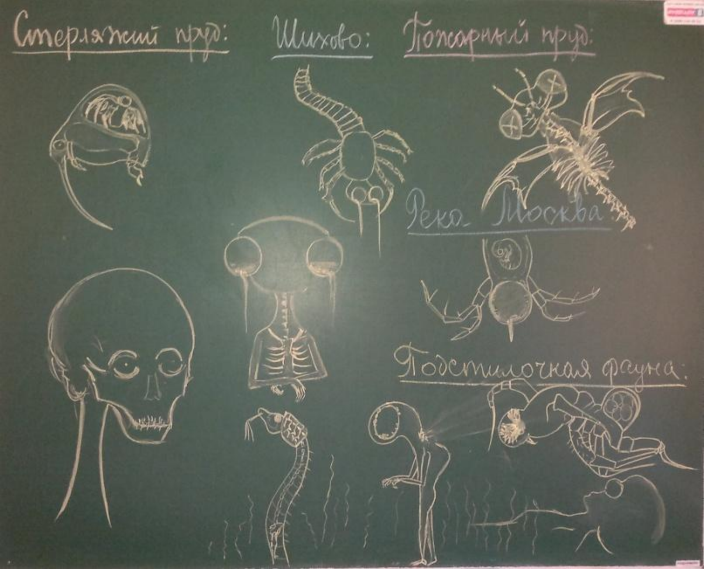

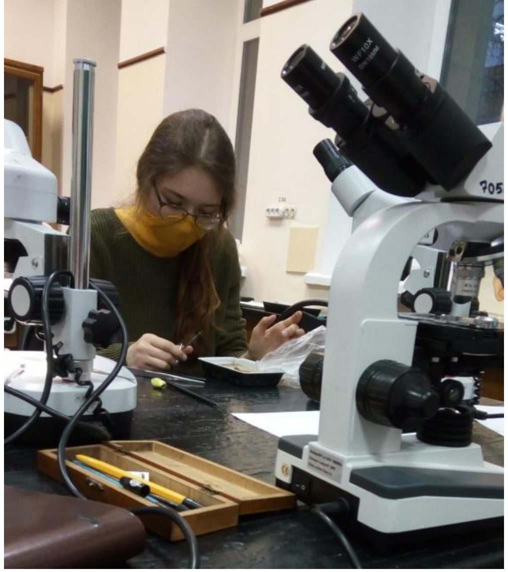
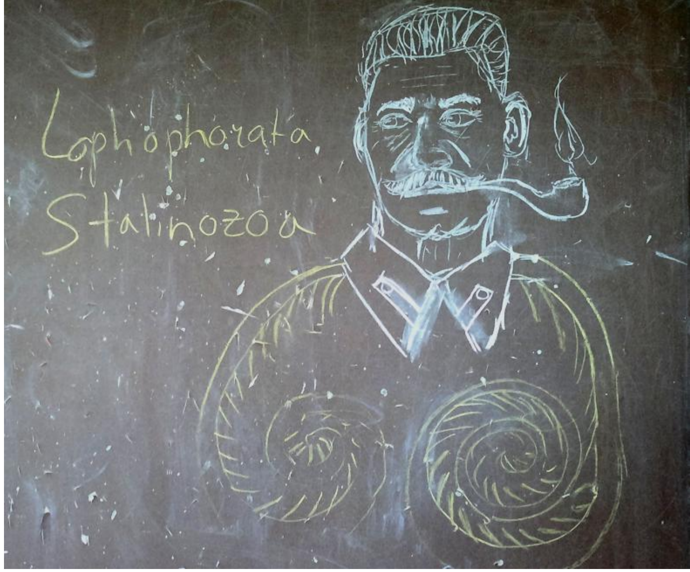

БЕСПОЗИУМ

5 апреля 2018: нервная система Cephalopoda


Budelmann B.U. 1995 Cephalopod Sense Organs, Nerves And The Brain: Adaptations For High Performance And Life Style

Marine and Freshwater Behaviour and Physiology, 25:13-33

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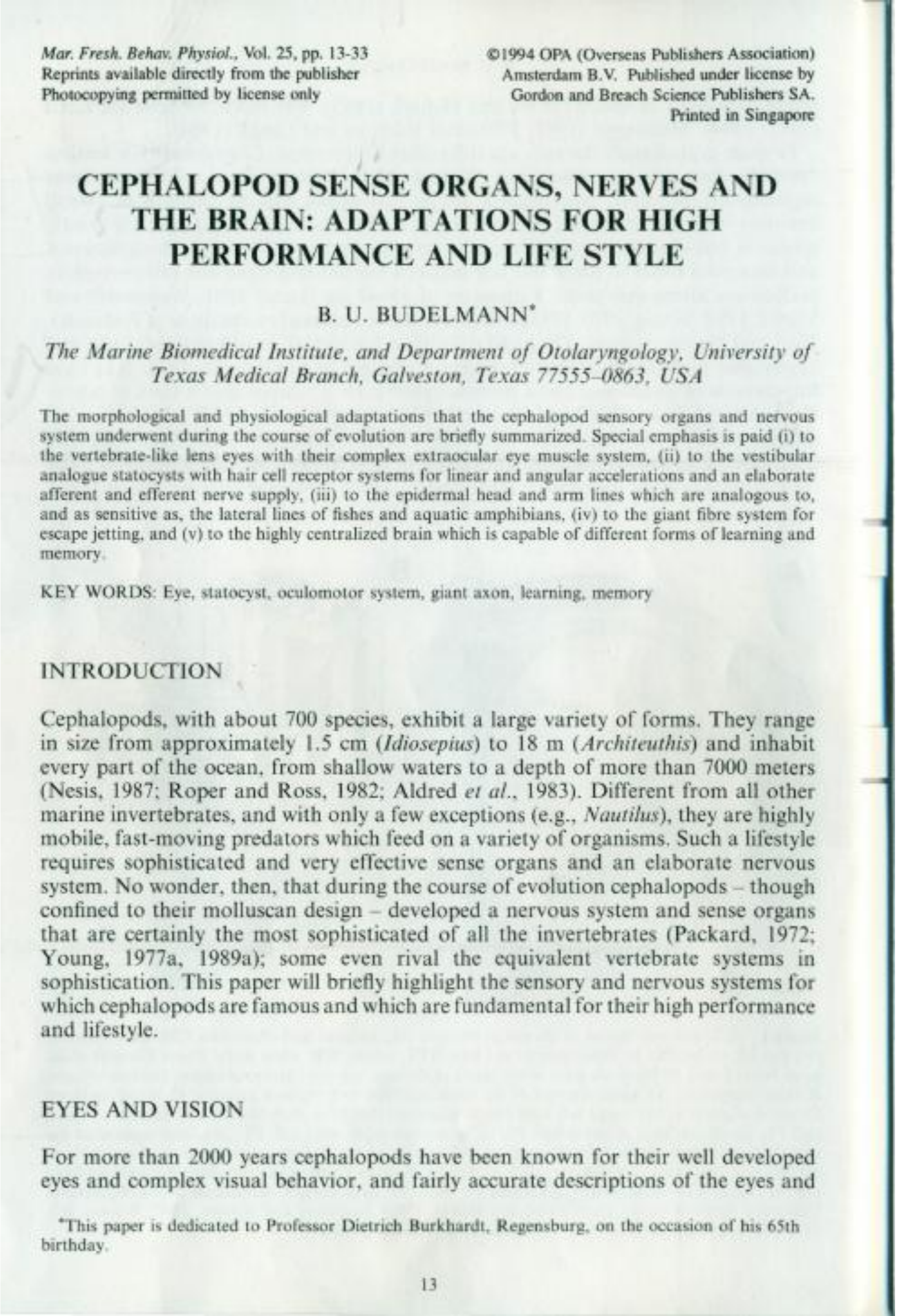

Mar. Fresh. Behav. Physiol., Vol. 25, pp. 13-33
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CEPHALOPOD SENSE ORGANS, NERVES AND THE BRAIN: ADAPTATIONS FOR HIGH PERFORMANCE AND LIFE STYLE

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The morphological and physiological adaptations that the cephalopod sensory organs and nervous system underwent during the course of evolution are briefly summarized. Special emphasis is paid (i) to the vertebrate-like lens eyes with their complex extraocular eye muscle system, (ii) to the vestibular analogue statocysts with hair cell receptor systems for linear and angular accelerations and an elaborate afferent and efferent nerve supply, (iii) to the epidermal head and arm lines which are analogous to, and as sensitive as, the lateral lines of fishes and aquatic amphibians, (iv) to the giant fibre system for escape jetting, and (v) to the highly centralized brain which is capable of different forms of learning and memory.

KEY WORDS: Eye, statocyst, oculomotor system, giant axon, learning, memory

INTRODUCTION

Cephalopods, with about 700 species, exhibit a large variety of forms. They range in size from approximately 1.5 cm (*Idiosepius*) to 18 m (*Architeuthis*) and inhabit every part of the ocean, from shallow waters to a depth of more than 7000 meters (Nesis, 1987; Roper and Ross, 1982; Aldred *et al.*, 1983). Different from all other marine invertebrates, and with only a few exceptions (e.g., *Nautilus*), they are highly mobile, fast-moving predators which feed on a variety of organisms. Such a lifestyle requires sophisticated and very effective sense organs and an elaborate nervous system. No wonder, then, that during the course of evolution cephalopods – though confined to their molluscan design – developed a nervous system and sense organs that are certainly the most sophisticated of all the invertebrates (Packard, 1972; Young, 1977a, 1989a); some even rival the equivalent vertebrate systems in sophistication. This paper will briefly highlight the sensory and nervous systems for which cephalopods are famous and which are fundamental for their high performance and lifestyle.

EYES AND VISION

For more than 2000 years cephalopods have been known for their well developed eyes and complex visual behavior, and fairly accurate descriptions of the eyes and

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*This paper is dedicated to Professor Dietrich Burkhardt, Regensburg, on the occasion of his 65th birthday.

