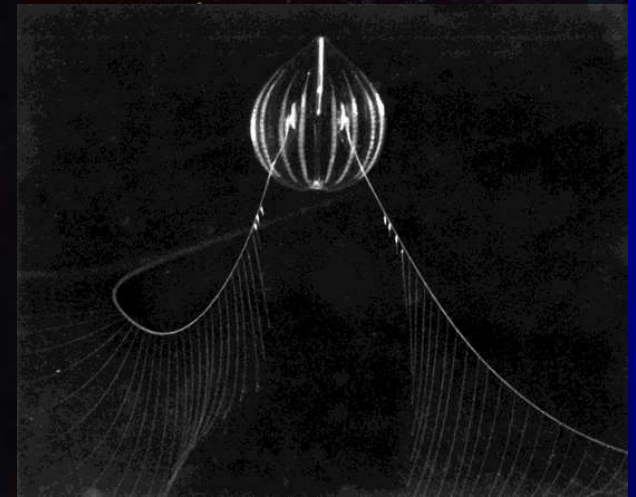
Mem. Acad. Imper. Sci. de  
St.Petersbourg, 1833.  
Ser.6. Vol.2. P.479-544

- *Карл Линней (Carl Linnaeus ) (1707-1778)*
  - Класс Vermes, отряды Intestina (*Lumbricus, Hirudo, волосатики, сипункулиды*), Mollusca (актинии, асцидии, *Terebella, Aphrodite, Nereis*), Testacea (*Chiton, двустворки, Nautilus, гастроподы*), Lithophyta (твердые кораллы), **Zoophyta** (*Volvox, губки, мягкие кораллы, книдарии и гребневики*).
- *Жорж Леопольд Кювье (G. Cuvier) (1769-1832)*
  - Класс **Ascalerphes** (медузы и корраллы), в группе Zoophyta
- *Жан Батист Пьер Антуан де Моне Ламарк (J.B.P.A.de M.Lamarck ) (1744-1829)*
  - Классы Mollusca, Crustacea, Arachnida, Insecta, Vermes, Polypi, **Radiata** (отряд **Mollasses** – мягкотелые, отряд **Иглокожие**)
- *Иоганн Фридрих фон Эшишольц (Johann Friedrich von Eschscholtz) (1793-1831)*
  - отряд **Stenophorae** (класс Ascalerpha, среди иглокожих и других беспозвоночных)
- *Фридрих-Сигизмунд Лейкарт (Rudolf Leuckart) (1794-1843 )*
  - **Stenophora** (в типе Coelenterata: книдарии и губки)
- *Фосмэр (Gualtherus Carel Jacob Vosmaer) (1854 – 1916)*
  - выделил губок из кишечнополостных
- *Бертольд Гатчек (Berthold Hatschek) (1854-1941)*
  - тип **Stenophora**.

*Pleurobrachia species*



*P.pileus*



*P.bachei*



~ 1.5-2 cm

*P.pileus*

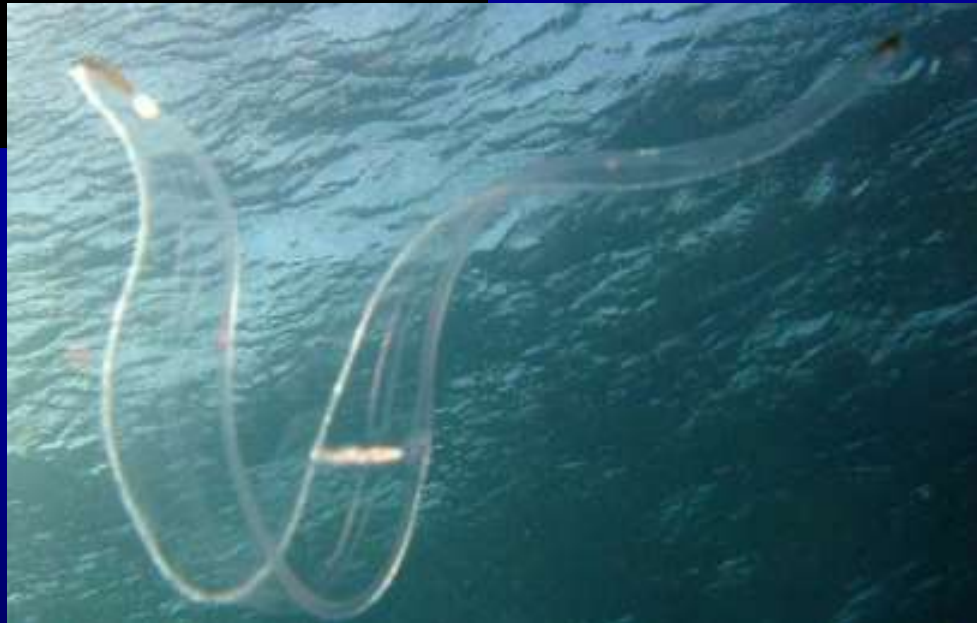
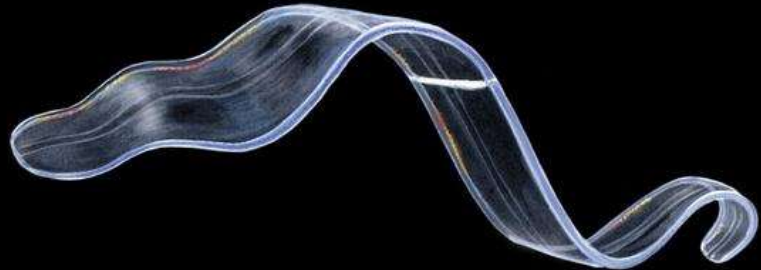
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*Velamen parallelum*

## Cestum species

*C. amphitrites*



*C. veneris*



*Tortugas*



*Eurhamphaea vexilligera*







*Beroe forskalli*



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# Тентиллы



*Pleurobrachia*

© Jim Mastro

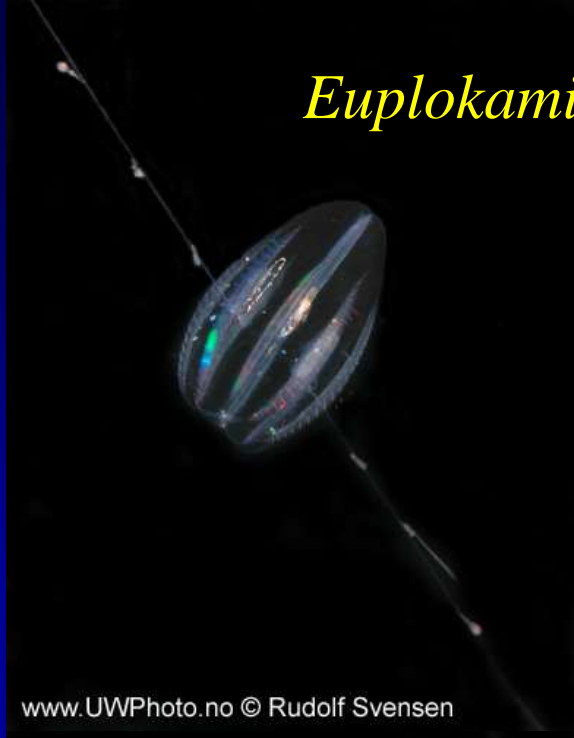


*Mertensia ovum* with  
*Clione antarctica*



*Tetrapphalia*

*Euplokamis dunlapae*



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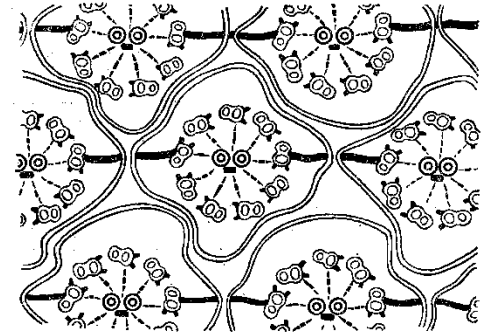
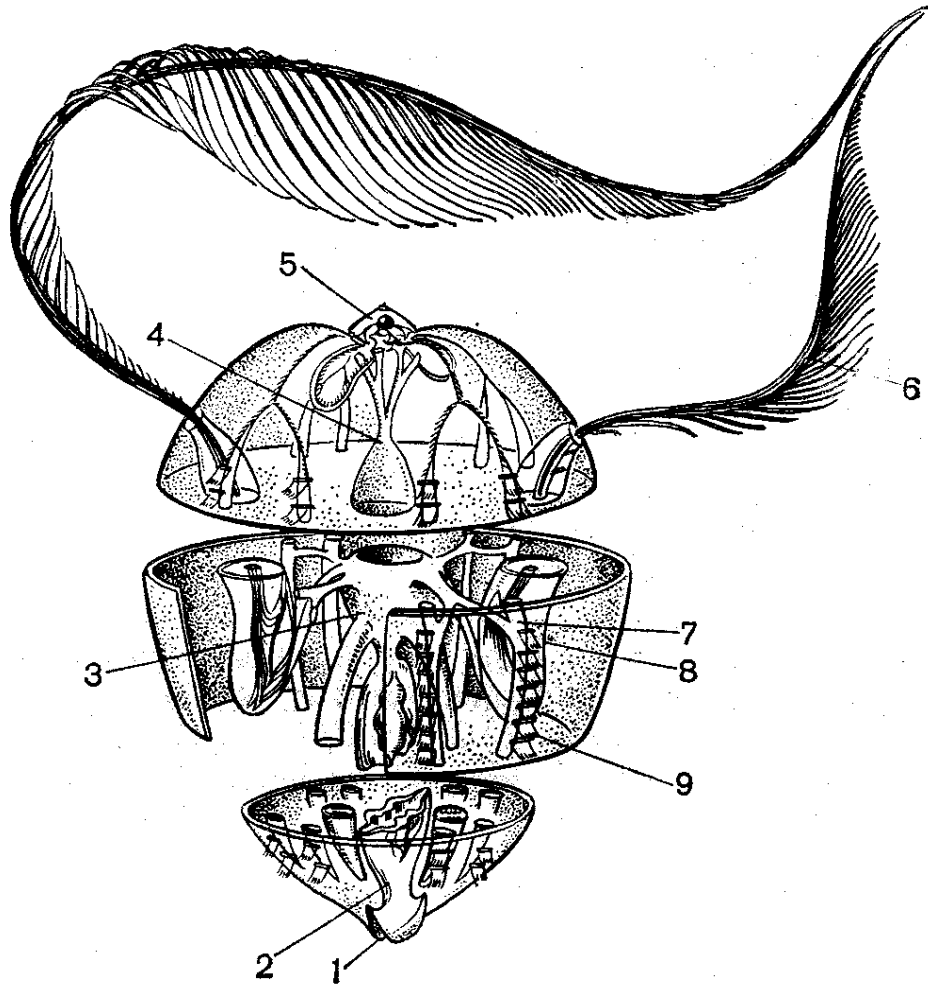
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### Схема строения гребневика:

1 — рот; 2 — глотка; 3 — желудок; 4 — аборальный гастральный канал; 5 — аборальный орган; 6 — щупальце; 7 — меридиональный гастральный канал; 8 — карман щупальца; 9 — ряд гребных пластинок.



Поперечный срез ребристой пластинки.

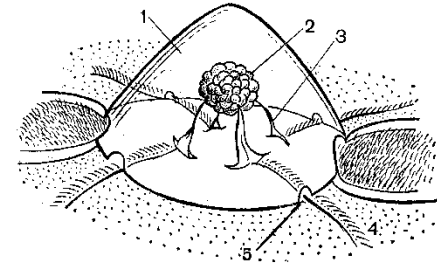
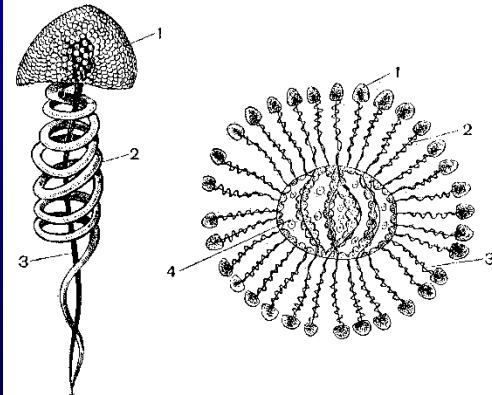