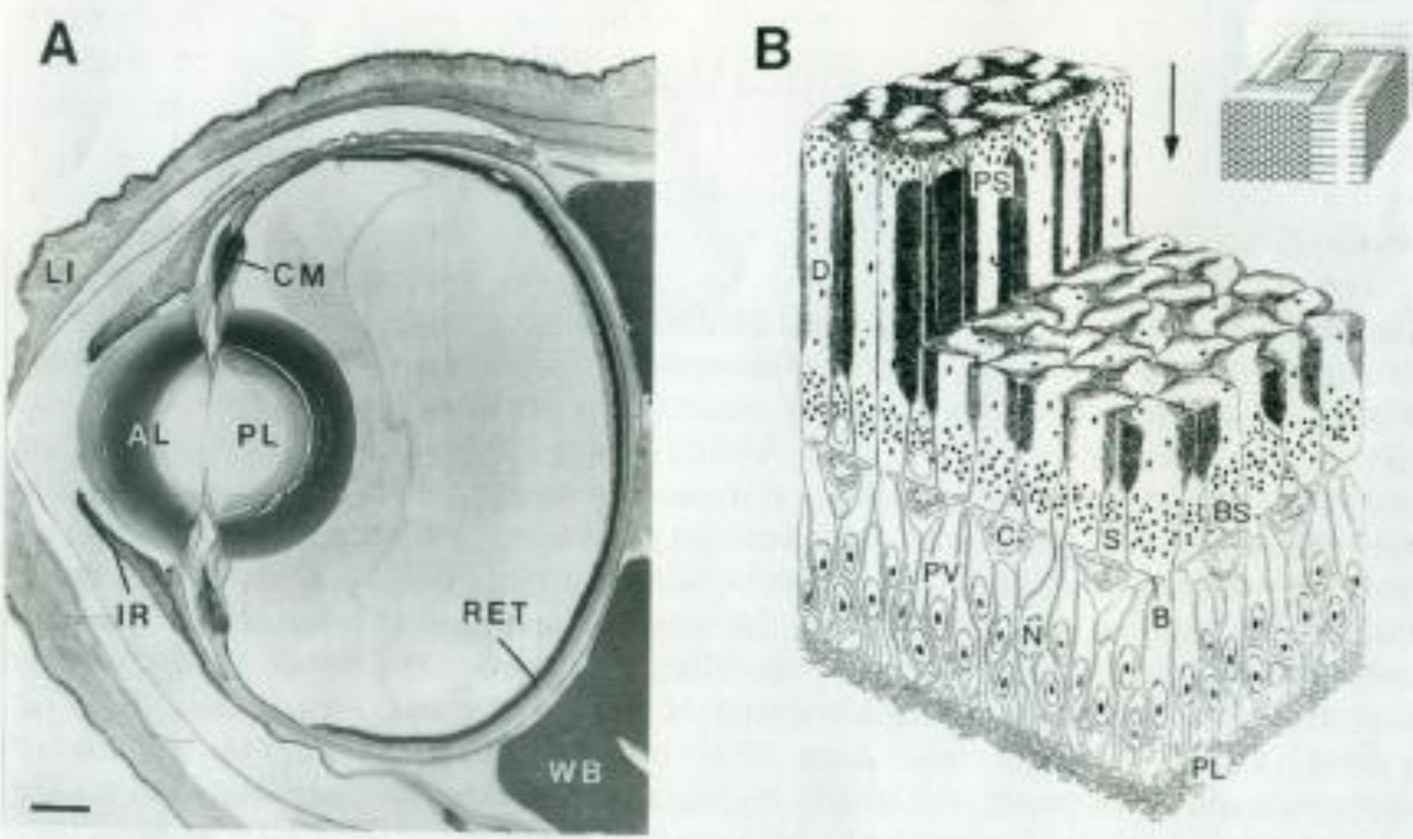

Figure 1 A: Transverse section of the eye of *Octopus*. AL, anterior part of eye lens; CM, ciliary muscle; IR, iris; LI, eyelid; PL, posterior part of eye lens; RET, retina; WB, white body. Borax Carmine stain. Scale bar is 1 mm. B: Block diagram of the retina of *Octopus vulgaris*. Arrow indicates direction of light. B, basal membrane; BS, basal segment of the visual cell filled with pigment granules; C, blood capillary; D, distal segment of the visual cell with lateral microvilli that form rhabdomeres; N, nucleus of visual cell; PL, plexiform layer of the retina; PS, tip process of supporting cell; PV, proximal segment of the visual cell; S, supporting cell. Inset upper right: Diagram of the orthogonal orientation of microvilli in neighboring visual cells. (A, courtesy of J. Z. Young; B, from Yamamoto *et al.*, 1965 Reproduced from the *Journal of Cell Biology*, 1965, Volume 25: 345–359, by copyright permission of the Rockefeller University Press. B (inset), from Saibil and Hewat, 1987) *Journal of Cell Biology*, 1987, Volume 105: 19–28, by copyright permission of the Rockefeller University Press.

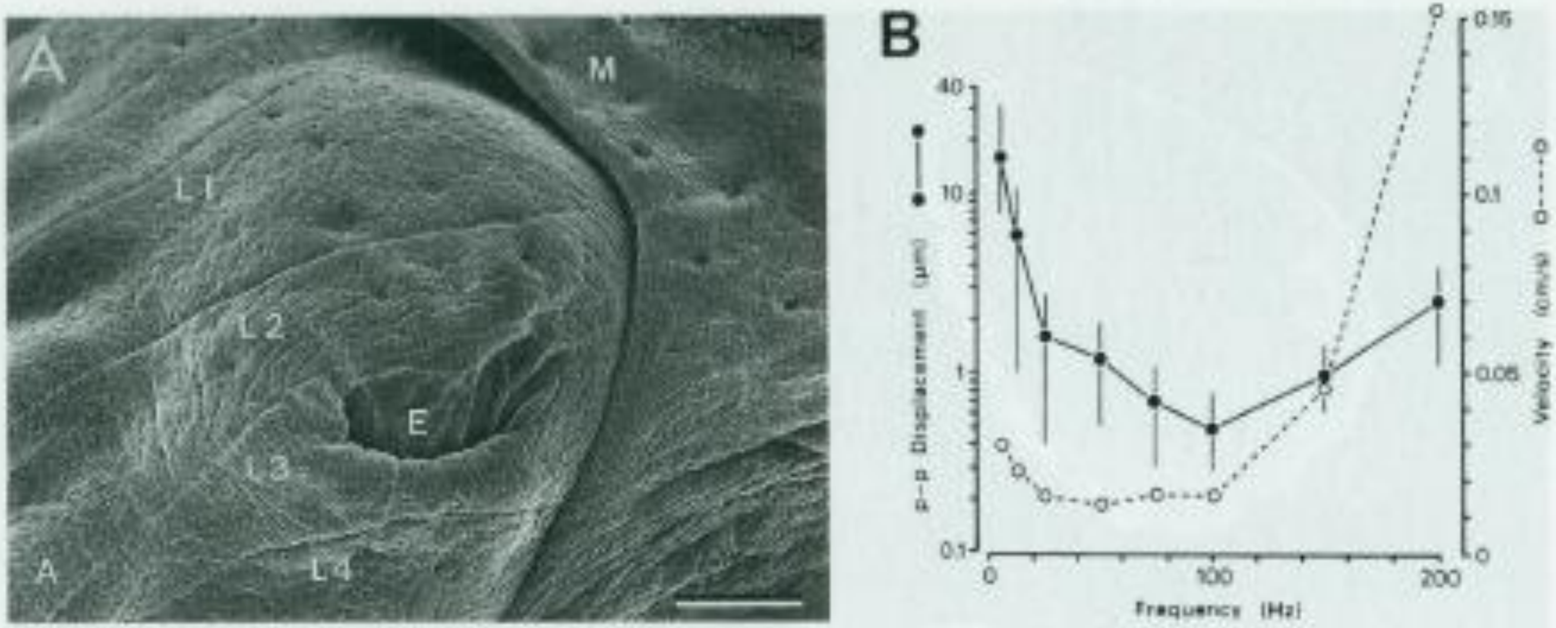

Figure 4 A: Epidermal lines (lateral line analogue) on the head of a 14-days old *Sepia officinalis*. Oblique lateral view to show the four lines (L1–L4) that run in anterior/posterior direction. Some lines continue onto an arm (A). E, eye; M, anterior edge of mantle. Scale bar is 0.5 mm. B: Thresholds of the dorsal head lines of *Sepia officinalis* to local water movements. The peak-to-peak water displacement (closed circles, solid line, left ordinate) and velocity (open circles, dashed line, right ordinate) are shown as a function of stimulus frequency (abscissa). (A, Budelmann and Fertl, unpublished; B, from Budelmann and Bleckmann, 1988;) Reproduced from the *Journal of Comparative Physiology A*, 1988, Volume 164: 1–5, by copyright permission of Springer Verlag

Figure 5 A: Cut-open cavity of the statocyst of *Nautilus* (scanning electron micrograph). The mass of statoconia is removed. K, opening of Kölliker's canal. Scale bar is 0.3 mm. B: The octopod-type of statocyst of *Octopus vulgaris* (photomicrograph). Lateral view of the left statocyst sac with the macula/statolith system and the crista/cupula system (divided into nine subsystems). Note that the cupulae are not seen in this and the next figure. S, statolith; 1–9, crista segments 1–9. Scale bar is 0.5 mm. C: The decapod-type of statocyst of *Sepia officinalis* (photomicrograph). The two statocyst cavities are cut open by a transverse vertical cut. To the left: Anterior view, showing the three macula/statolith (statoconia) systems in each cavity and two of the four crista segments. To the right: Posterior view, showing the remaining two crista segments. In the cavity on the right, some of the cartilaginous anticrista lobes have been removed to show the course of the crista segments. 1, crista transversalis anterior; 2, crista longitudinalis; 3, crista transversalis posterior; 4, crista verticalis; I, statoconial layer of macula neglecta inferior; P, statolith of macula statica princeps; S, statoconial layer of macula neglecta superior. Scale bar is 1 mm. (A, Budelmann, unpublished; B, from Budelmann *et al.*, 1987a; C, from Budelmann, 1976). Reproduced from the *Philosophical Transactions of the Royal Society of London*, 1987, Volume 315: 305–343, by copyright permission of The Royal Society. Reproduced from the *Structures and Function of Proprioceptors in the Invertebrates* (Mill, P. J., ed.), 1976, pp. 529–566, by copyright permission of Chapman and Hall.

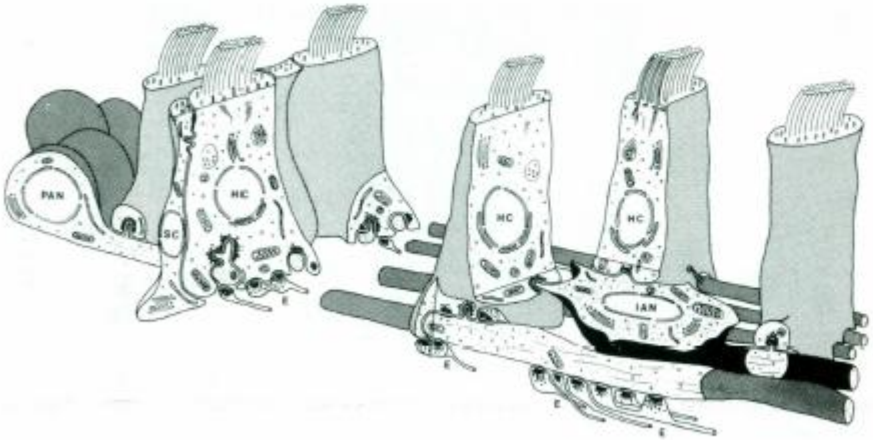

Figure 6 Diagram of the cellular, neuronal and synaptic organization of the macula of the statocyst of *Octopus vulgaris*. The secondary sensory hair cells (HC) are in afferent synaptic contact with two types of first-order afferent neurons (IAN, intramacullar afferent neurons; PAN, perimacular afferent neurons). Hair cells and neurons receive many efferent endings (E). (From Colmers, 1981). Reproduced from the *Journal Comparative Neurology*, 1981, Volume 197: 385–394, by copyright permission of Alan R. Liss Inc.

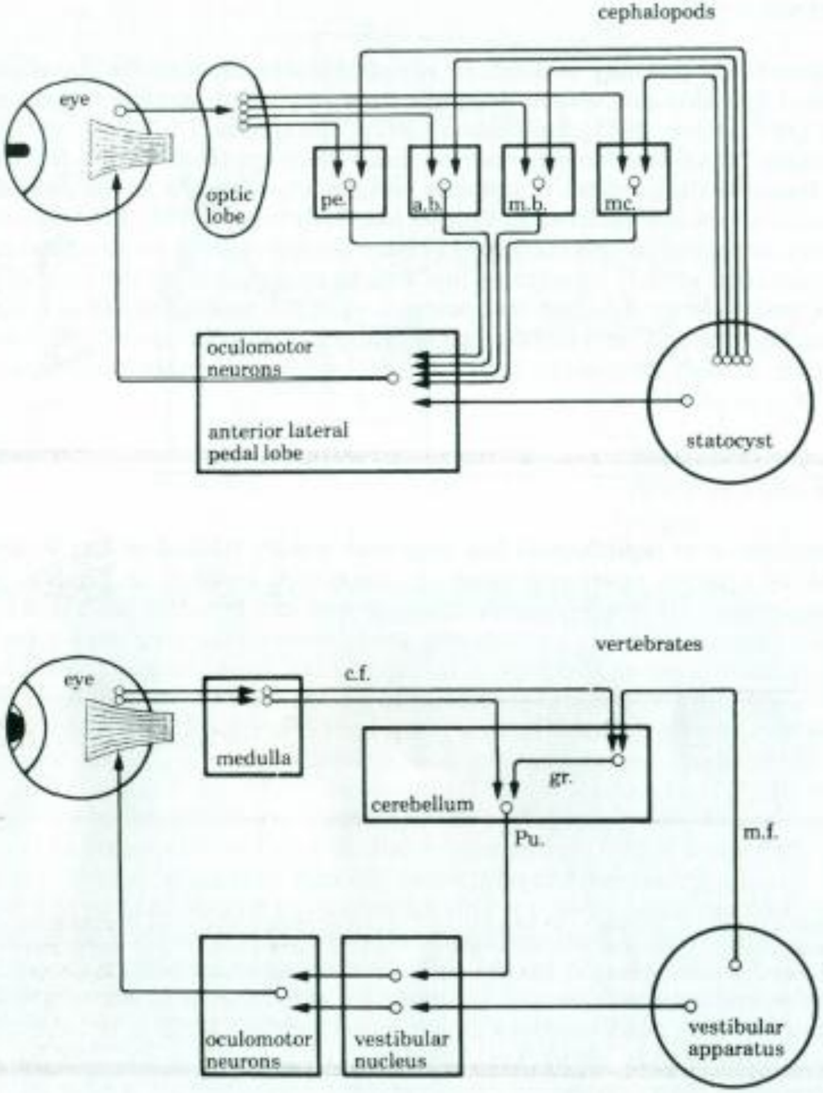

Figure 8 Brain pathways of the oculomotor control system in cephalopods and vertebrates. Simplified diagrams to show the direct and indirect pathways from the equilibrium receptor organs to the motoneurons of the eyes in the statocyst-oculomotor reflex of *Octopus* (top) and the vestibulo-ocular reflex (VOR) of vertebrates (bottom). a.b., anterior basal lobe; c.f., climbing fibres; gr., granule cells; m.b., median basal lobe; m.c., magnocellular lobe; m.f., mossy fibres; pe., peduncle lobe; Pu., Purkinje cell. (From Budelmann and Young, 1984). Reproduced from the *Philosophical Transactions of the Royal Society of London*, 1984, Volume 306: 159–189, by copyright permission of The Royal Society.

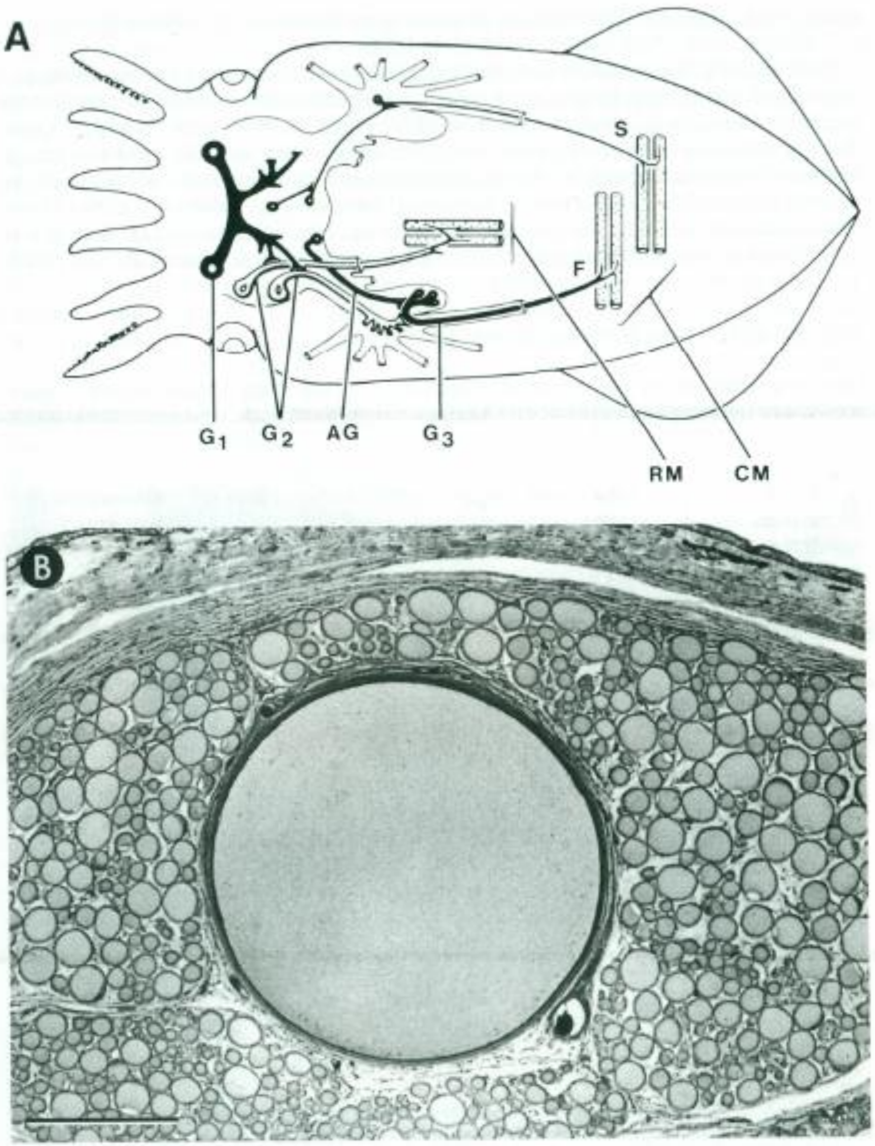

Figure 9 A: Diagram of the giant fibre system of *Loligo*, showing the neuronal pathways to the slow (S; top) and fast (F; bottom) circular muscle system. AG, accessory giant cell; CM, circular muscles; G1, first-order giant cell; G2, second-order giant cell; G3, third-order giant cell; RM head retractor muscle. B: Cross section of the third-order giant fibre of *Lolliguncula brevis*. Scale bar is 100 μm. (A, from Mackie, 1990, based on Young, 1936; B, courtesy of K. Cooper.) Reproduced from the *Canadian Journal of Zoology*, 1990, Volume 68: 799–805, by copyright permission of National Research Council of Canada.

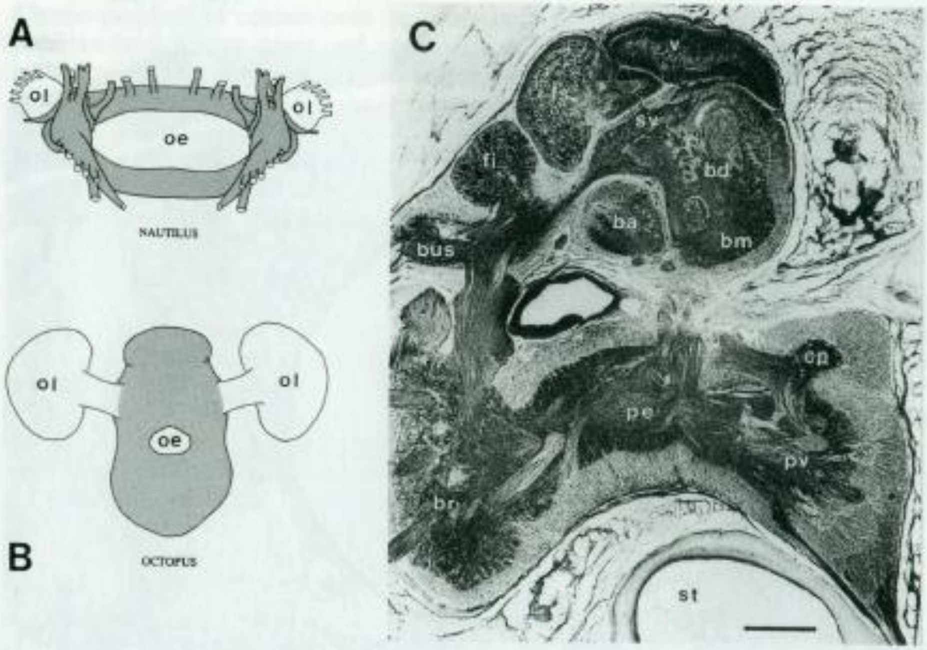

Figure 10 A, B: Diagrammatic anterior views of the central nervous systems of *Nautilus* (A) and *Octopus* (B), demonstrating the degree of centralization of the central nervous system around the oesophagus (oe) and the size relation between the central brain (stippled) and the optic lobes (ol). C: Sagittal section of the central nervous system of *Octopus vulgaris*, showing the various lobes in the supra- and suboesophageal masses of the brain. ba, anterior basal lobe; bd, dorsal basal lobe; bm, median basal lobe; br, brachial lobe; bus, superior buccal lobe; cp, posterior chromatophore lobe; fi, inferior frontal lobe; fs, superior frontal lobe; pe, anterior and posterior pedal lobes; pv, pallioviisceral lobe; st, statocyst cavity; sv, subvertical lobe; v, vertical lobe. Scale bar is 1 mm. (A, based on Young, 1965; C:, courtesy of J. Z. Young.)

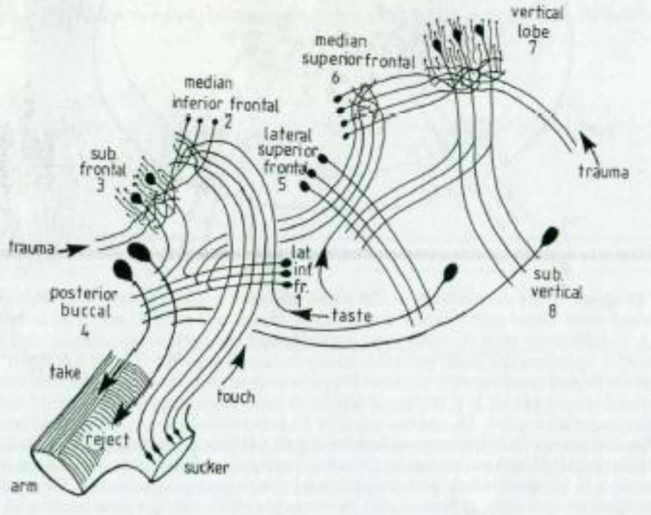

Figure 11 Diagram of the connections of the tactile memory system of *Octopus*.The successive matrices are labelled 1–8. (From Young, 1991b.) Reproduced from the *Biological Bulletin*, 1991, Volume 180: 200–208, by copyright permission of Marine Biology Laboratory.