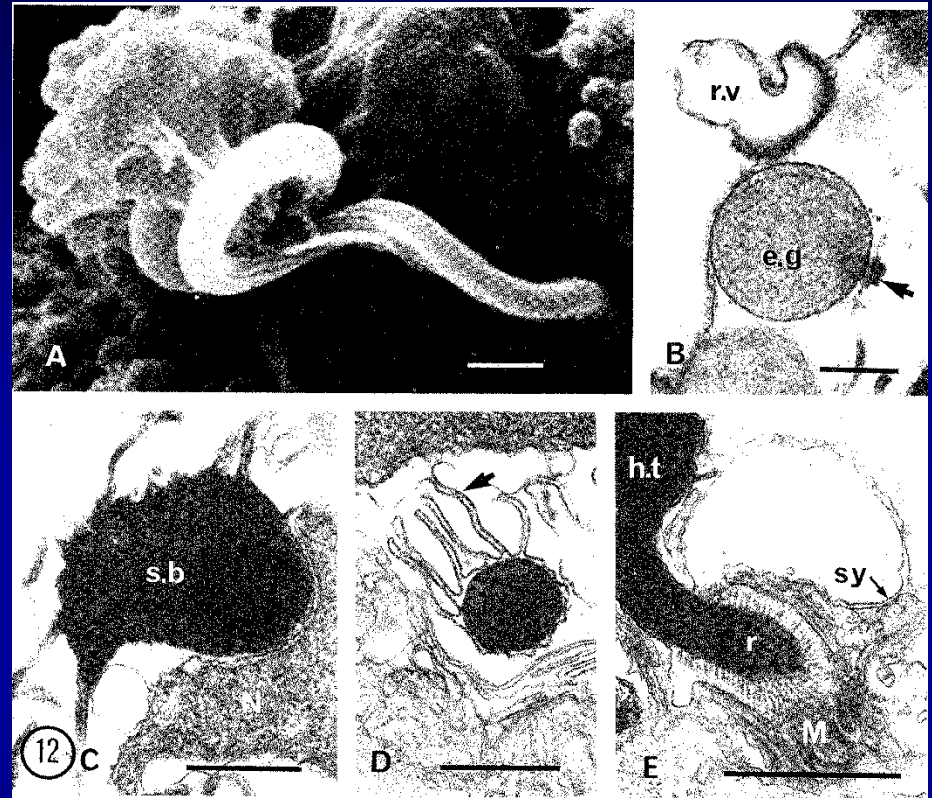
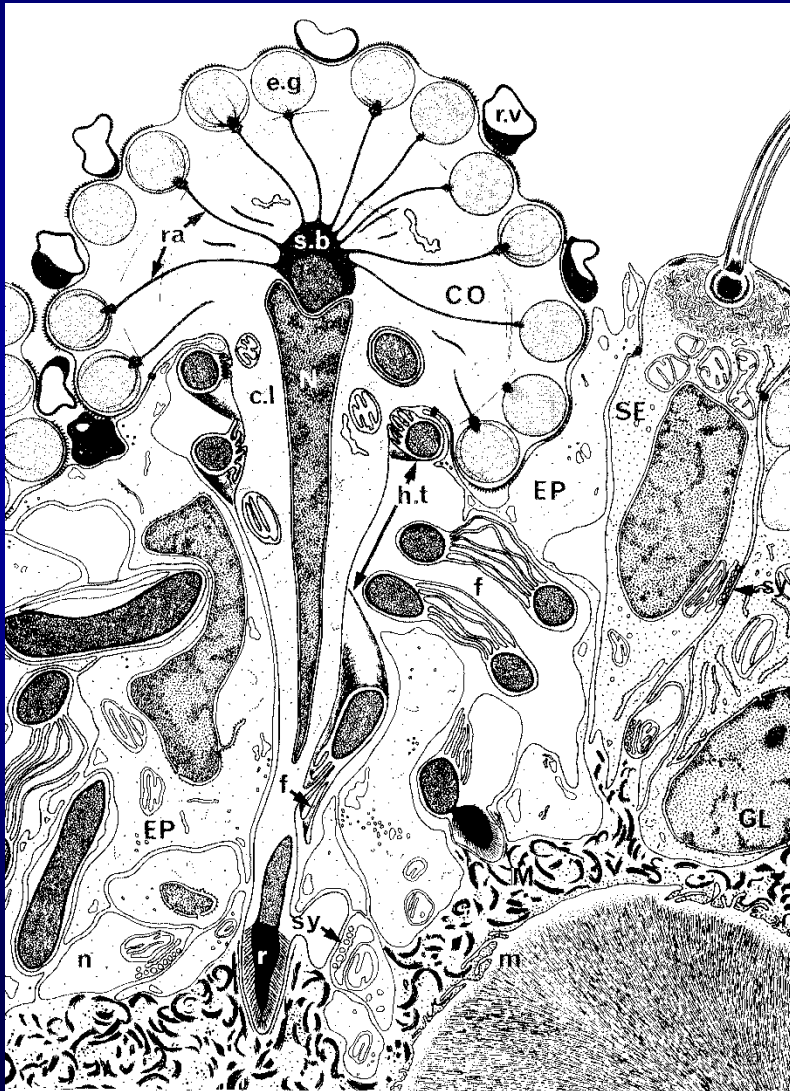
Схема строения аборального органа (сбоку): 1 — ресничный купол (шапер); 2 — статолит; 3 — пружинящие дужки; 4 — мерцательные бороздки; 5 — поры купола.

Строение клейкой клетки гребневика (слева) и поперечный срез щупальца (справа): 1 — клейкая клетка головки; 2 — спиральный тяж; 3 — прямой тяж; 4 — мышечный цилиндр щупальца.



# Стенка тела, коллобласты

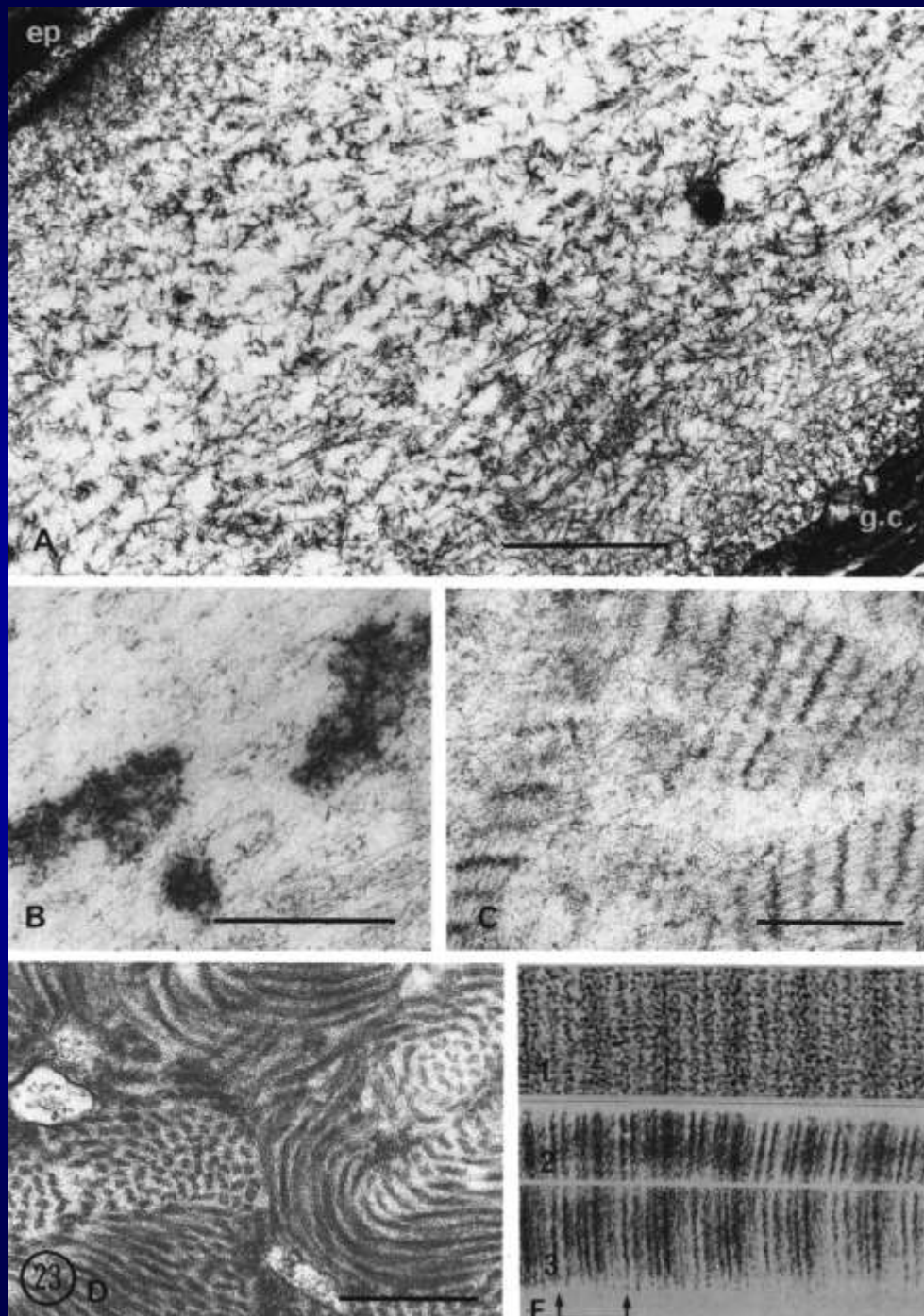
Diagram of the tentillar epithelium of *Pleurobrachia*, reconstituted from TEM. CO, colloblast; c.l, connecting lamella; e.g., eosinophilic granule; EP, supporting epithelial cell; F, membrane folds of the helical thread; GL, mucous gland cell; h.t., helical thread; m, smooth muscle cell; M, mesoglea; n, neurite; N, nucleus; r, root, ra, radius; r.v, refractory vesicle; s.b., spheroidal body; SE, sensory ciliated cell; sy, synapse.



Ultrastructural features of the colloblasts of *Pleurobrachia rhodopis*. A. SEM of a colloblast partially removed from the tentacle. The stalk has been broken so that the membrane folds running along the helical thread are visible. The bulges on the colloblast head correspond to the eosinophilic granules. Bar=1 mkm. B. Detail of an eosinophilic granule. Note the dense structures (arrow) associated with the attachment patch to the radius and the thick cell coat above the granule. Bar= 1 mkm. C. Spheroidal body with fibrous radii radiating from it. The spheroidal body lies in a groove at the surface of the nucleus and is in close contact with the nuclear envelope. Bar=0.5 mkm. D. Transverse section of the helical thread from a colloblast. Several folds (arrow) are visible on both sides of the connecting lamella. Bar=0.5 mkm. E. Longitudinal section of the root: it prolongs the helical thread and is embedded in the mesoglea between muscle cells. A neurite makes syntic contact (arrow) with a bulbous expansion of the colloblast stalk. Bar=2 mkm. (from Franc, 1978).

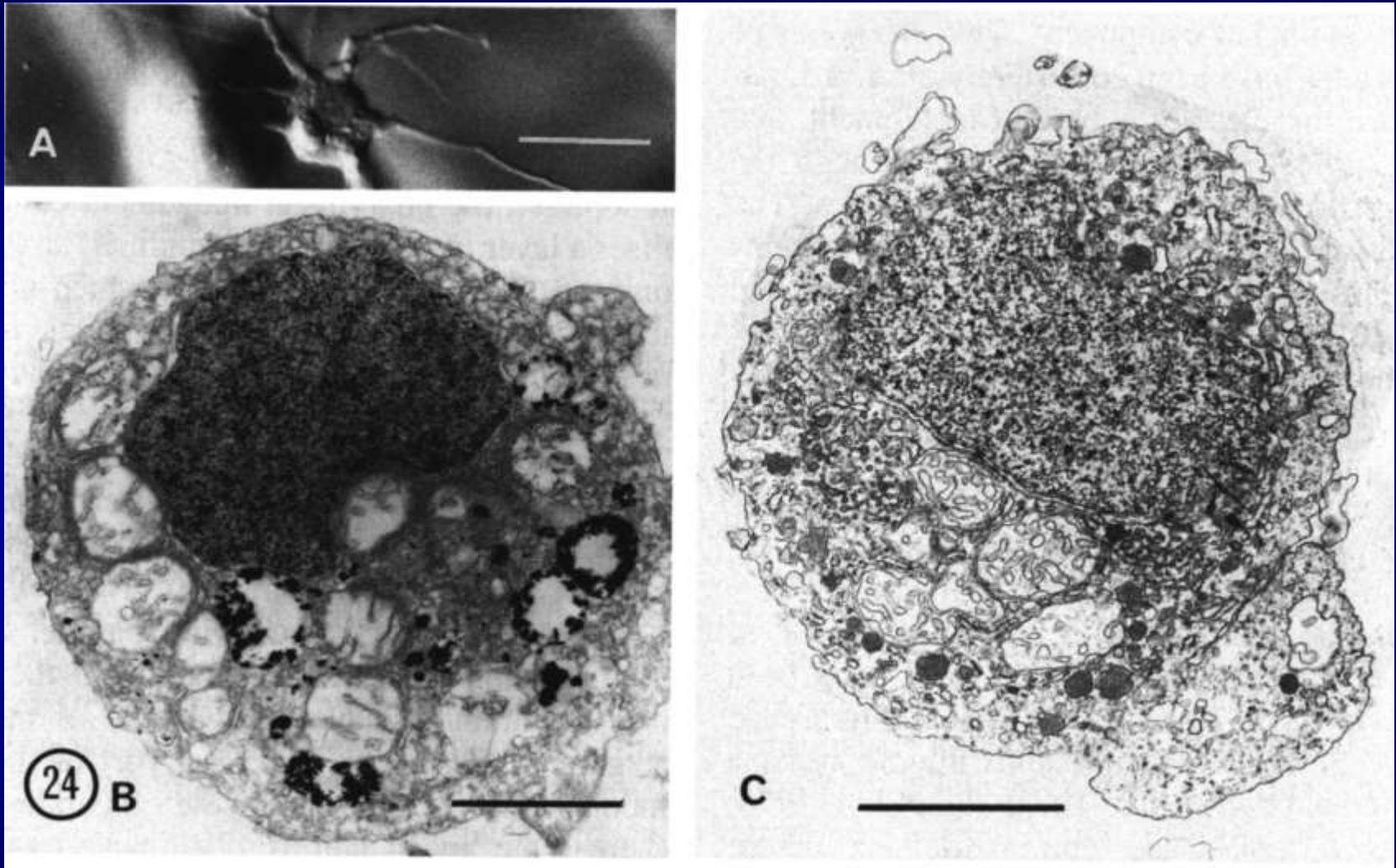
# Мезоглея - ВНЕКЛЕТОЧНЫЙ МАТРИКС:

разные варианты  
организации фибрилл  
мезоглеи из разных частей  
тела гребневиков.



Ultrastructure of the extracellular matrix of Ctenophora. A. Fibrillar nonstriated bundles in the mesoglea of *Pleurobrachia*, between a comb row (ep) and the underlying meridional canal (g.c). Bar=1 mkm. B. Particulate component of the mesoglea of *Pleurobrachia*. Bar=0.5 mkm. C. Native periodically striated bundles in the mesoglea of a regenerating tentacle of *Pleurobrachia*. Bar=0.5 mkm. D. Coiled bundles of nonstriated fibrils in the mesoglea of a tentacle of *Cestum*. Bar=0.5 mkm. E. Collagen striation. 1: Electron micrograph of native collagen from the mesoglea of *Euplokamis*. 2, 3: Extracted, purified, and reconstituted collagen fibers from *Beroe* and calf skin respectively.

# Мезенхимные клетки

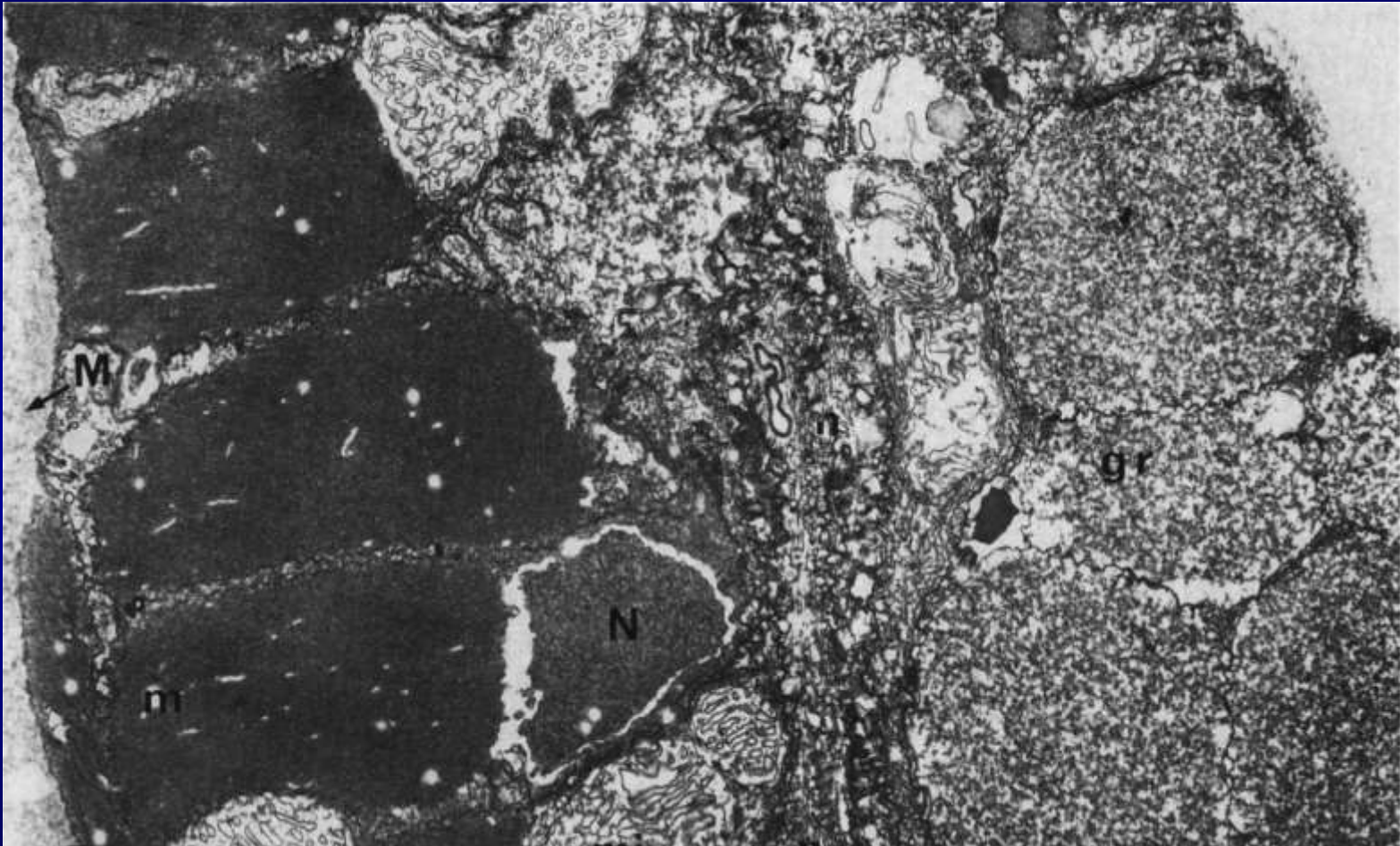


Mesenchyme cells in the mesoglea of *Beroë ovata*. A, Micrograph of a living mesenchyme cell, Nomarski optics. Bar=20 mkm. B, Acid phosphatase activity in the vacuoles of a mesenchyme cell. Bar=2 mkm. C, Vacuolated mesenchyme cell. Bar=2 mkm.



# Мышечная система

## Париетальная мускулатура

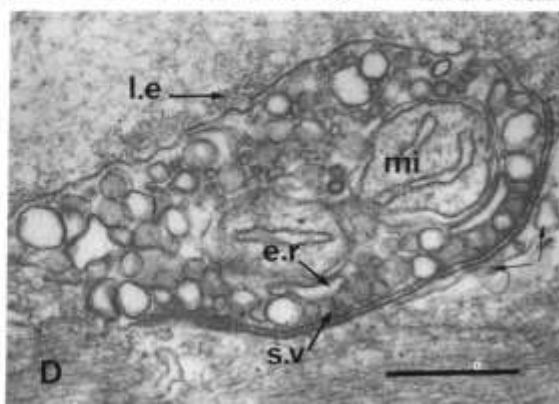
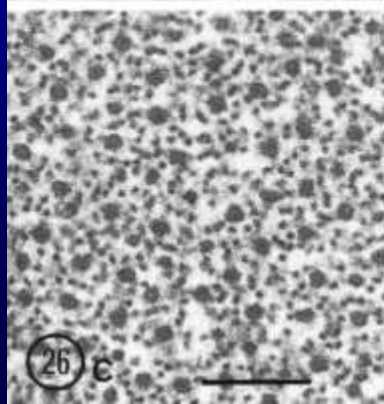
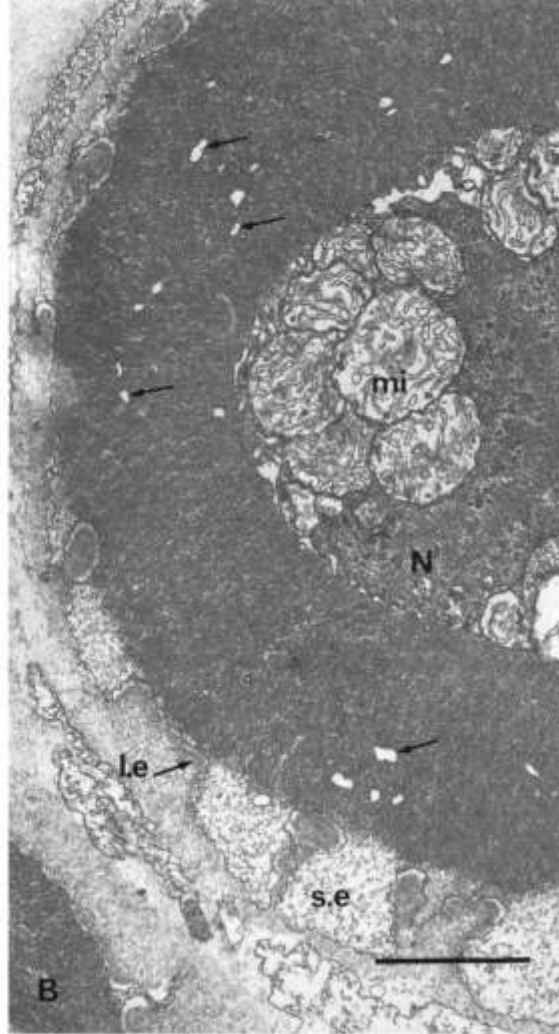


Section through the epidermis of *Cestum veneris* orthogonal to the body longitudinal axis and parietal muscle cells. M, mesoglea; m, contractile base of parietal muscle cell; N, nucleus of muscle cell; n, neurites; gr, mucus-containing granules of a gland cell. Bar=2 mkm.

# Мышечная система:

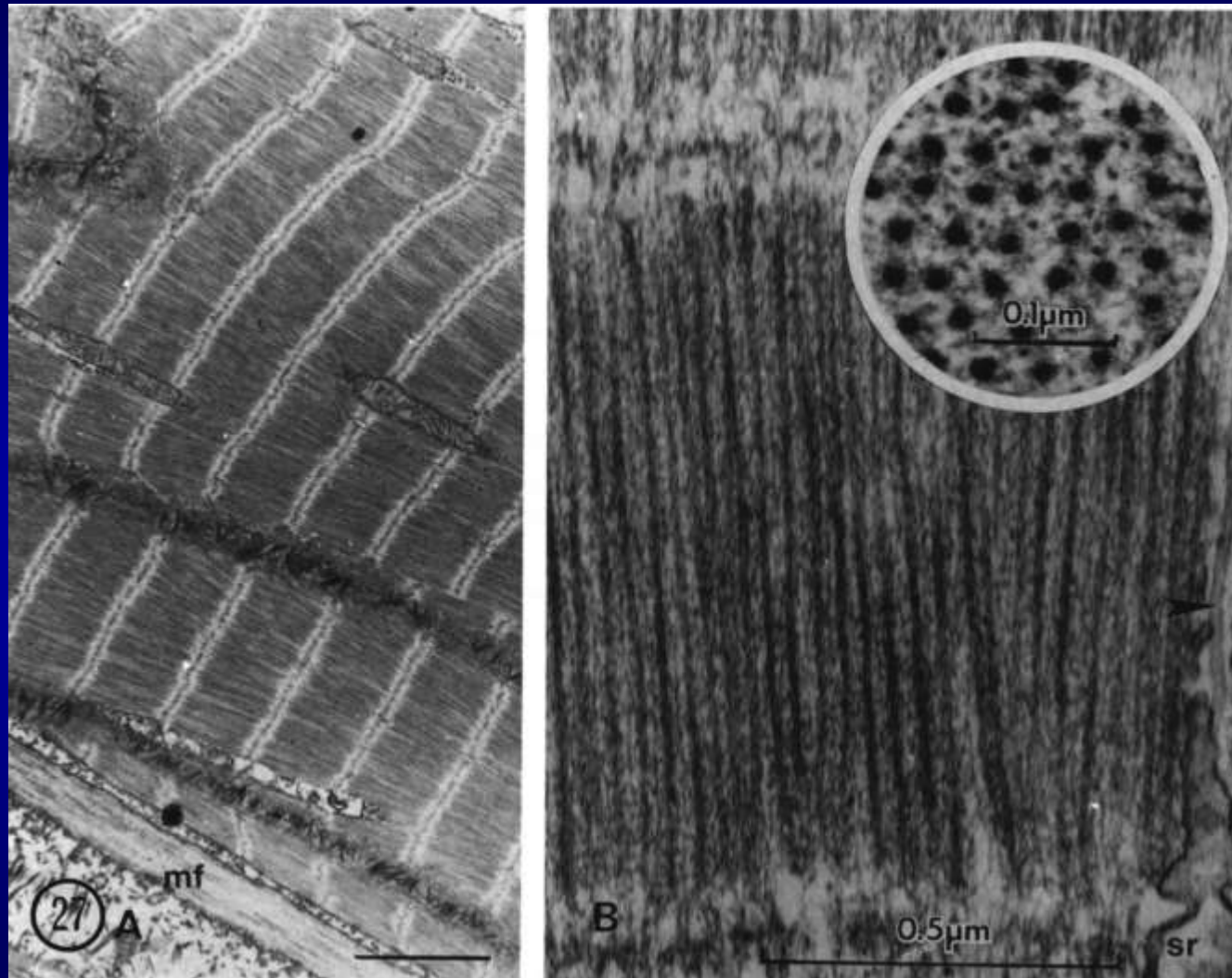
## Мезоглеальные гигантский мышечные фибриллы *Beroe ovata*.

Mesogleal giant fiber of *Beroe ovata*. A. Interference contrast photomicrograph of a living radial muscle showing the extensive branching under the pharyngeal epithelium. Note the multiple nuclei (arrowheads) and the thin sarcolemmal evaginations (s.e.). Bar=20 mkm. B. Cross section of a radial fiber displaying sarcolemmal infoldings characteristic of contracted fibers. The axial core contains a nucleus (N) and mitochondria (mi). Numerous sections of sarcoplasmic reticulum tubules (arrows) are interspersed among the myofilaments. Note the thick lamina externa (l.e.). Bar=2mkm. C. Cross section of myofilaments. Bar=0.1 mkm. D. Neuromuscular junction. L.e., lamina externa; mi, mitochondrion; e.r., endoplasmic reticulum; s.v., synaptic vesicle. Note the subsarcolemmal cistern (arrows). Bar=0.5 mkm.