Cephalopod Chromatophores

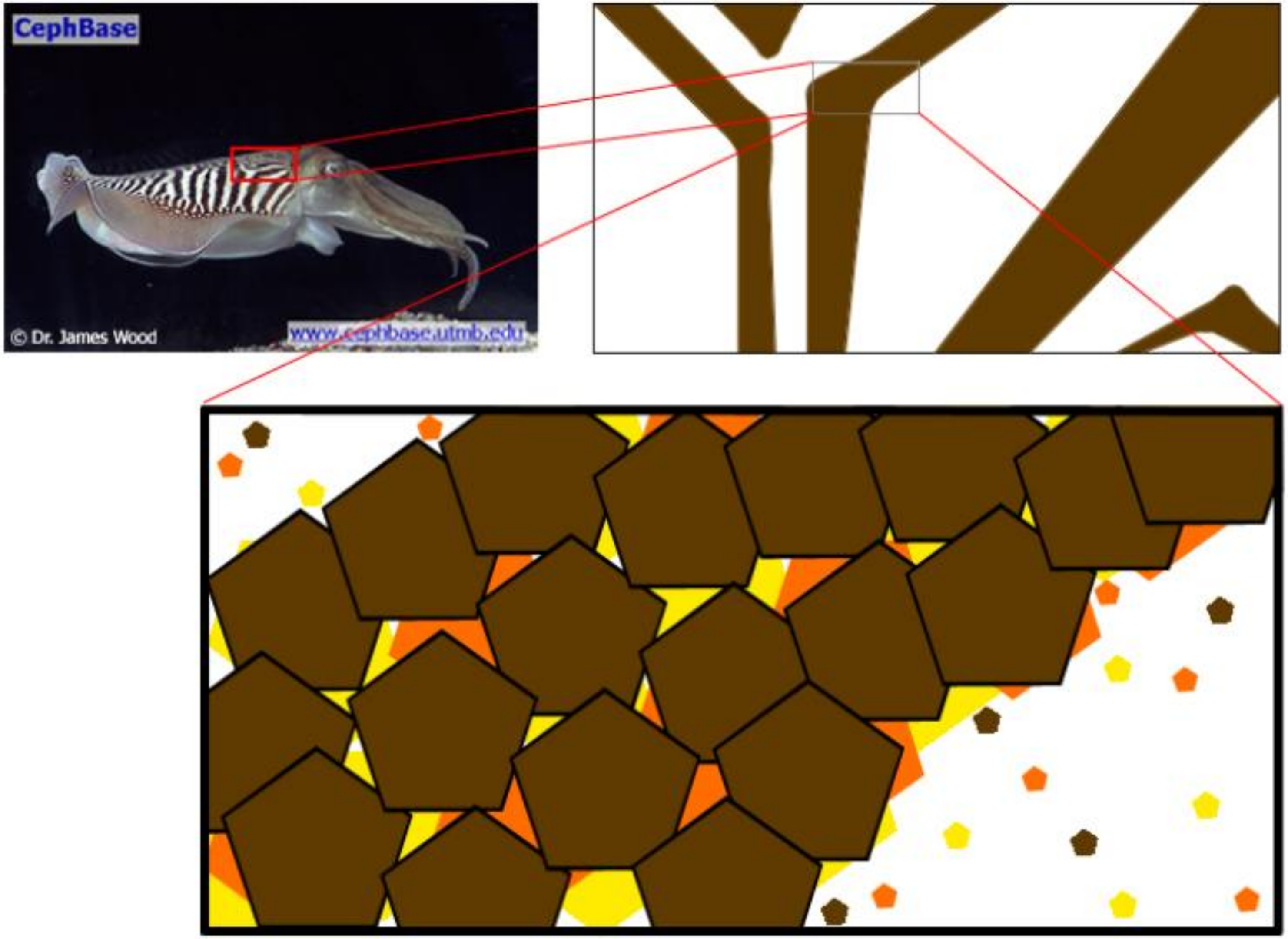

Figure 3. A) Iridophores and chromatophores on skin of Sepioteuthis sepioidea (CephBase image No. 287 by Roger T. Hanlon) . B) Red and green iridophores visible on head of cuttlefish, sepia officinalis (CephBase image No. 1378 by James B. Wood).

Figure 4. A) Leucophores (white areas) visible on skin of Octopus burryi (CephBase image No. 294 by Roger T. Hanlon). B) Octopus burryi showing white spots due to leucophores (CephBase image No. 42 by Martin A. Wolterding).

Figure 5. Histioteuthis sp. (CephBase image No. 577 unknown photographer) with numerous photophores.

Shigeno S. and Yamamoto M. 2002 Organization of the Nervous System in the Pygmy Cuttlefish, *Idiosepius paradoxus* Ortmann (Idiosepiidae, Cephalopoda)

Journal of Morphology 254(1):65-80
DOI: 10.1002/jmor.10020

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Research Article

Organization of the nervous system in the pygmy cuttlefish, *Idiosepius paradoxus* ortmann (Idiosepiidae, cephalopoda)

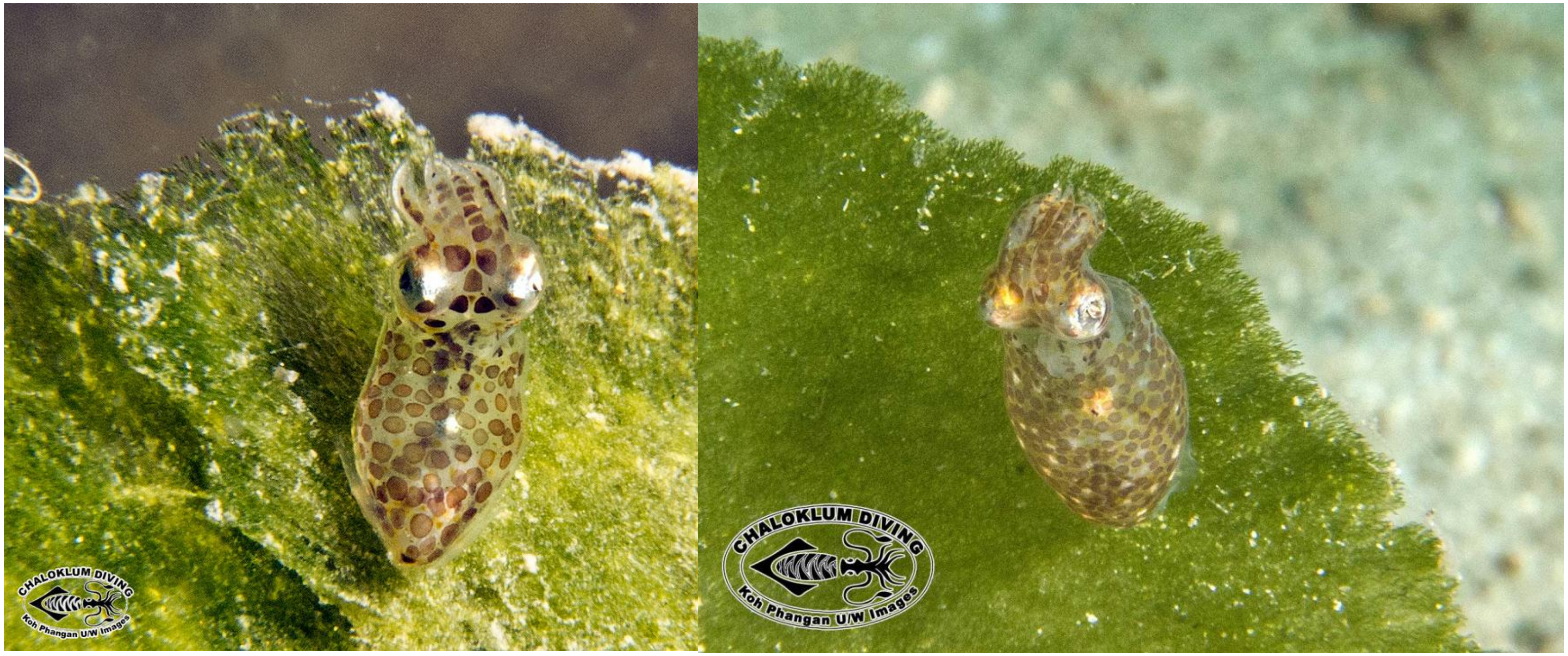
Shuichi Shigeno, Masamichi Yamamoto

First published: 31 July 2002 | https://doi.org/10.1002/jmor.10020 | Cited by:31

Abstract

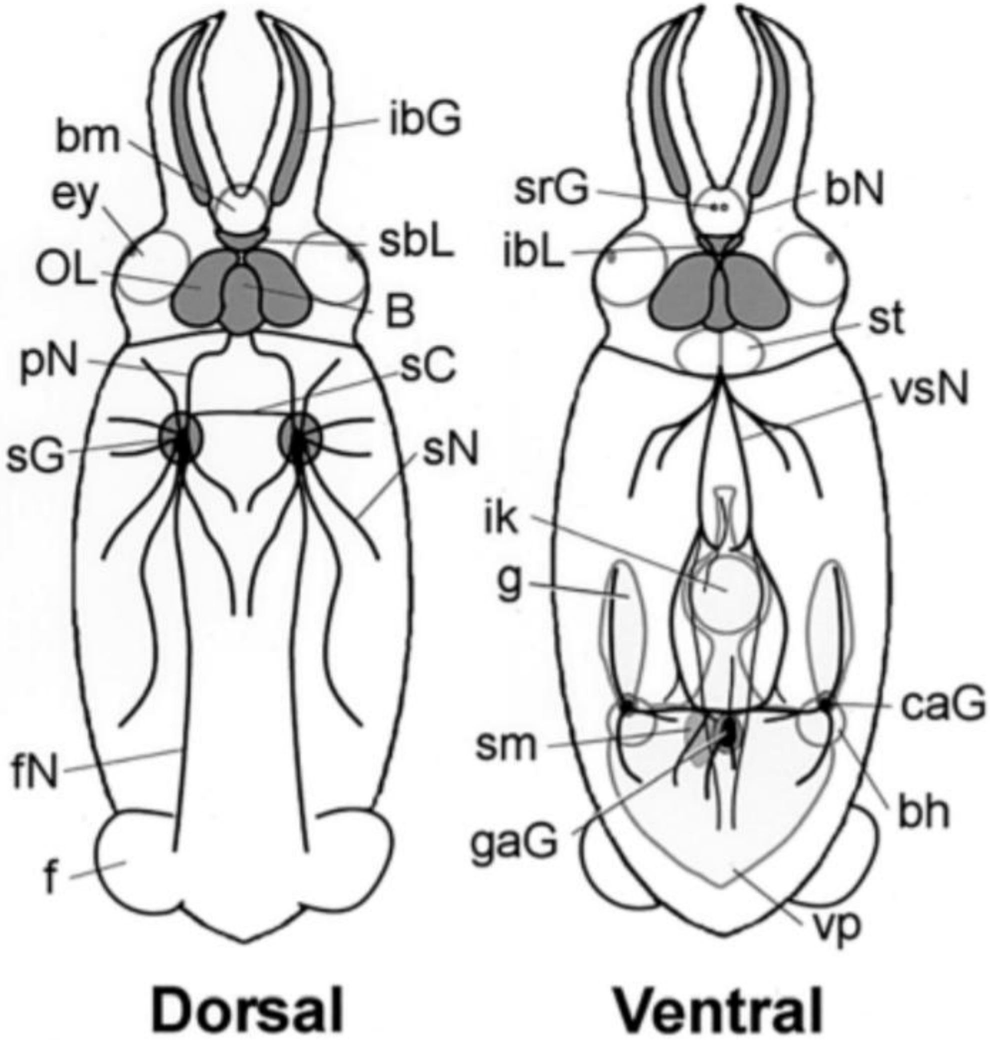
The idiosepiid cuttlefish is a suitable organism for behavioral, genetic, and developmental studies. As morphological bases for these studies, organization of the nervous system was examined in *Idiosepius paradoxus* Ortmann, 1881, using Cajal's silver technique and immunohistochemical staining with anti-acetylated α-tubulin antibody. The nervous architecture is generally identical to that described in *Sepia* and *Loligo*, but some features characterize the idiosepiid nervous system. The olfactory system is highly developed in the optic tract region. The dorsolateral lobes show large neuropils, connected with each other by a novel well-fasciculated commissure. Each olfactory lobe is subdivided into two lobules. The neuropils of the anterior and the posterior chromatophore lobes are very poorly developed. Neuronal gigantism is not extensive in the brain; enlarged neuronal cells are visible only in the perikaryal layer of the posterior subesophageal mass. The giant nerve fiber system is of the *Sepia* type; the axons are not markedly thick and the first-order giant fibers do not fuse with each other at the chiasma. Three-dimensional images by whole-mount immunostaining clarified the innervation pattern in the peripheral nervous system in detail. Two commissural fibers link the left and right posterior funnel nerves ventrally and dorsally. The stellate commissure, which is absent in *Sepia* and *Sepiola*, connects the stellate ganglia with each other. A branch of the visceral nerve innervating the median pallial adductor muscle is characteristically thick. Tubulinergic reactivity of the cilia and axons reveals the presence of many ciliated cells giving off an axon toward brain nerves in the surface of the funnel, head integument, arm tips, and epidermal lines. Some of these features seem to reflect the inactive nekto-benthic life of the idiosepiid cuttlefish in the eelgrass bed. J. Morphol. 254:65–80, 2002. © 2002 Wiley-Liss, Inc.

Cuttlefish? More like cutefish!



Схематичное изображение нервной системы *Idiosepius paradoxus*

S. Shigeno and M. Yamamoto, 2002



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The Cephalopod Nervous System: What Evolution Has Made of the Molluscan Design

In: Breidbach O., Kutsch W. (eds) The Nervous Systems of Invertebrates: An Evolutionary and Comparative Approach. Experientia Supplementum, vol. 72, pp 115-138

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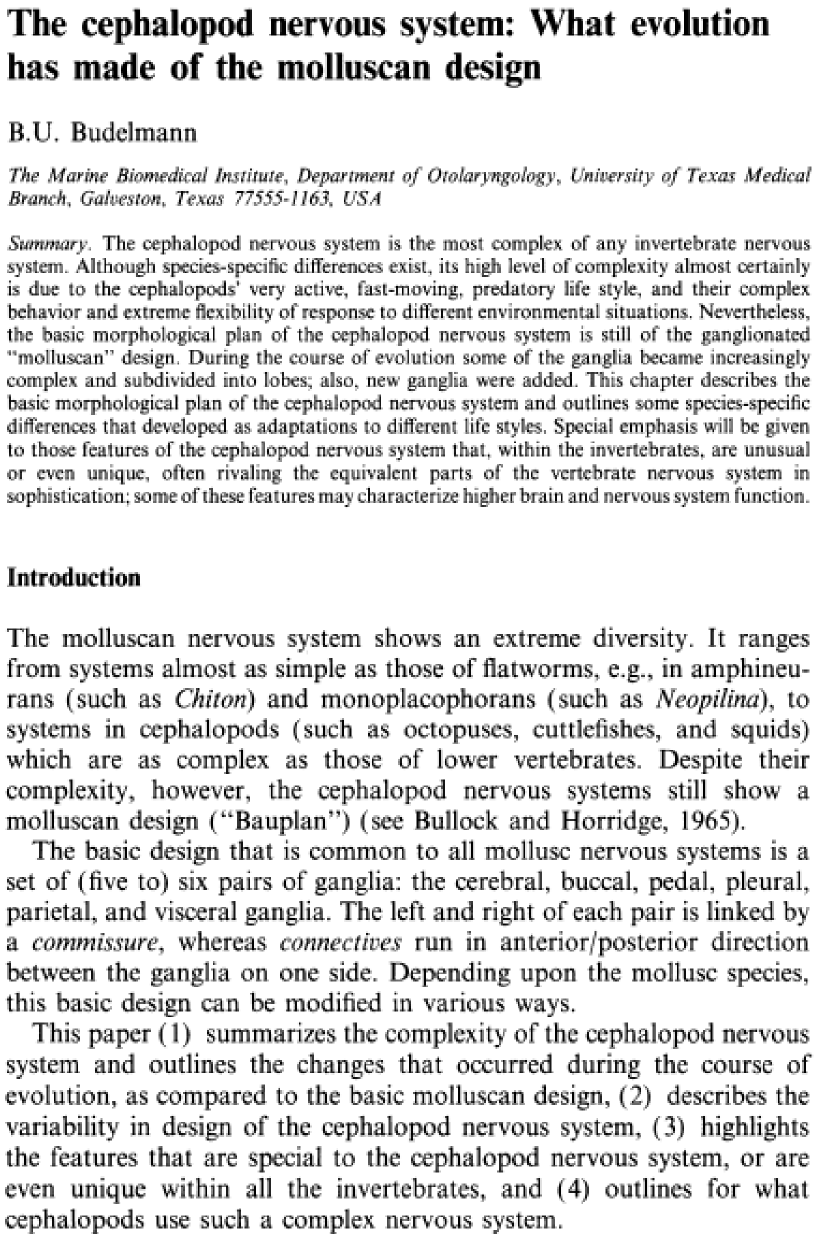

The cephalopod nervous system: What evolution has made of the molluscan design

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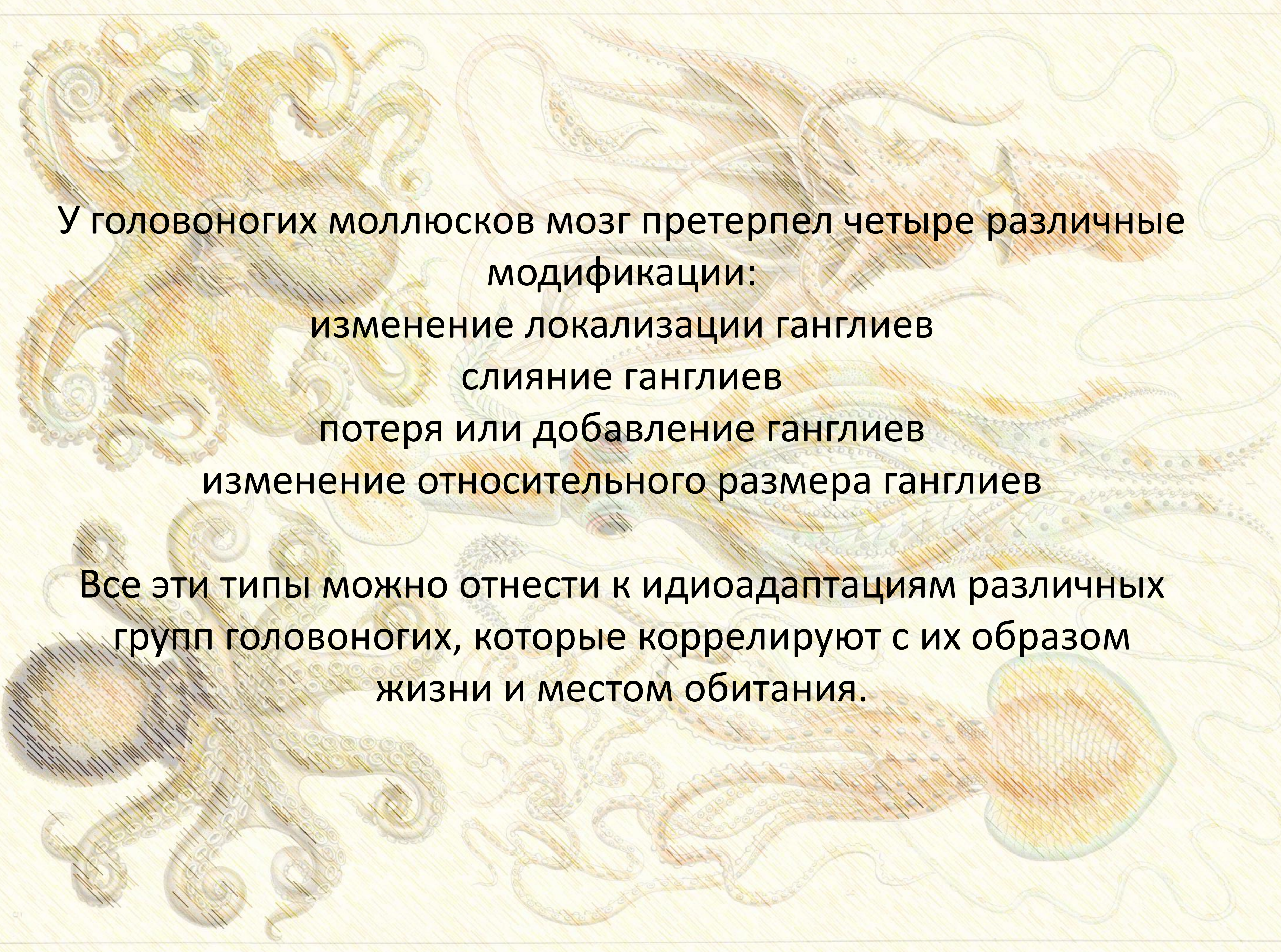
Summary. The cephalopod nervous system is the most complex of any invertebrate nervous system. Although species-specific differences exist, its high level of complexity almost certainly is due to the cephalopods' very active, fast-moving, predatory life style, and their complex behavior and extreme flexibility of response to different environmental situations. Nevertheless, the basic morphological plan of the cephalopod nervous system is still of the ganglionated "molluscan" design. During the course of evolution some of the ganglia became increasingly complex and subdivided into lobes; also, new ganglia were added. This chapter describes the basic morphological plan of the cephalopod nervous system and outlines some species-specific differences that developed as adaptations to different life styles. Special emphasis will be given to those features of the cephalopod nervous system that, within the invertebrates, are unusual or even unique, often rivaling the equivalent parts of the vertebrate nervous system in sophistication; some of these features may characterize higher brain and nervous system function.

Introduction

The molluscan nervous system shows an extreme diversity. It ranges from systems almost as simple as those of flatworms, e.g., in amphineurans (such as *Chiton*) and monoplacophorans (such as *Neopilina*), to systems in cephalopods (such as octopuses, cuttlefishes, and squids) which are as complex as those of lower vertebrates. Despite their complexity, however, the cephalopod nervous systems still show a molluscan design ("Bauplan") (see Bullock and Horridge, 1965).

The basic design that is common to all mollusc nervous systems is a set of (five to) six pairs of ganglia: the cerebral, buccal, pedal, pleural, parietal, and visceral ganglia. The left and right of each pair is linked by a *commissure*, whereas *connectives* run in anterior/posterior direction between the ganglia on one side. Depending upon the mollusc species, this basic design can be modified in various ways.

This paper (1) summarizes the complexity of the cephalopod nervous system and outlines the changes that occurred during the course of evolution, as compared to the basic molluscan design, (2) describes the variability in design of the cephalopod nervous system, (3) highlights the features that are special to the cephalopod nervous system, or are even unique within all the invertebrates, and (4) outlines for what cephalopods use such a complex nervous system.



У головоногих моллюсков мозг претерпел четыре различные модификации:

изменение локализации ганглиев

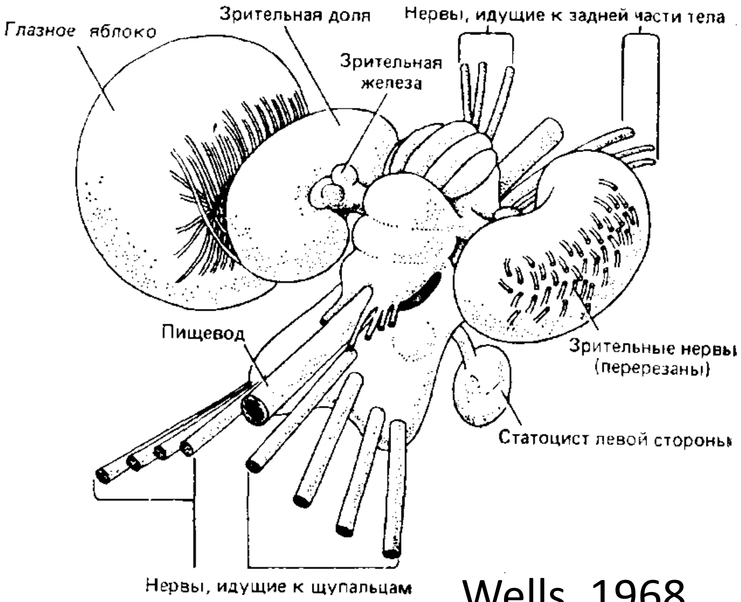
слияние ганглиев

потеря или добавление ганглиев

изменение относительного размера ганглиев

Все эти типы можно отнести к идиоадаптациям различных групп головоногих, которые коррелируют с их образом жизни и местом обитания.

Доли и их функции



Wells, 1968

25 основных долей, среди которых некоторые подразделяются вторично - так, число долей может доходить до 38!

За анализ тактильных ощущений, обучение, краткосрочную и долгосрочную память ответственны vertical, subvertical, subpedunculate, precommissural superior frontal, inferior frontal, sub-frontal, часть posterior buccal lobes и optic lobes.

Высшие моторные центры расположены в dorsal, median, anterior, lateral, and inter-basal и peduncle долях.

Median basal доля отвечает за дыхание и движения при плавании.