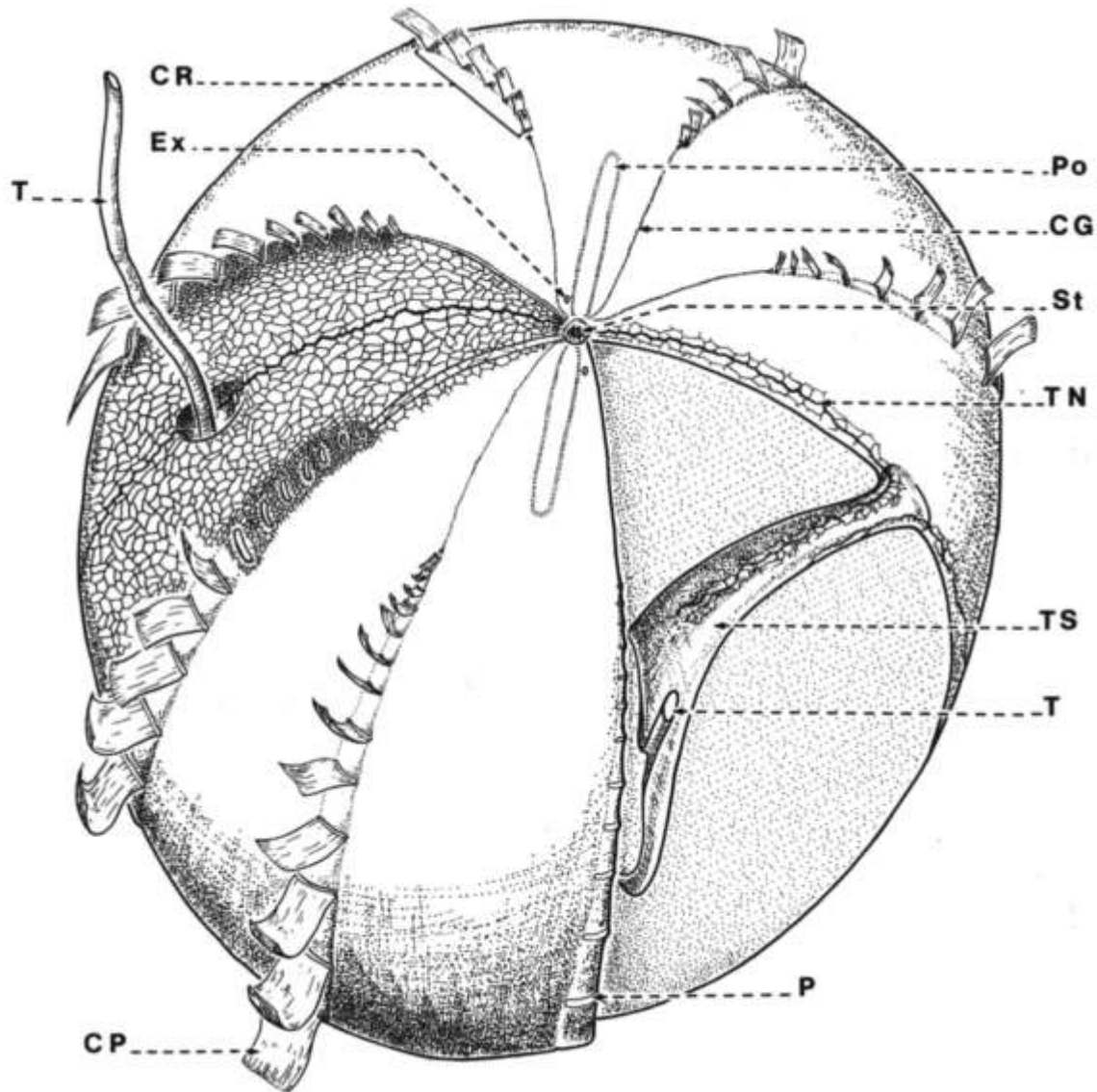
# *Euplokamis dunlapae*:

## поперечно-полосатая мускулатура в тентиллах

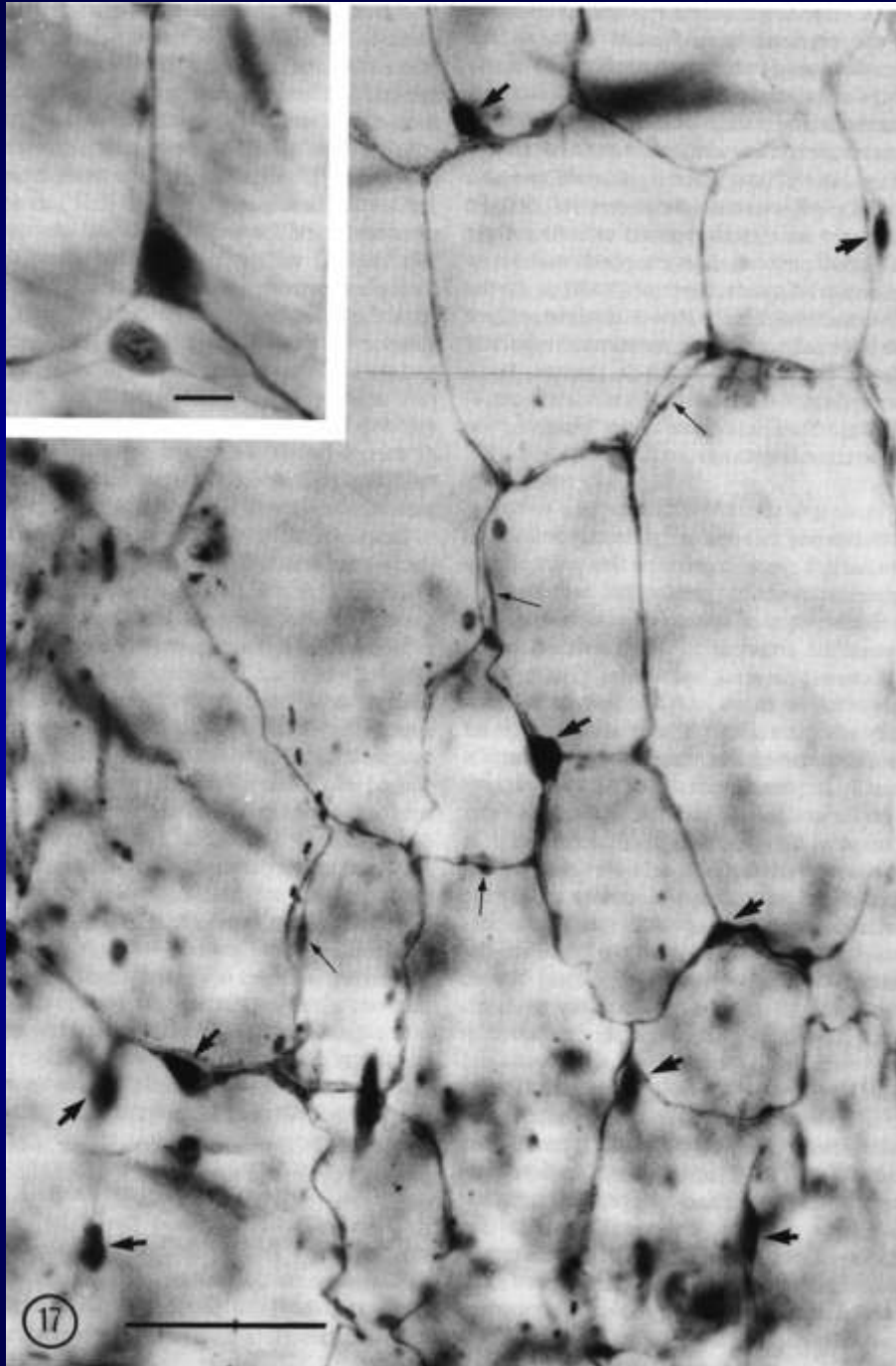


Striated muscle in tentillum of *Euplokamis*. A. longitudinal section of striated muscle fibers, also showing a myofilament cell (mf). Bar=2 μm. B. detail of a sarcomere. Note at the periphery of sarcomere an axial smooth endoplasmic reticulum tubule (sr) and a microtubule (arrowhead). Inset shows cross section of myofilaments. Bar=0.5 μm/

# Нервная система



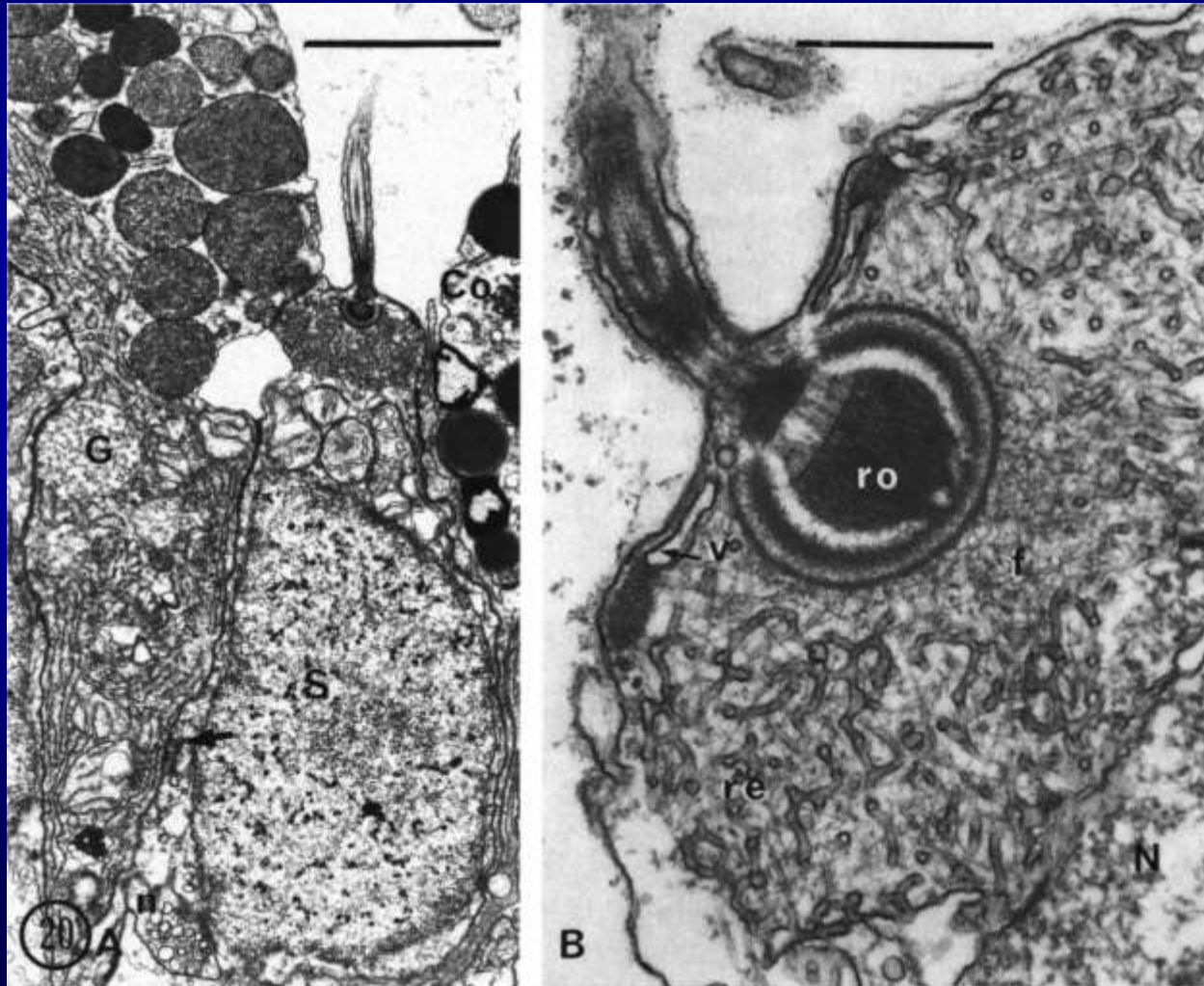
# Нервный плексус



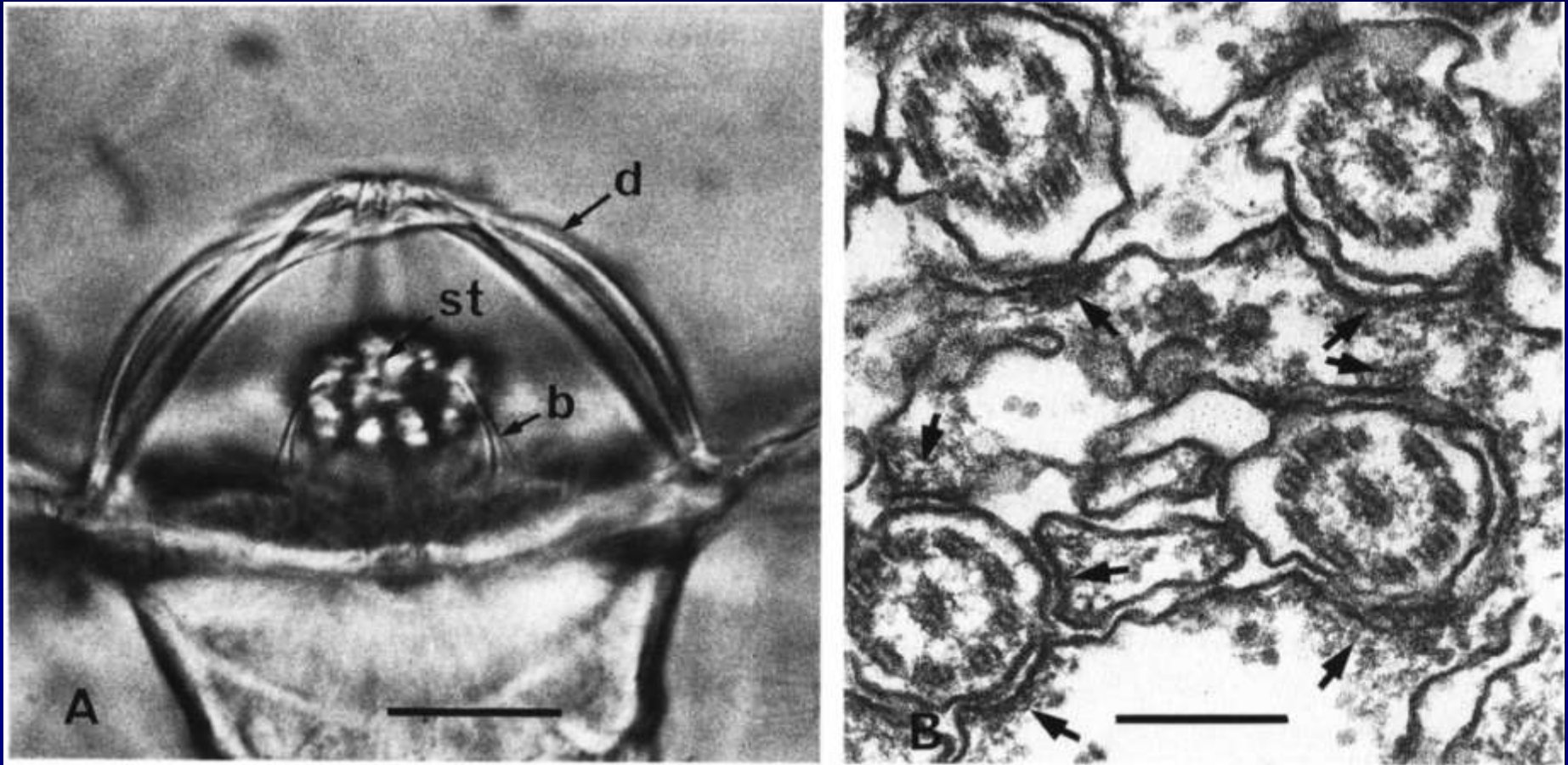
Subpharyngeal nerve net of *Beroë ovata*, vitally stained with reduced methylene blue. The net displays a polygonal pattern with bipolar and tripolar neurons (thick arrows, and inset) generally located at the nodes. Two parallel neurites may be observed in various meshes (thin arrows) of the net. Bar=50 mkm.