Lateral basal доля – за хроматофоры и мышцы кожи

Superior buccal доля - за моторные функции при питании

Magnocellular доля – за промежуточный моторный центр + молниеносная защита или уплывание и при нападении

Sub-esophageal доли – моторные центры (brachial доли – промежуточные, chromatophore и funnel доли – нижние моторные центры, vasomotor доля – кровообращение, anterior lateral pedal доля – глазодвигательная, pedal и palliovisceral доли – промежуточные и нижние моторные центры

Зрительная доля

700% у *Grimalditeuthis bonplandi*

15% у *Cirrothauma* “дамбо” *murrayi*

Вертикальная доля

(чувствительность и память)

3% у *Cirrothauma murrayi*

28% у Адского вампира
Vampyroteuthis infernalis

Плечевые доли

(промежуточные моторные центры)

30% у *Architeuthis*

5% у *Sepioteuthis*

Централизация/Цефализация

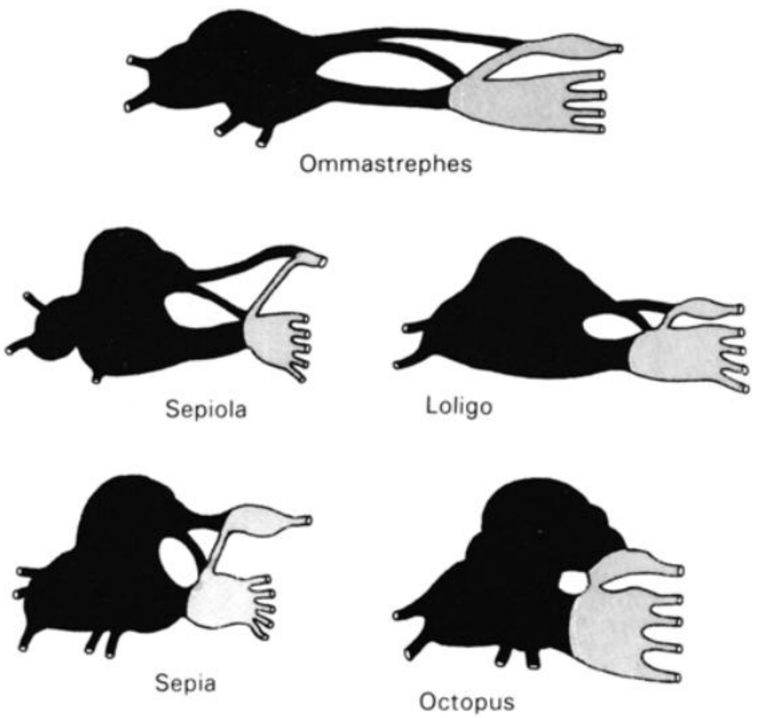
Существует три главных типа мозга головоногих:

Примитивный наутилоидный тип

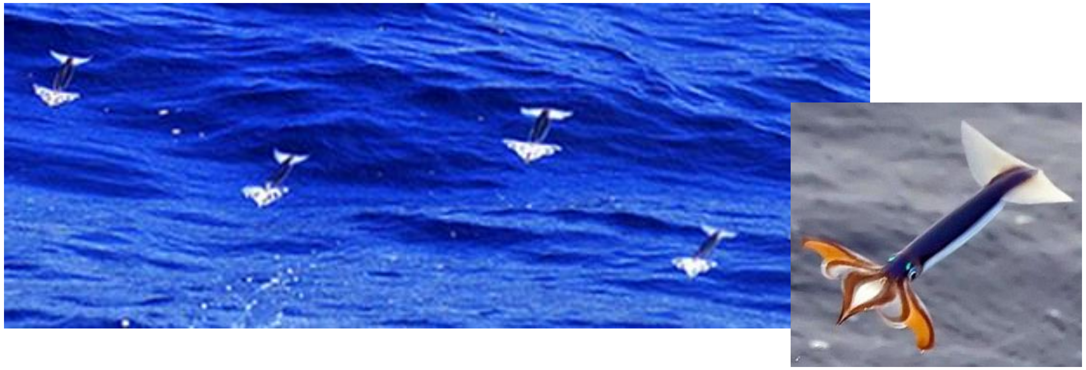
Тип, присущий десятируким головоногим (decapoda) – это каракатицы, белемниты, кальмары.

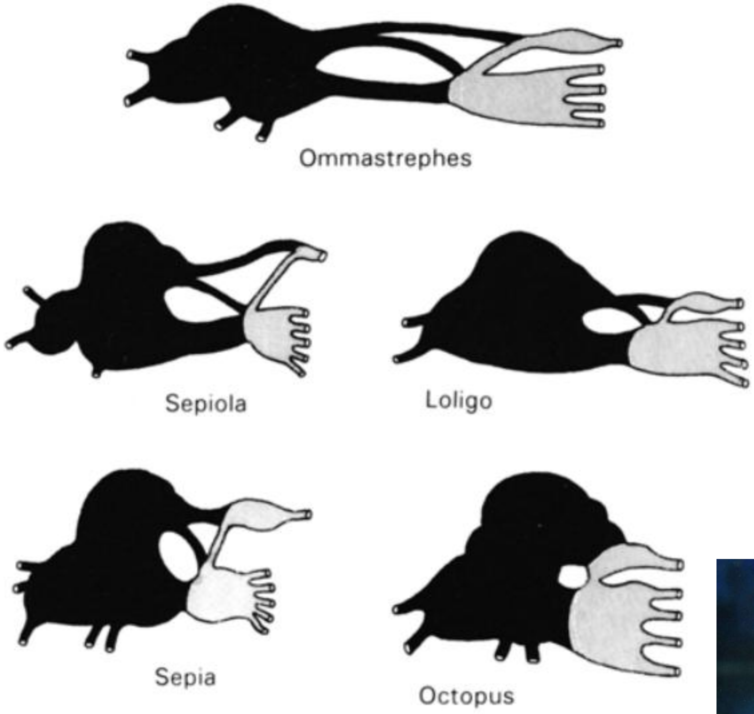
Тип, присущий восьмируким головоногим (octopoda) – это осьминоги и вампиры.

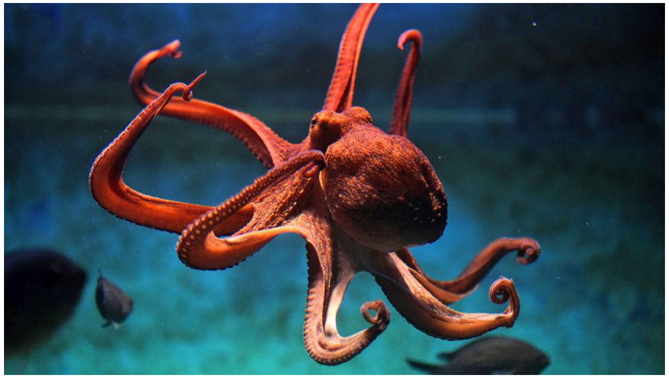
Именно в таком порядке идет увеличение «централизации» мозга



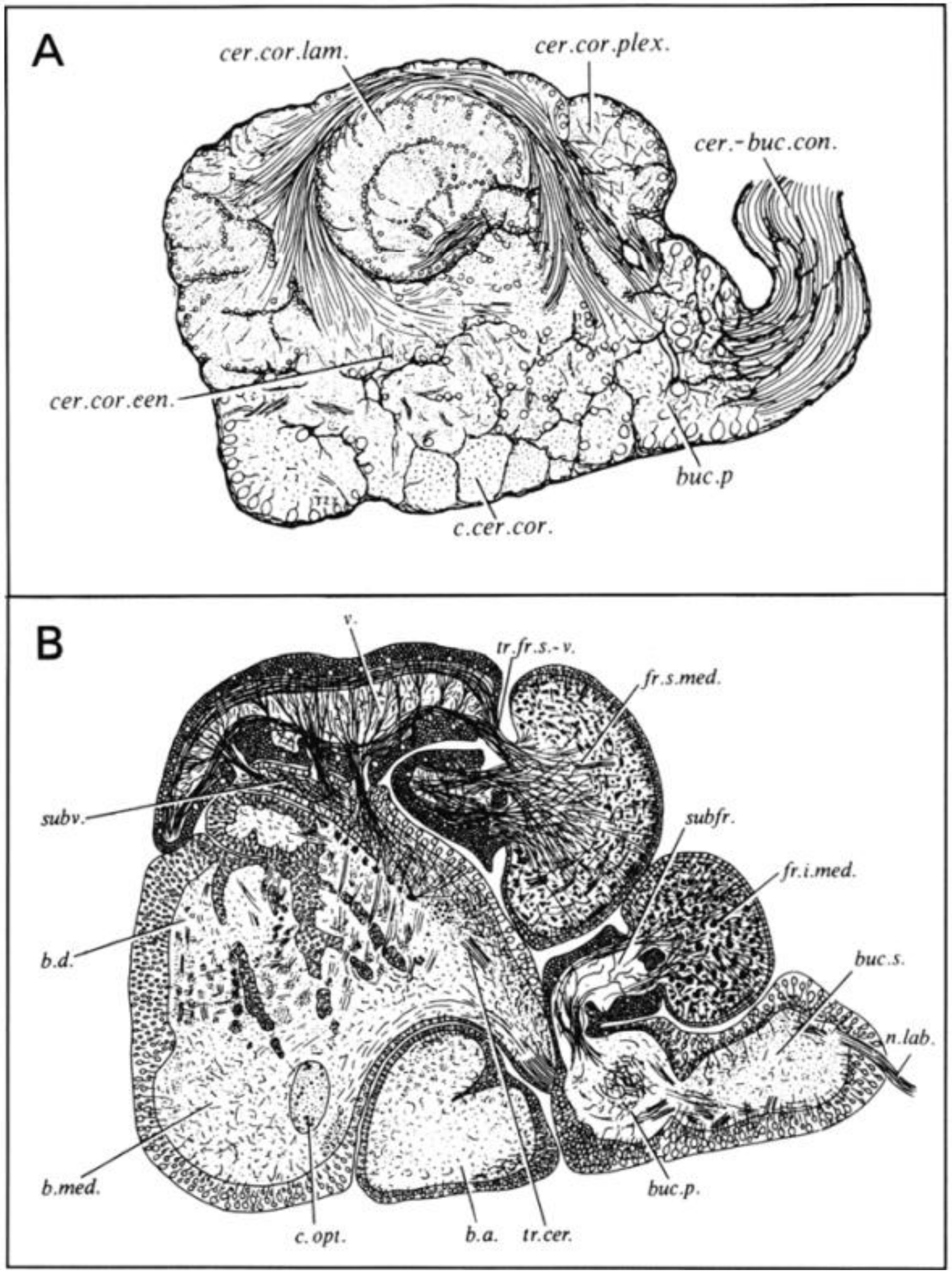
Кстати, нервная система головоногих является самой централизованной среди всех моллюсков и (в вместе с насекомыми) среди всех беспозвоночных




Ommastrephes
Sepiola
Loligo
Sepia
Octopus

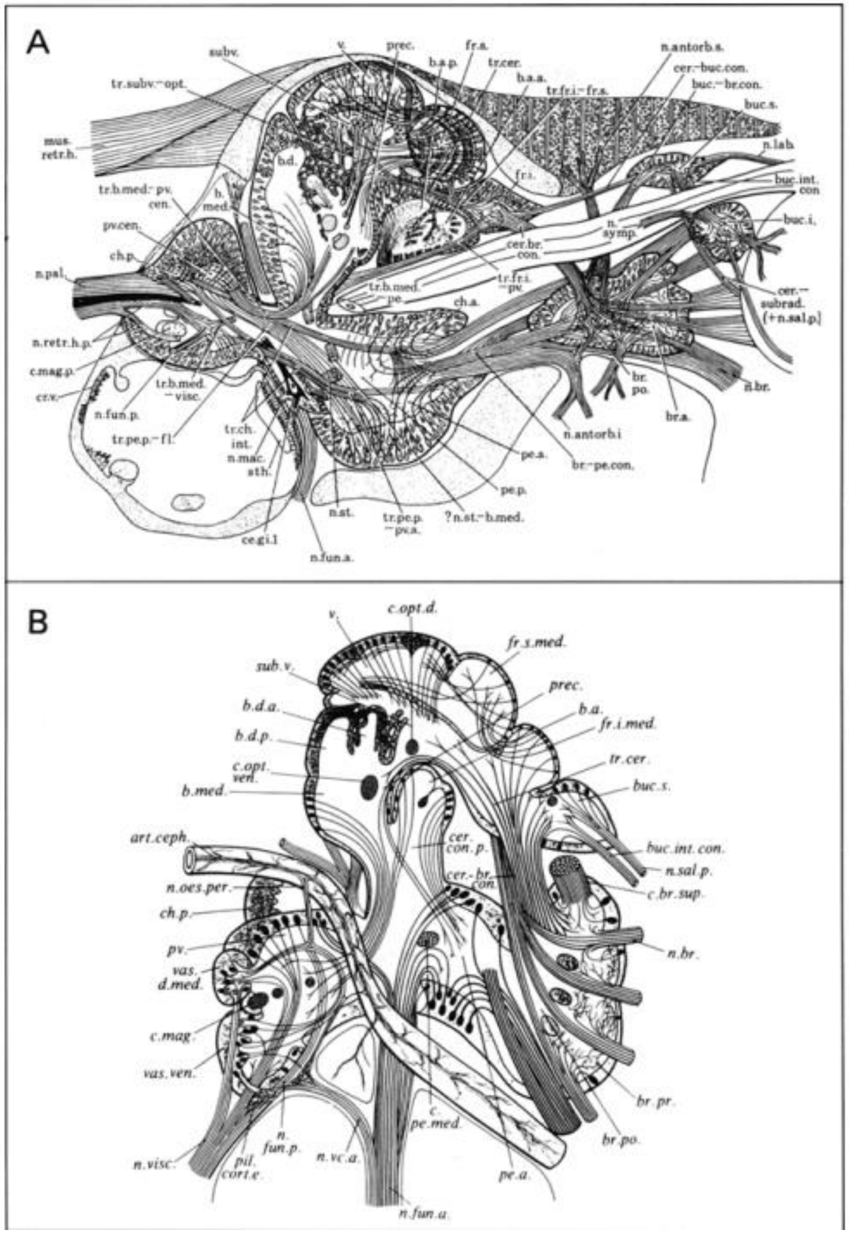


Мозг наутилуса и октаподы



Ему не хватает структур мозга для продуманного моторного контроля над щупальцами, высших центров мозга для обучения и памяти. Оптические доли намного меньше.