# ЧУВСТВИТЕЛЬНЫЕ КЛЕТКИ

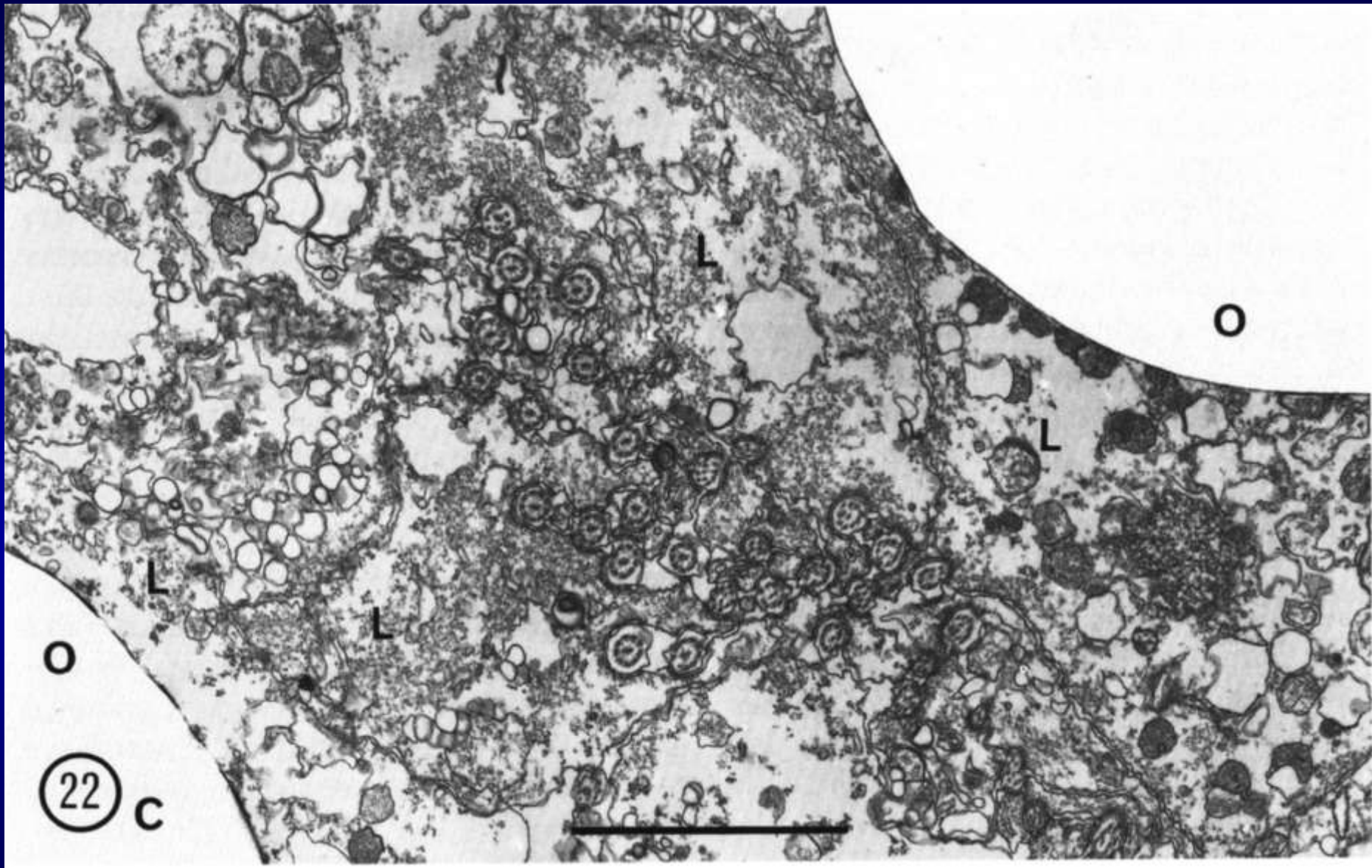
Ciliated sensory cells. A. Epidermis of tentilla of *Lampetia pancerina*. The sensory cell (S) synapses (arrow) upon an adjacent granular gland cell (G). It is separated from a neighboring colloblast (Co) by supporting cell processes. A neurite (n)-to-sensory cell synapse is cut tangentially. Bar=2 mkm. B. Longitudinal section through the apex of a ciliated sensory cell from the labial rim of *Beroe ovata*. f, microfilaments linking the root to the tubule network; ro, honeycomb array of smooth reticulum tubules; N, nucleus; re, striated spherical ciliary root; v, circular vacuole. Bar=0.5 mkm.



# Аборальный орган



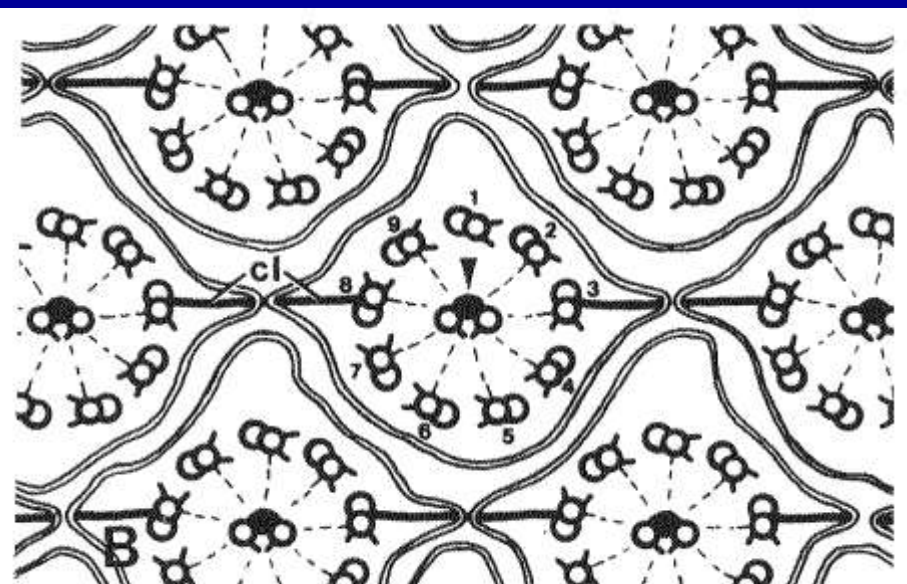
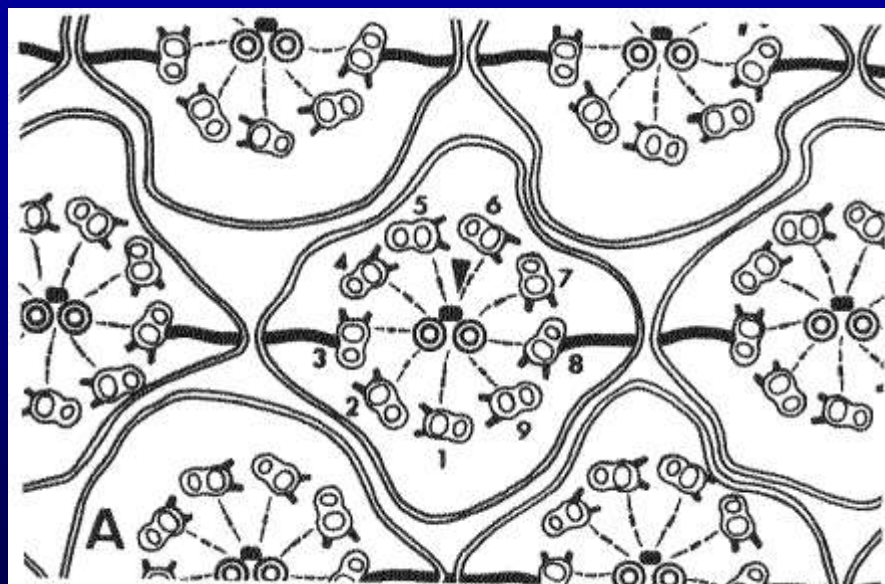
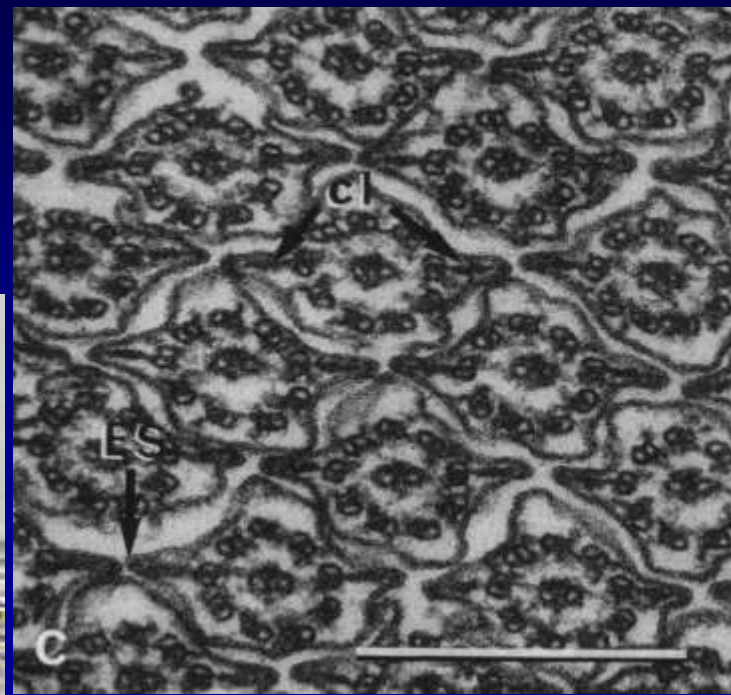
Aboral organ. A. Aboral pole of a living *Charistephane*. Two balancers (b) supporting the statocyst (st) are clearly visible. d, ciliary dome. Bar=50 mkm. B. Detail of the junctions established between the balancer cilia and the lithocytes. Numerous fine filaments (arrows) coat the junctional membrane of lithocytes. Bar=0.2 mkm.



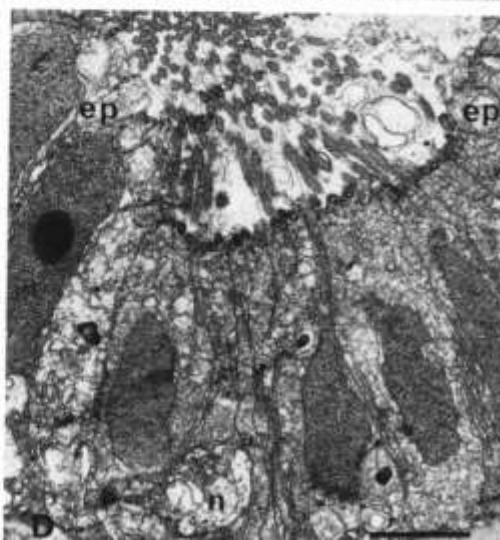
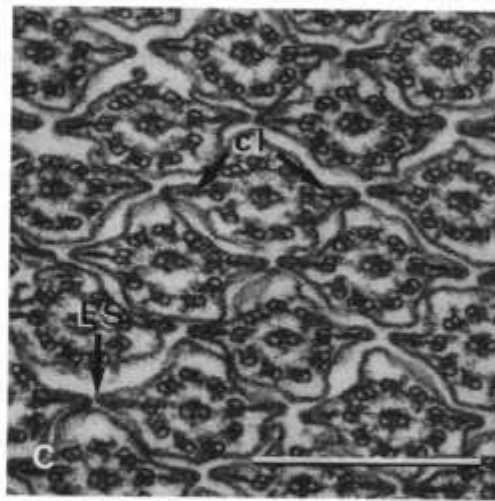
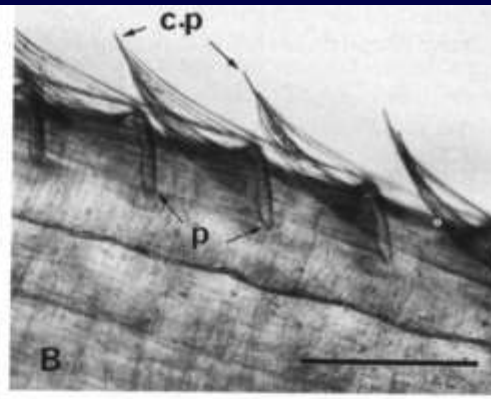
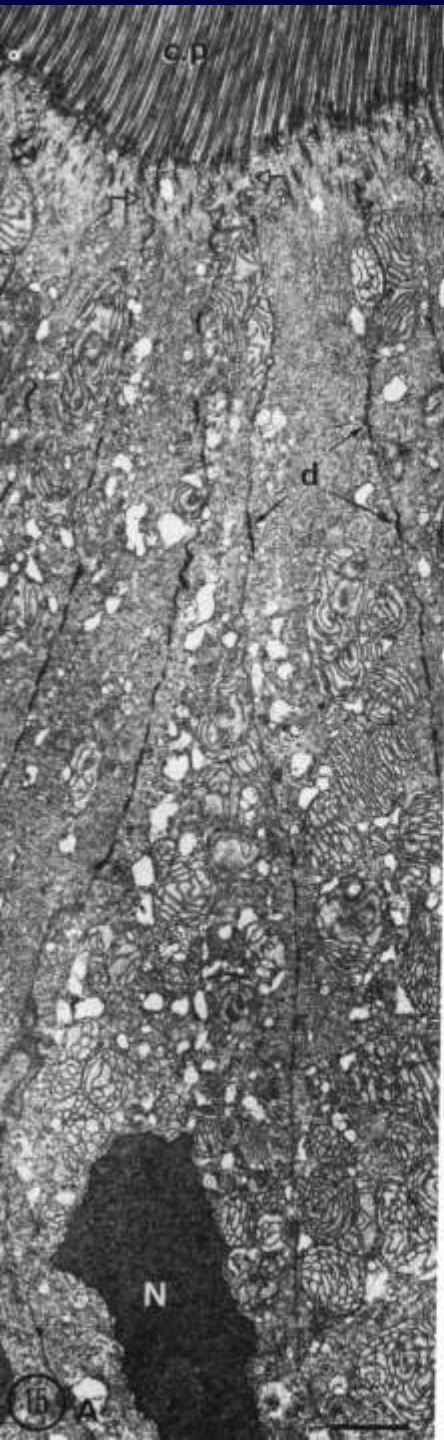
Aboral organ (continuation). C. Section through the statocyst, at the level of attachment of balancer cilia. Each lithocyte (L) contains many small vesicles and granules, and a huge empty vacuole left by the otolith (O). The membrane of the lithocytes invaginates deeply to accommodate the balancer cilia. Bar=2 mkm.



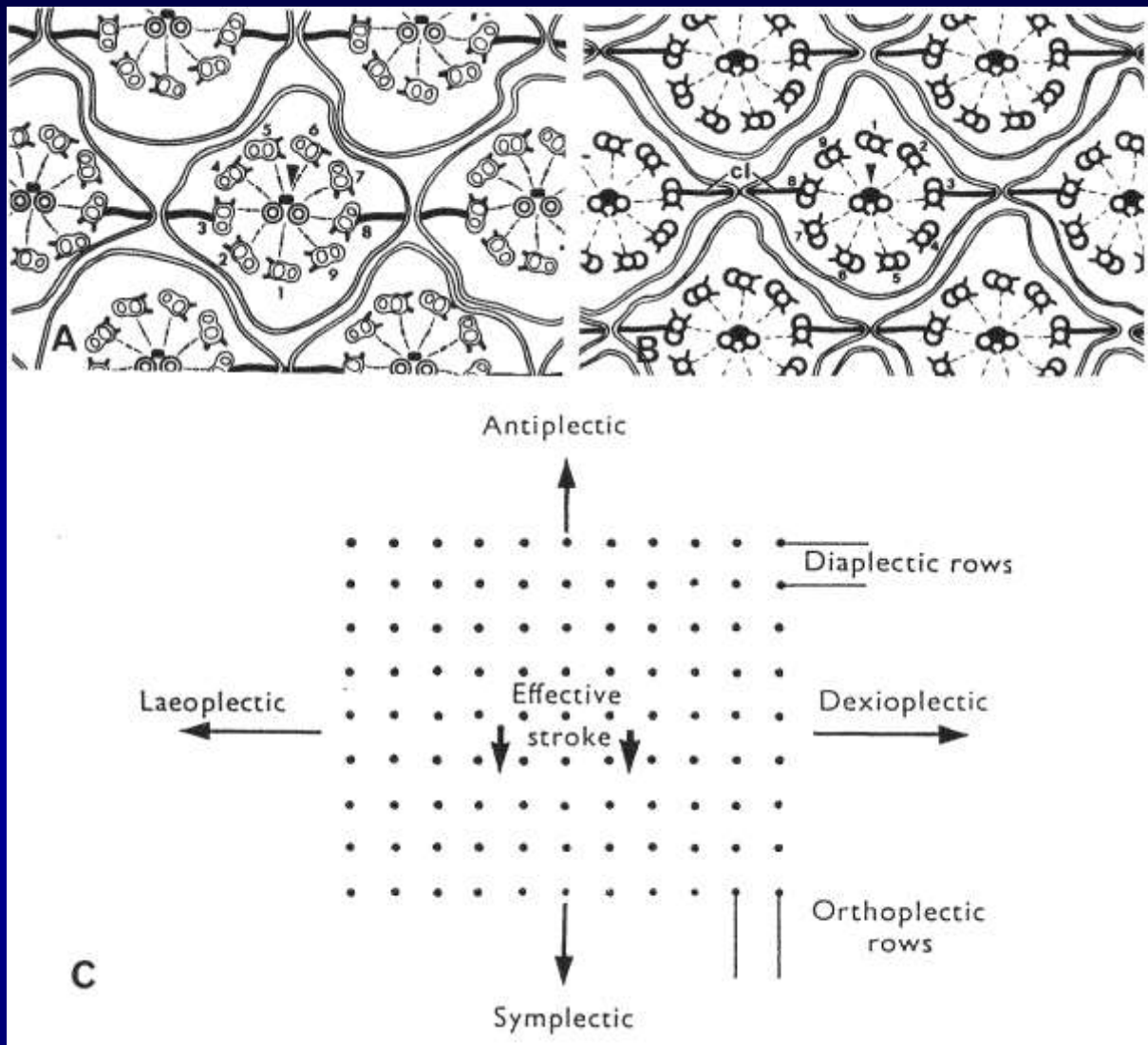
# Гребная пластинка



# The locomotor system of *Beroe ovata*

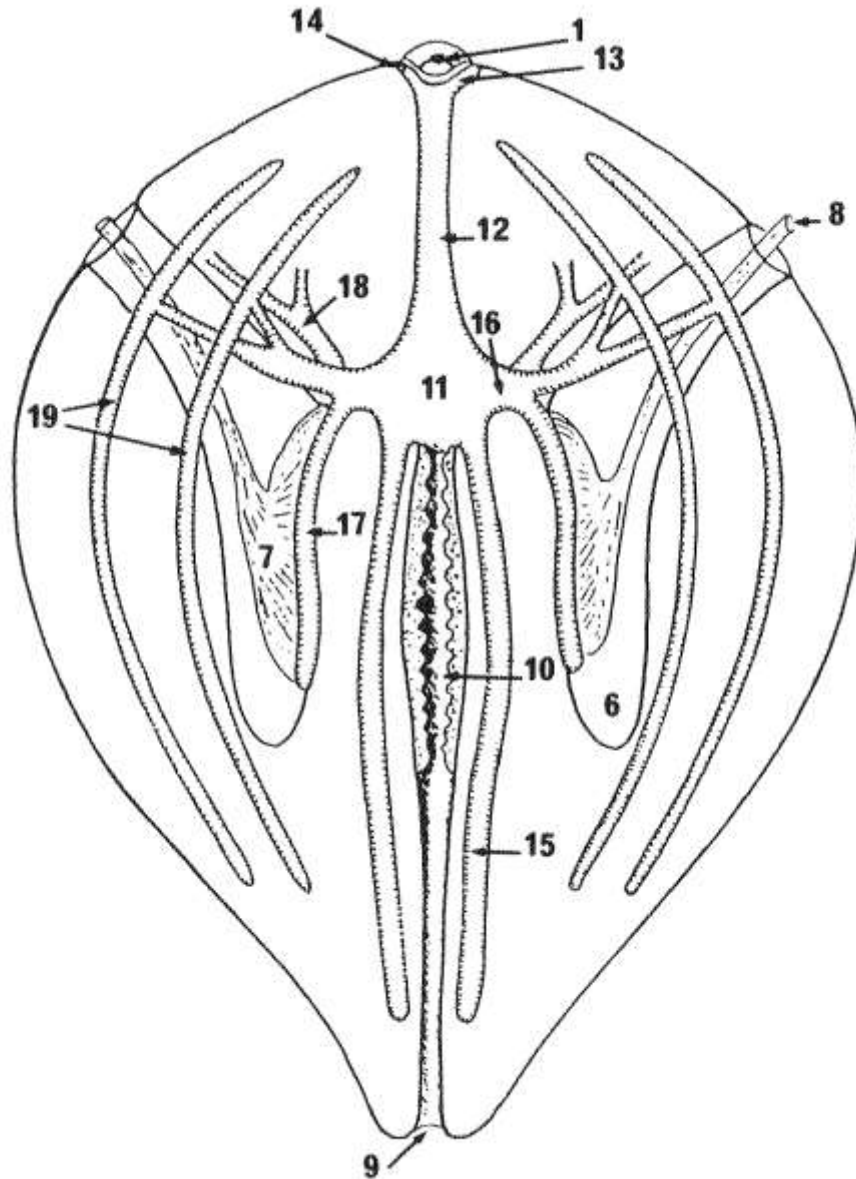


The locomotor system of *Beroe ovata*. A. Ciliated comb cells, from a meridional section through a polster. Open arrows, apical belt junction; d, desmosomes; N, nucleus. Note the numerous large mitochondria. Bar=3 mkm. B. Ciliated comb plates (c.p.) at rest in a living *Beroe*. The ridge (p) at the base of each plate is the apex of the polster emerging from the epidermis. The aboral organ is at the right. Bar=0.5 mkm. C. Cross section through a comb plate of a forward-swimming *Pleurobrachia* larva. The aboral direction is toward the bottom of figure. Cl, compartmenting lamella; ES, direction of effective stroke. Bar=0.5 mkm. D. Frontal section through a ciliated groove. Note the striking difference in size of the polster cills. N, nerve; ep, epithelial cells adjacent to the ciliated cells. Bar=3 mkm.



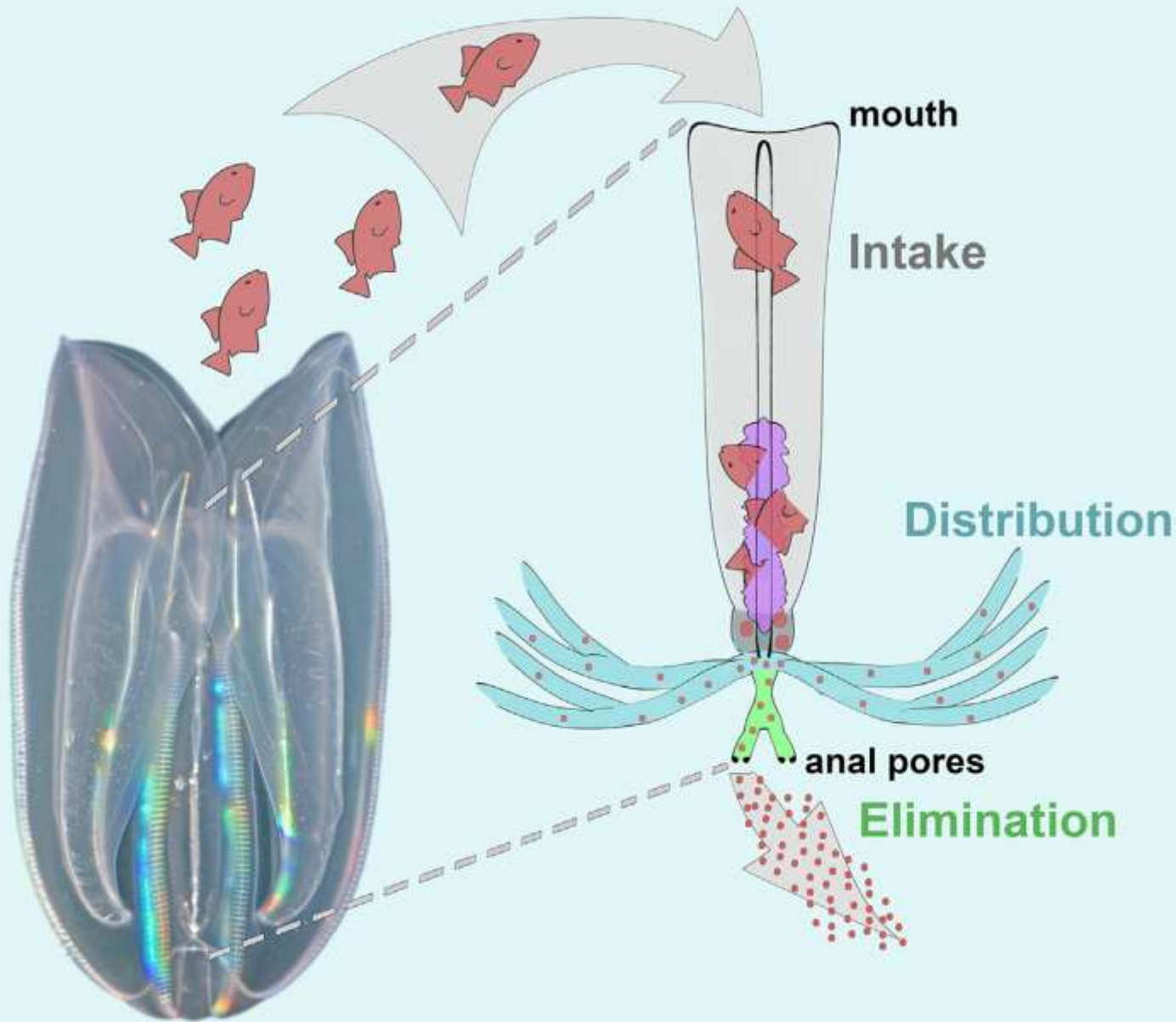
Diagrammatic cross section through comb plate cilia. The effective stroke takes place in a plane (arrowhead) perpendicular to the axis of the central pair of tubules. The beat is directed aborally during forward swimming. Compartmenting lamellae (cl) link adjacent axonemes into rows perpendicular to the plane of beat. A. Adult ctenophore: the central dense "midfilament" faces the aboral pole. B. Cydippid larva: the central midfilament faces the oral pole. C. The nomenclature of ciliary patterns and metachronal patterns (data from Knight-Jones, 1954). Arrows indicate the movement of metachronal waves. Metachronal waves usually travel along rows that run in the plane of the effective stroke of cilia (orthoplectic rows). In this case, sympleptic waves move in the same direction of the beat, while antipleptic waves travel in the opposite direction. Both patterns occur along the comb rows of ctenophores, while macrocilia display antipleptic metachronism. When the ciliary tract is wide and short, metachronal waves run along rows that are at right angles to the effective stroke (diaplectic rows). The metachronism in this case is either laeoplectic or dexioplectic. The beating of the auricular ciliated plates of lobate ctenophores is an example of laeoplectic and dexioplectic metachronism (data from Tamm, 1982).