Различия мозга Decapoda(a) и Octapoda(b)

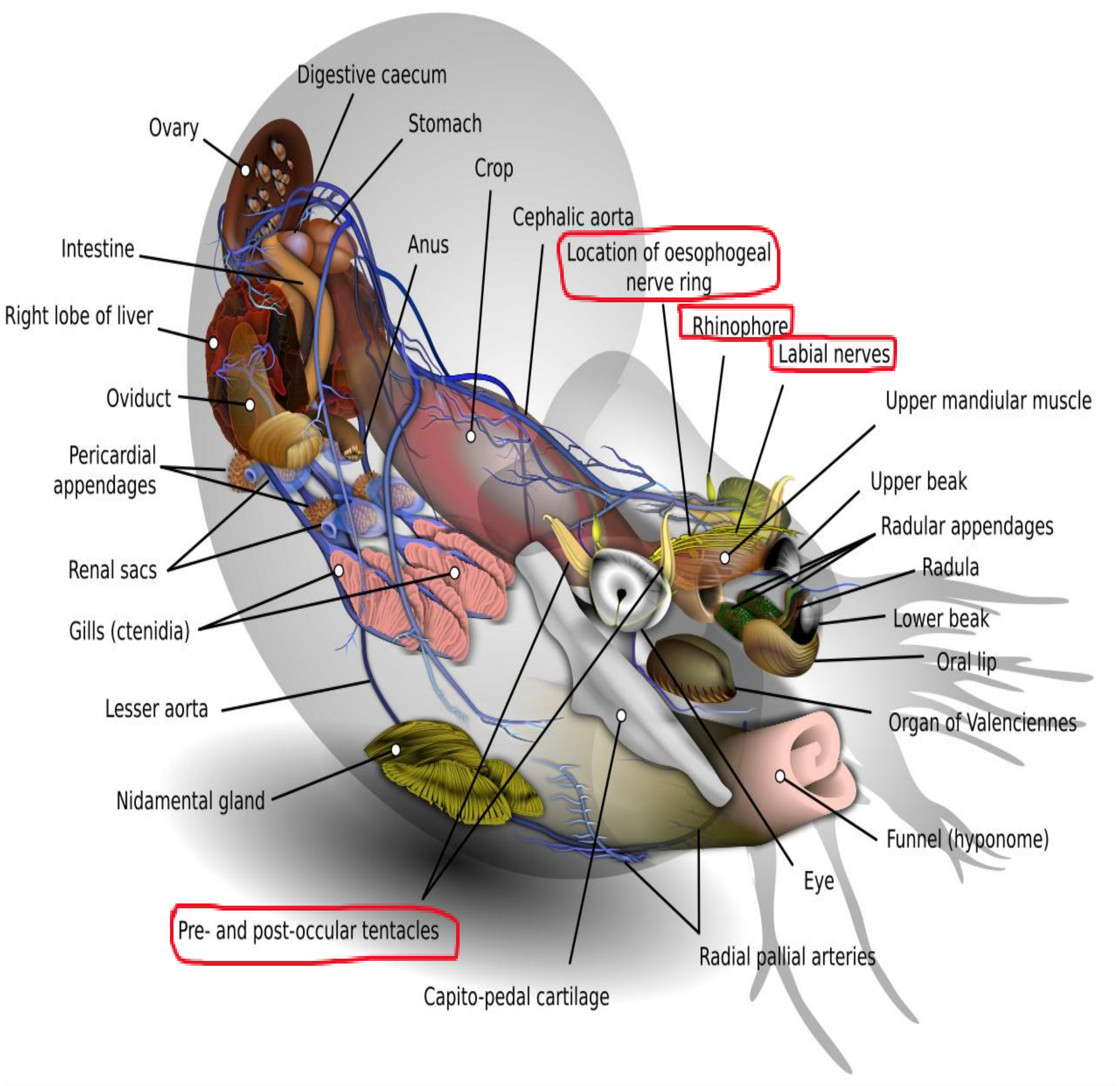


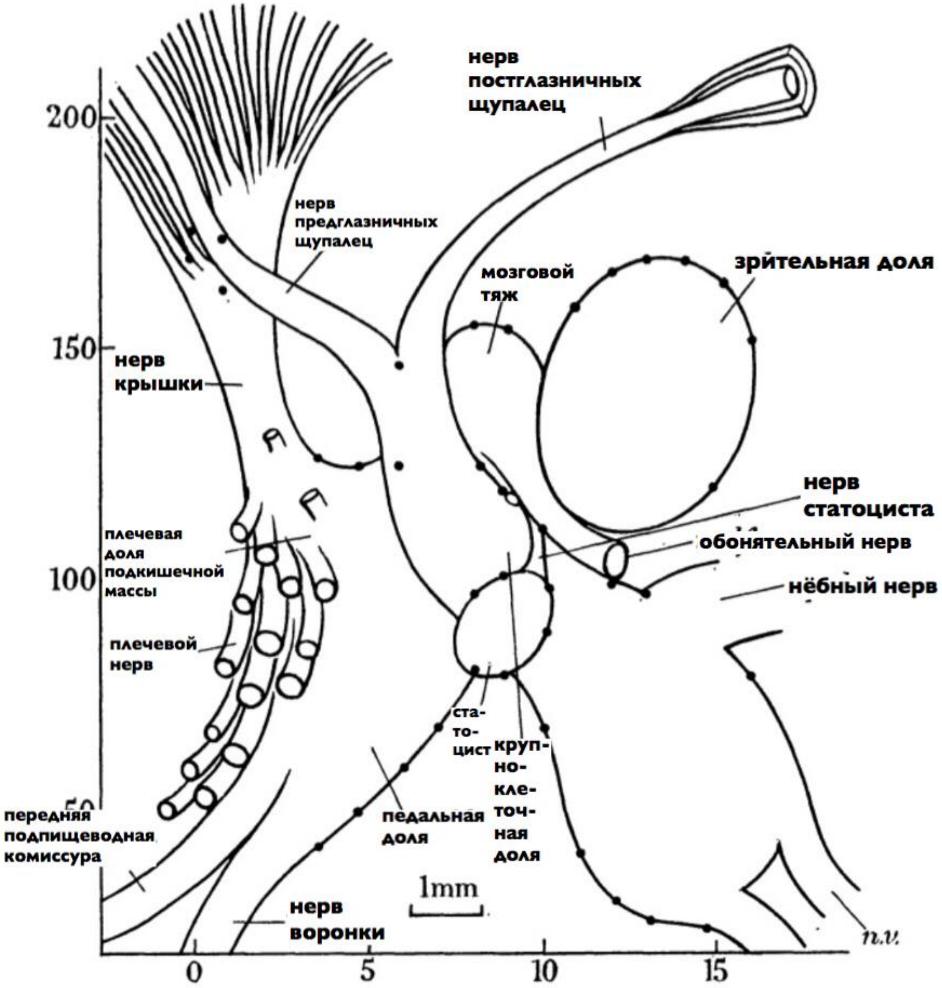
Мозг октапод более централизован, чем мозг декапода. У октапод плечевые, а также педальные лепестки и нижняя система долей больше, чем у декапод из-за более сложного использования их рук и их способности к тактильному обучению.

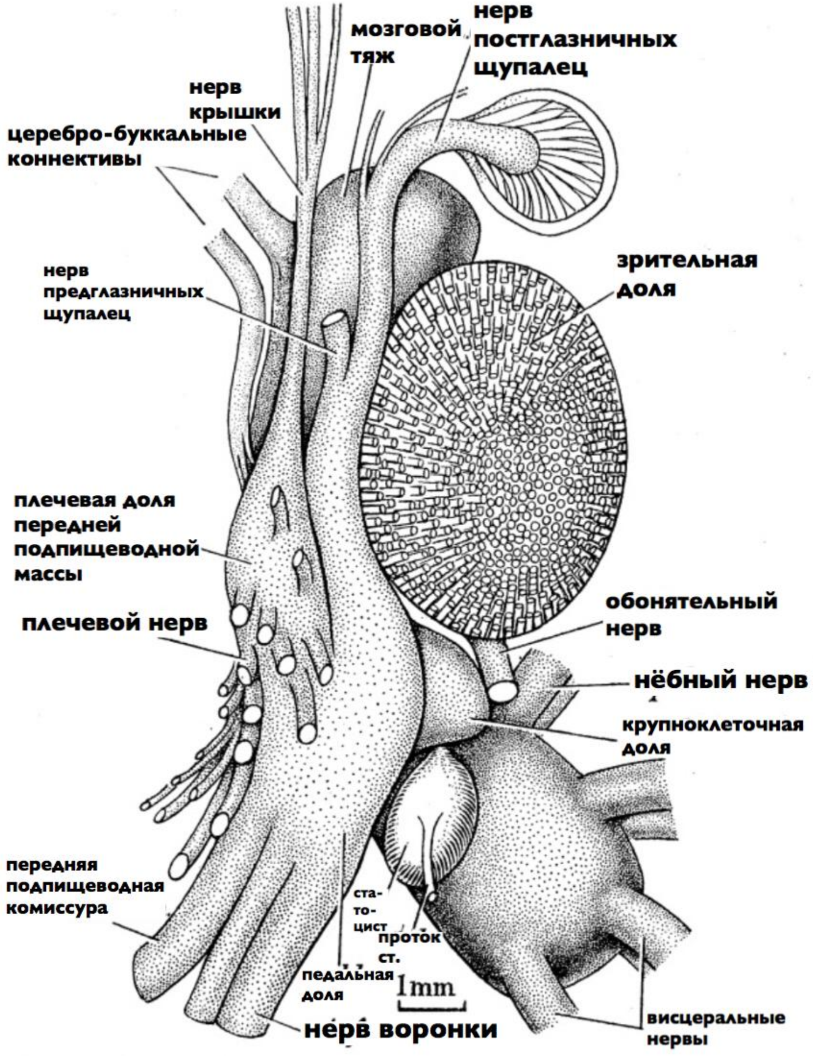
У декапод, напротив, есть большие оптические лопасти, более крупные базальные дольки и большая, но развернутая вертикальная доля; их нижняя система долей много Упрощена, и у них нет надглазничной комиссуры. В отличие от осьминогов, они имеют вентральную магноцеллюлярную комиссуру. Чтобы контролировать двигательную активность плавников, декаподы получили дополнительную плавниковую долю и периферийную гигантскую волоконную систему для высокопроизводительного плавания с реактивным движением

Индриксон Яна

ПРОСТО КРАСИВЫЙ НАУТИЛУС




нерв постглазничных щупалец
нерв предглазничных щупалец
мозговой тяж
зрительная доля
200
150
нерв крышки
нерв статоциста
обонятельный нерв
плечевая доля подкишечной массы
100
нёбный нерв
плечевой нерв
ста-то-цист
круп-но-кле-точ-ная доля
50
передняя подпищеводная комиссура
педальная доля
1mm
нерв воронки
n.v.
0
5
10
15