# План строения целентерона, симметрия

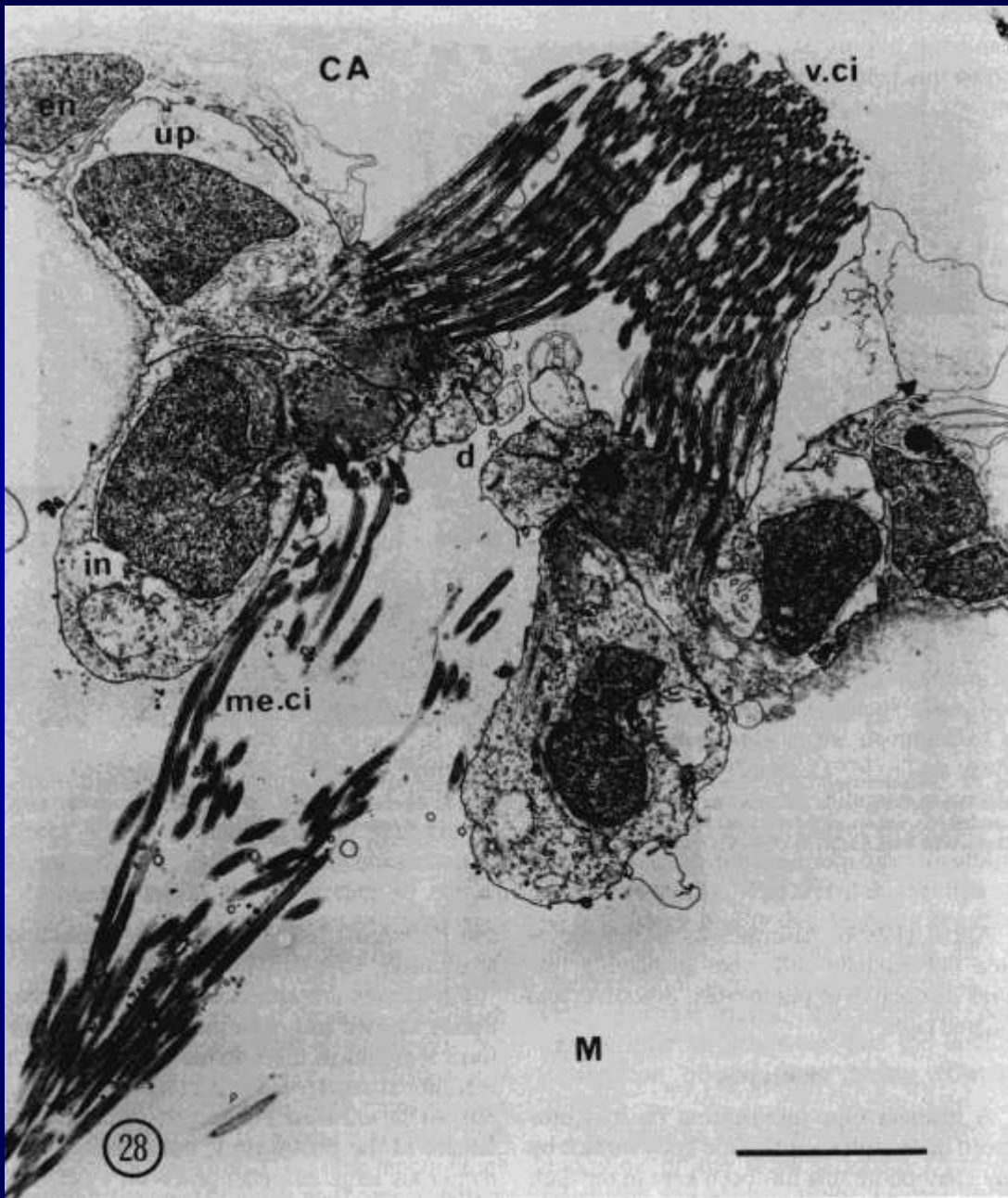


1, статоцист; 6, влагалище щупальца; 8, щупальце; 9, ротовое отверстие; 10, глотка (фаринкс); 11, инфундибулум («желудок»); 12, аборальный канал; 13, анальный канал; 14, анальная пора; 15, парагастральный канал; 16, перрадиальный канал; 17, тентакулярный канал; 18, интеррадиальный канал с дихотомией на адрадialные каналы; 19, меридианальные каналы.

# Functionally tripartite ctenophore through-gut



Ctenophores have historically been described as having a blind, sac-like gut. Using live imaging of ctenophore digestion in their report, Presnell et al. demonstrate that ctenophores possess a functionally tripartite through-gut, challenging the current paradigm that assumes that the through-gut originated within Bilateria (Presnell et al., 2016. *Current Biology* 26, 1–7.).



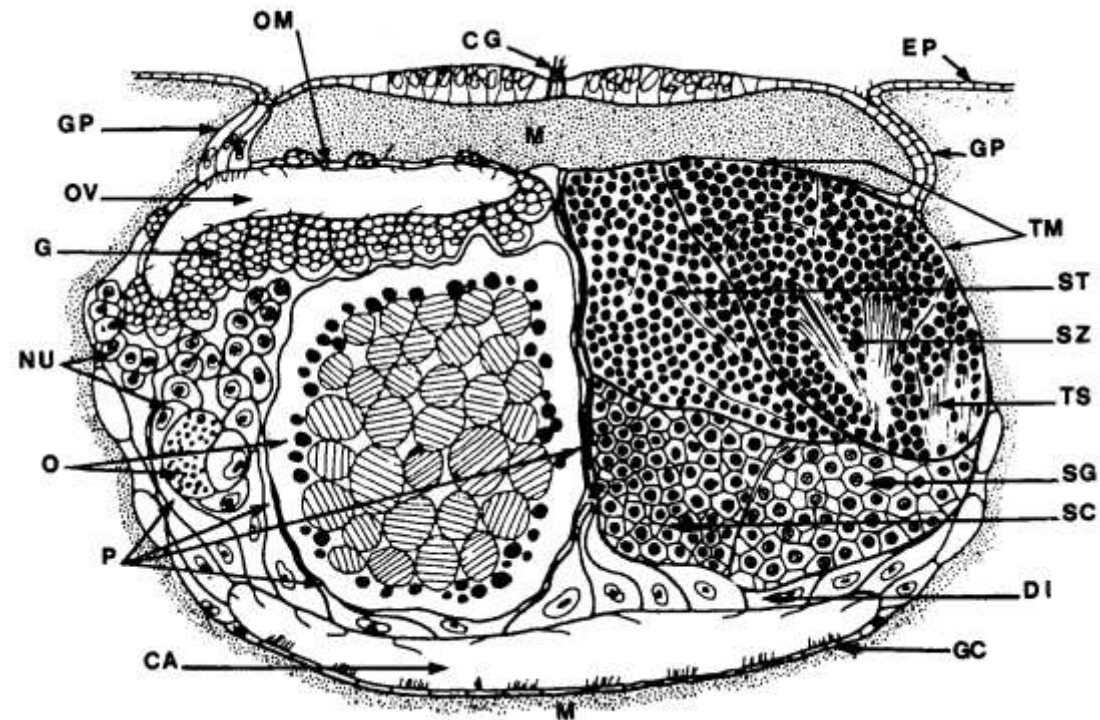
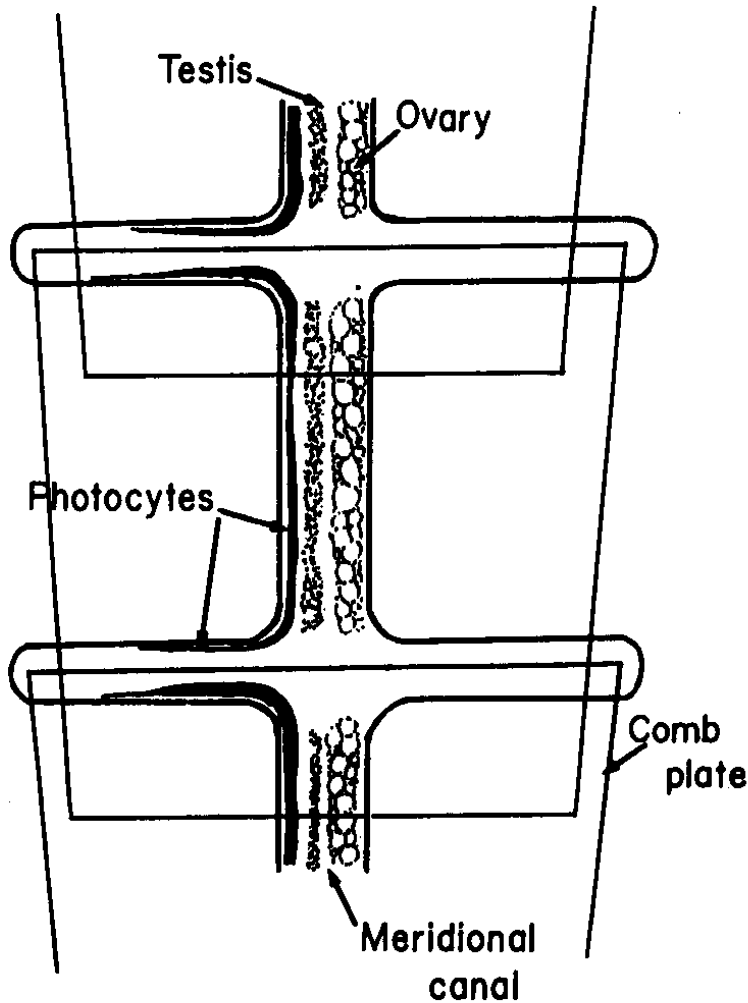
## Цилиарная розетка

### *Beroë ovata*

Longitudinal section through a ciliated rosette of *Beroë ovata*. CA, lumen of gastrovascular canal; d, diaphragm formed by the apices of "upper ring" cells (up) of the rosette; en, flat endodermal cell; in, "inner ring" cell of the rosette; M, mesoglea; me.ci, intramesogleal cilia; v.ci, intravascular cilia. Bar=5 mkm.

# Гермафродитная система

## *Bolinopsis*



## *Mnemiopsis*

Diagram of a cross section of a meridional canal of *Bolinopsis*, taken at the level of the gonopores. CA, lumen of meridional canal; CG, ciliated groove; DI, digestive cells; EP, epidermis; G, glandular epithelium; GC, ciliated gastrodermal cell (the rosettes are omitted); GP, gonopore; M, mesoglea; NU, nurse cells; O, oocytes; OM, ovarian membrane; OV, oviduct; P, interstitial processes of digestive cells; SC, spermatocystes; ST, spermatids; SG, spermatogonis; SZ, mature spermatozooids; TM, testicular membrane; TS, testicular sinus .

# План строения, симметрия

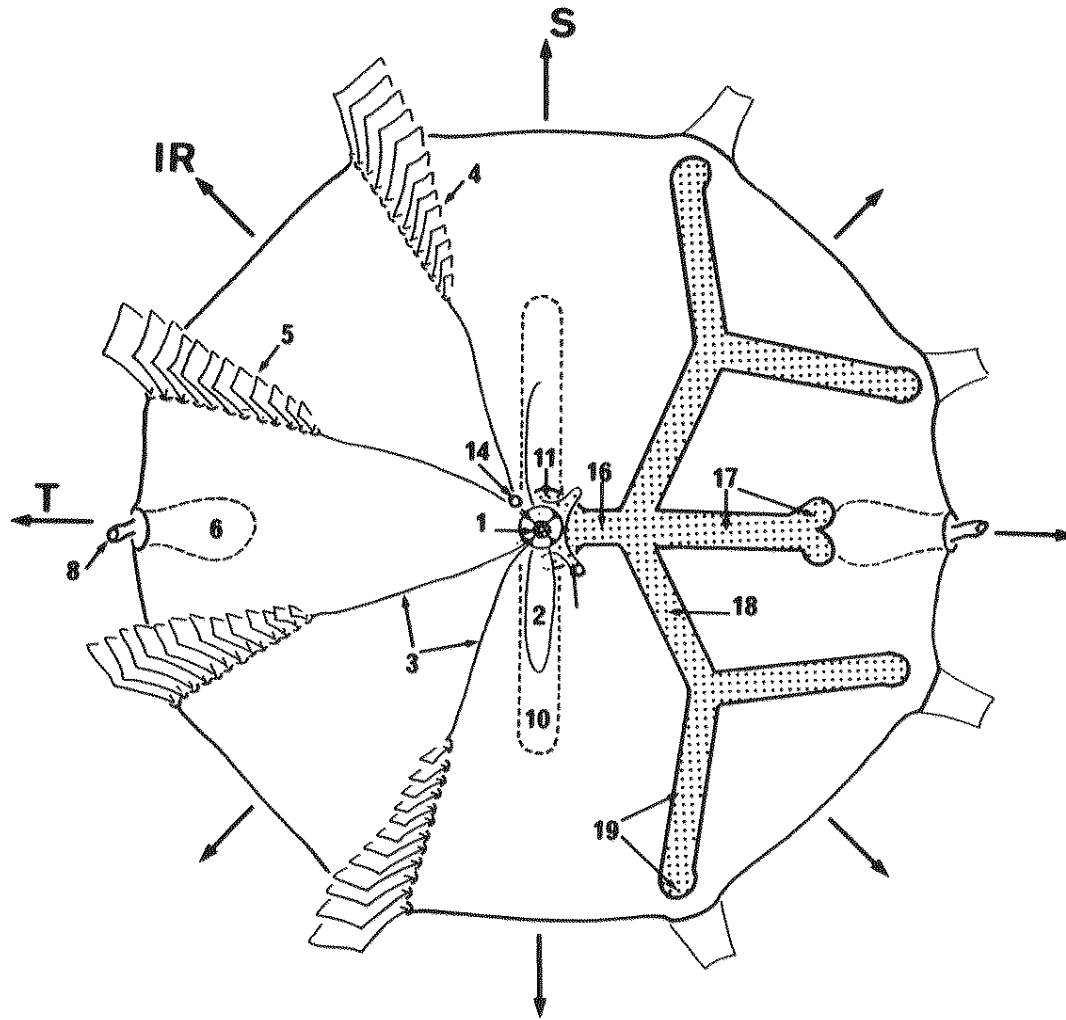


Fig. 2. Cydippid type: diagrammatic view from aboral pole (left half, locomotor system; right half, gastrovascular system). Abbreviations for Figures 2 and 3: IR, interradial plane; S, sagittal plane; T, tentacular (or transverse) plane; 1, statocyst; 2, polar field; 3, ciliated groove; 4, subsagittal comb row; 5, subtentacular comb row; 6, tentacle sheath; 7, tentacle base; 8, tentacle; 9, mouth; 10, pharynx; 11, infundibulum; 12, infundibulum canal; 13, excretory canal; 14, anal (or excretory) pore; 15, paragastric canal; 16, transverse canal; 17, tentacular canal; 18, interradial canal; 19, meridional canal. (Modified from Pavans de Ceccatty and Hernandez, 1965, with permission of the publisher.)



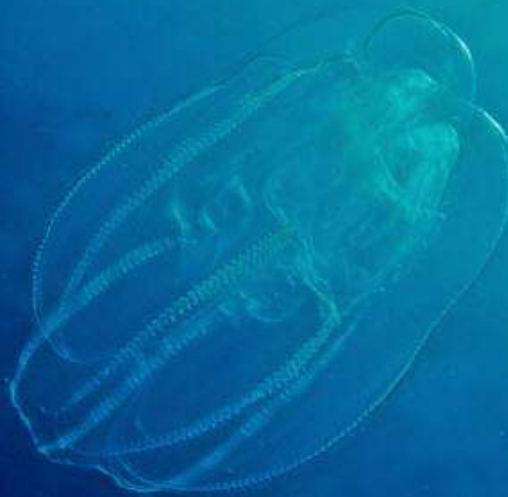
# Гребневики – голопланктонические животные



Ювенильная форма



*Bolynopsis*



1.5 см

# Тип Stenophora

КЛАССЫ

- Tentaculata  
(Tentaculifera)

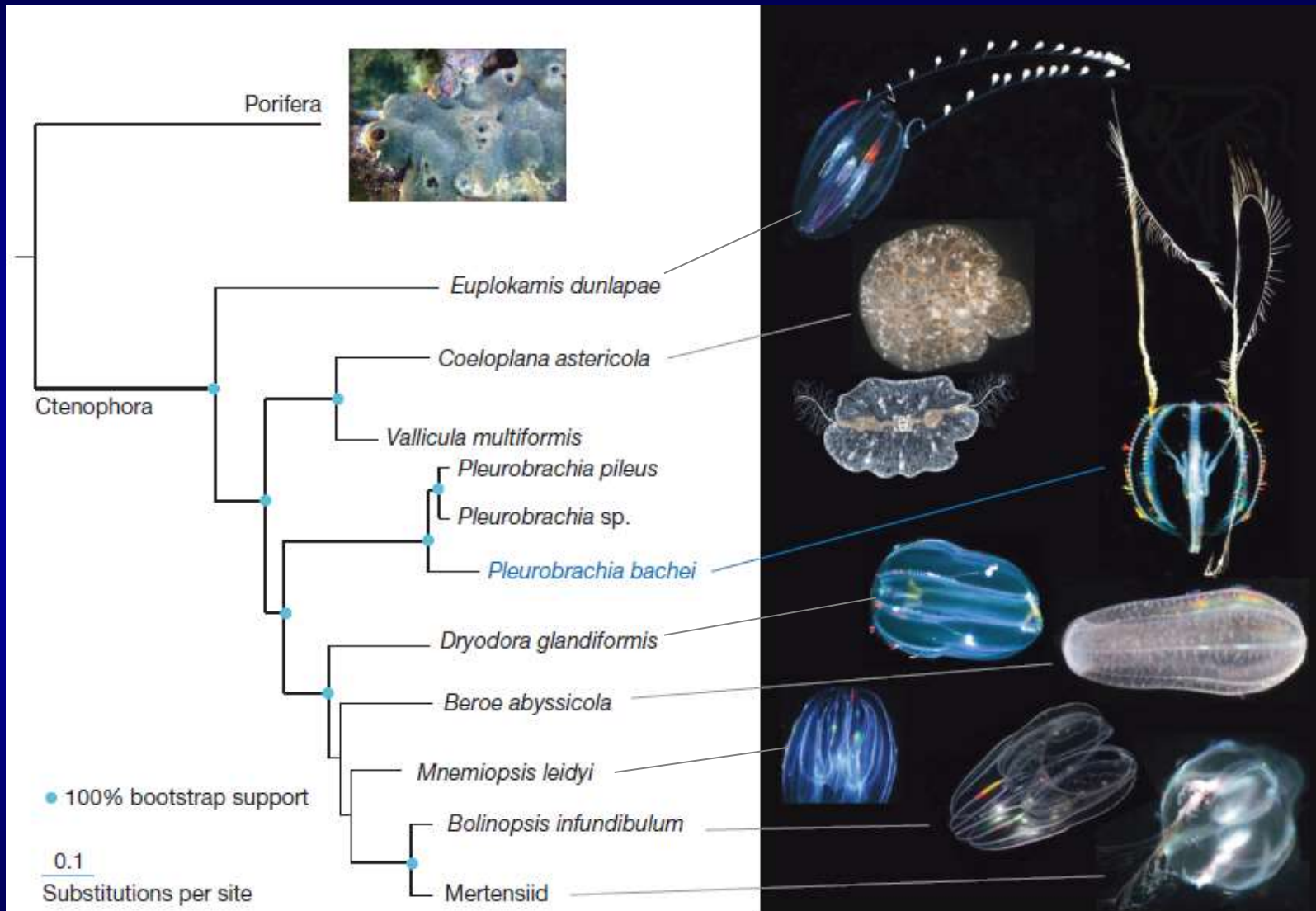
Nuda  
(Atentaculata)

Или

- Typhlocoela

Cyclocoela

# Phylogenomic reconstruction among major ctenophore lineages



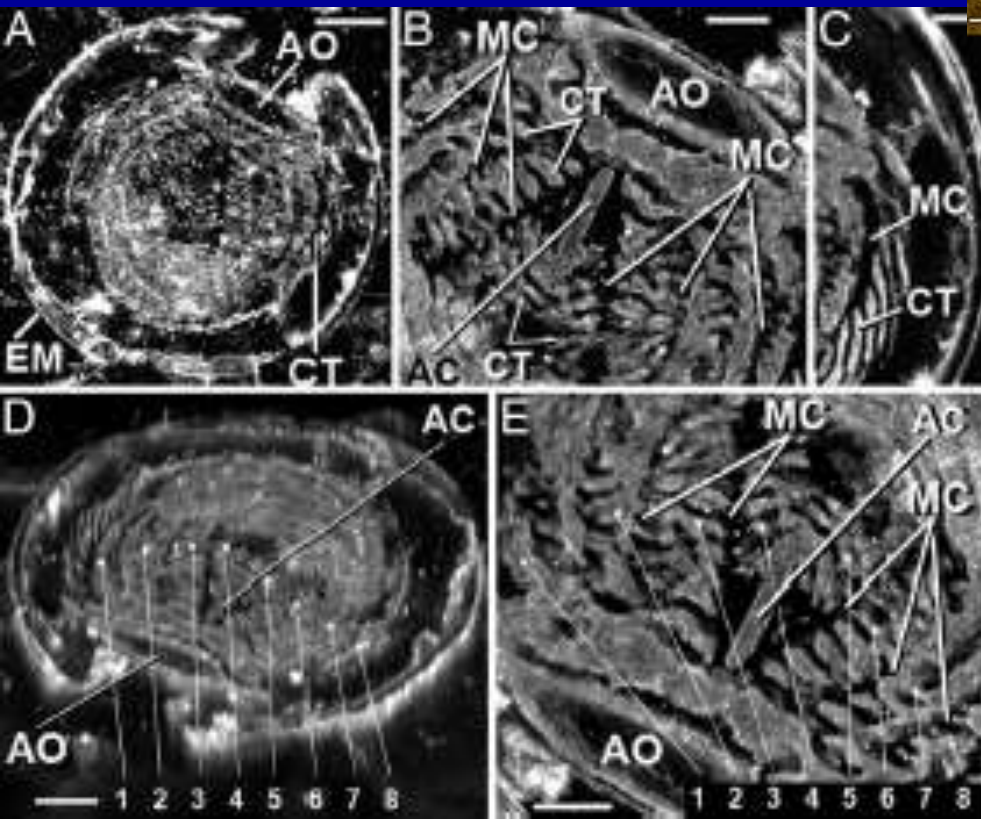
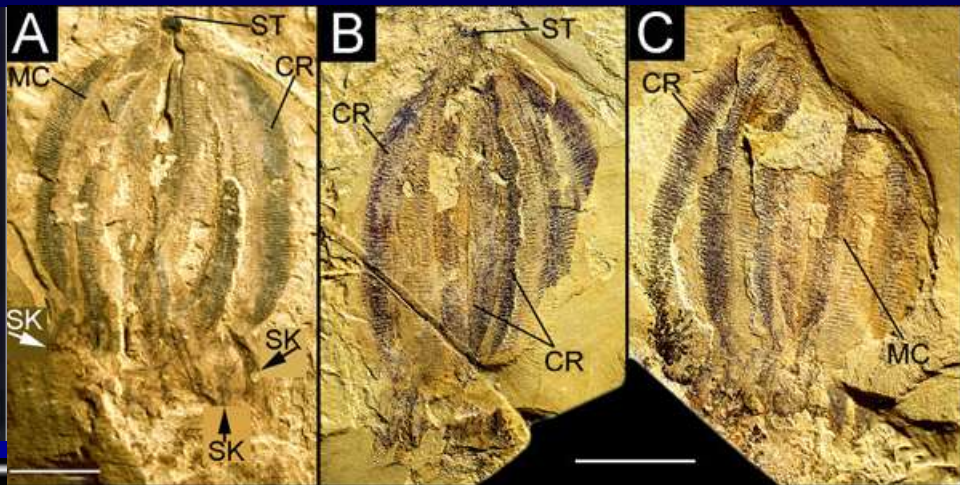
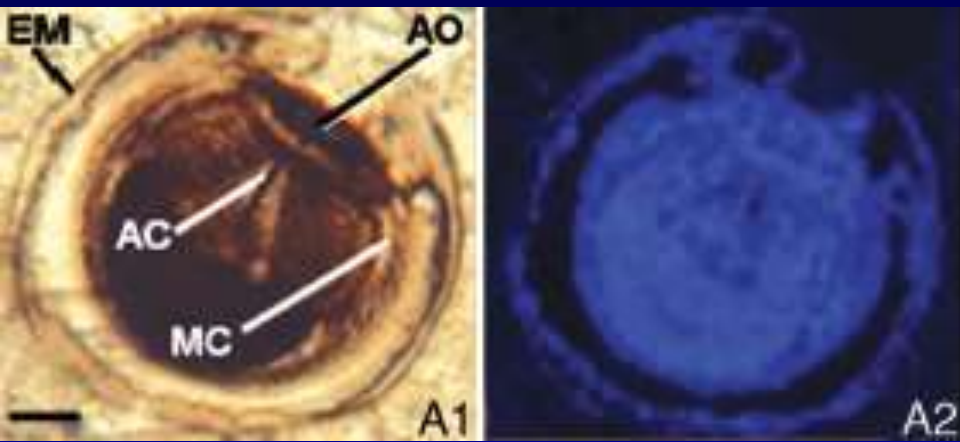
Cydippid (*Euplokamis*, *Pleurobrachia*, *Dryodora* and Mertensiidae) and lobate (*Mnemiopsis* and *Bolinopsis*) ctenophores were polyphyletic, suggesting independent loss of both cydippid larval stage and tentacle apparatus as well as independent development of bilateral symmetry in benthic ctenophores, *Vallicula* and *Coeloplana* (Moroz et al., 2014).

# Raman spectra of a Lower Cambrian ctenophore embryo from

southwestern Shaanxi, China

*Maotianoascus octonarius*

(Chen et al, 2007)



Optical and Raman images of a thin section-embedded ctenophore embryo from the Lower Cambrian Kuanchuanpu Formation of Ningqiang, Shaanxi Province, China. [Scale bars, 25  $\mu$ m (A)]

*Maotianoascus octonarius* from Lower Cambrian Maotianshan shale at Mt. Maotian, Chengjiang, Yunnan. (Scale bars, 10 mm.) (A and B) Part and counterpart of the holotype in this species. (C) A paratype specimen of this species. ST, statolith; CR, comb row; MC, meridional canal; SK, skirt-like possible oral lobe.

Confocal laser scanning microscopic images of the thin section-embedded embryo, obtained by recently documented techniques (12). [Scale bars, 25  $\mu$ m (A and D); 10  $\mu$ m (B, C, and E)]. Because such CLSM images record the laser-excited fluorescence emitted by the kerogen that comprises such fossils, they provide a proxy for direct chemical analyses that show the carbonaceous composition of a specimen analyzed. (A) CLSM image of the complete embryo (see Fig. 1A). The aboral region (B) and middle-right region (C) (see Fig. 1C) of the specimen show the fine-scale morphological information provided by CLSM images. (D) Rotated CLSM image showing comb rows, numbered 1–8, that overlie meridional canals. (E) Higher-magnification image of the aboral region showing the numbered comb rows. AO, apical (aboral) organ; EM, egg membrane; CT, ctenes; AC, aboral canal; MC, meridional canal.