мозговой тяж
нерв постглазничных щупалец
нерв крышки
церебро-буккальные коннективы
зрительная доля
нерв предглазничных щупалец
плечевая доля передней подпищеводной массы
обонятельный нерв
плечевой нерв
нёбный нерв
крупноклеточная доля
передняя подпищеводная комиссура
ста-то-цист
проток ст.
педальная доля
1mm
нерв воронки
висцеральные нервы

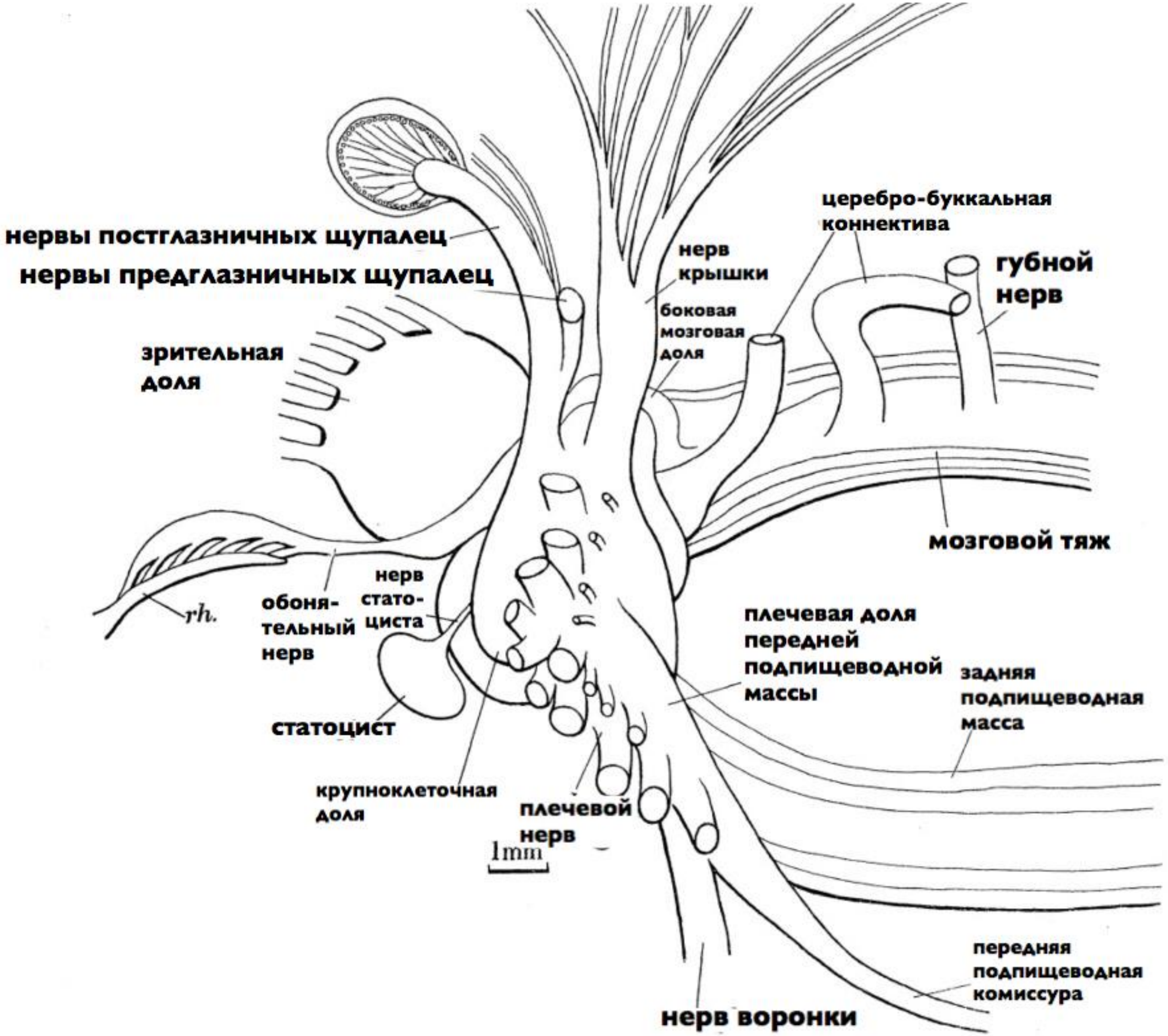
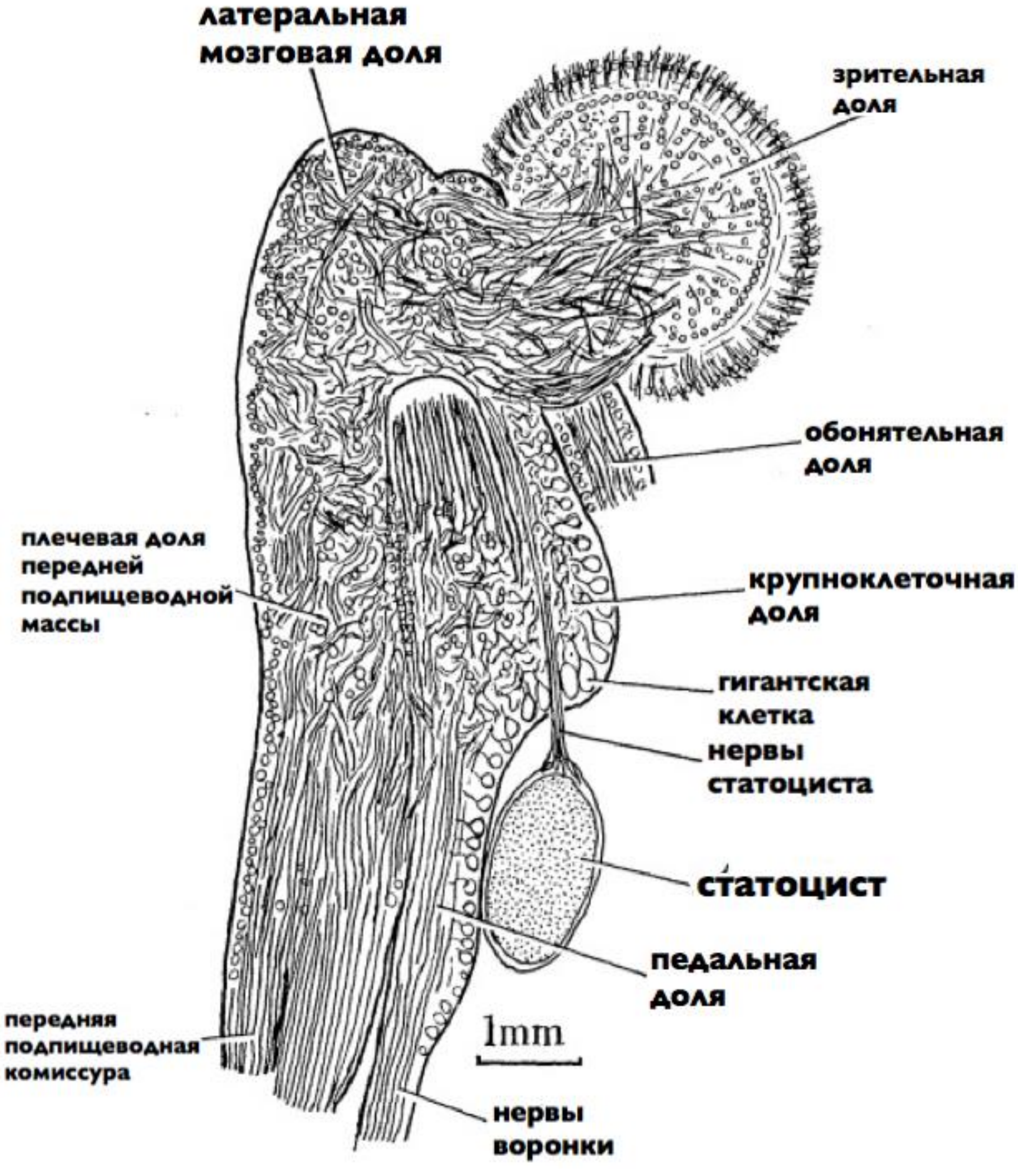
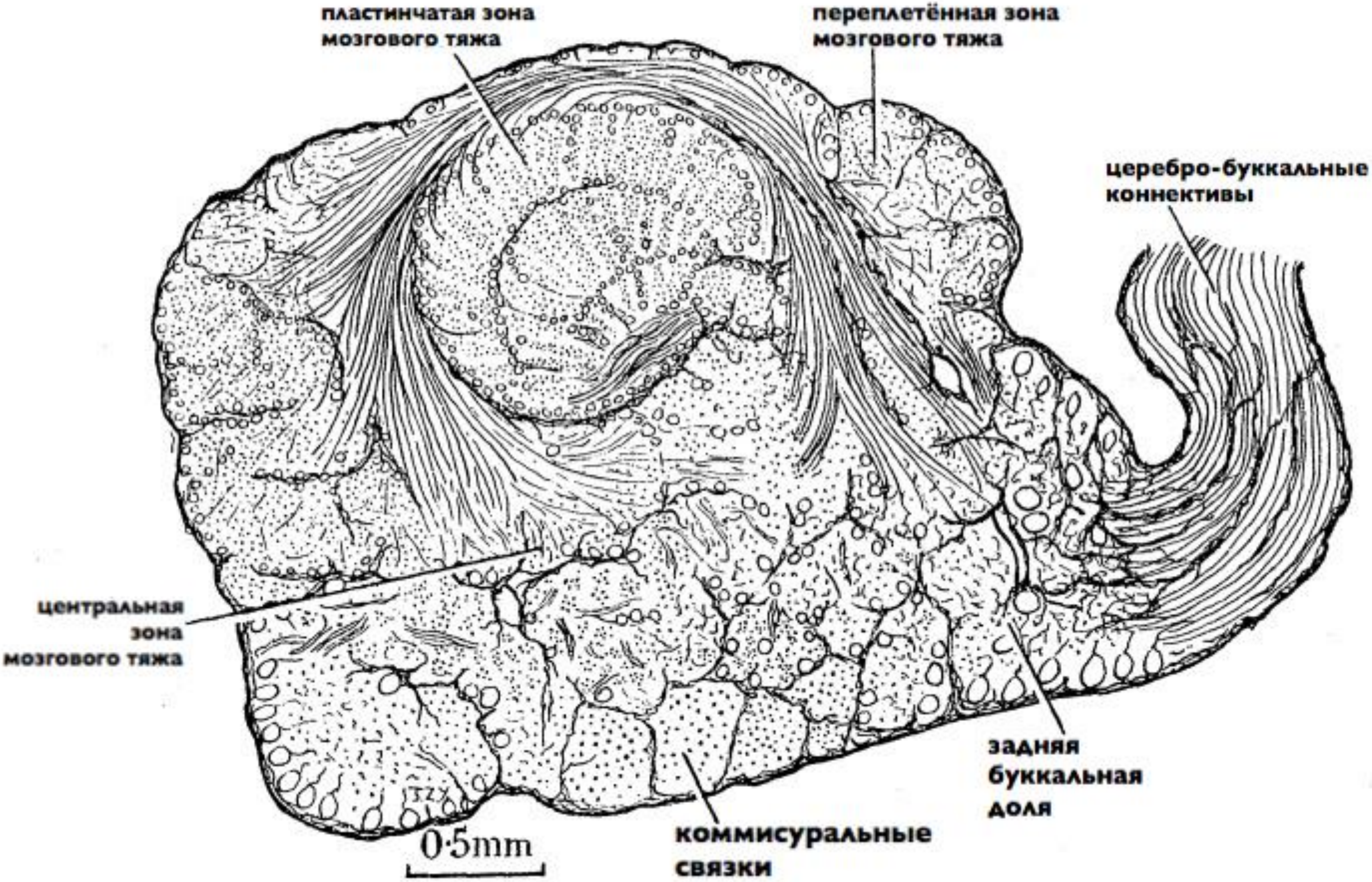
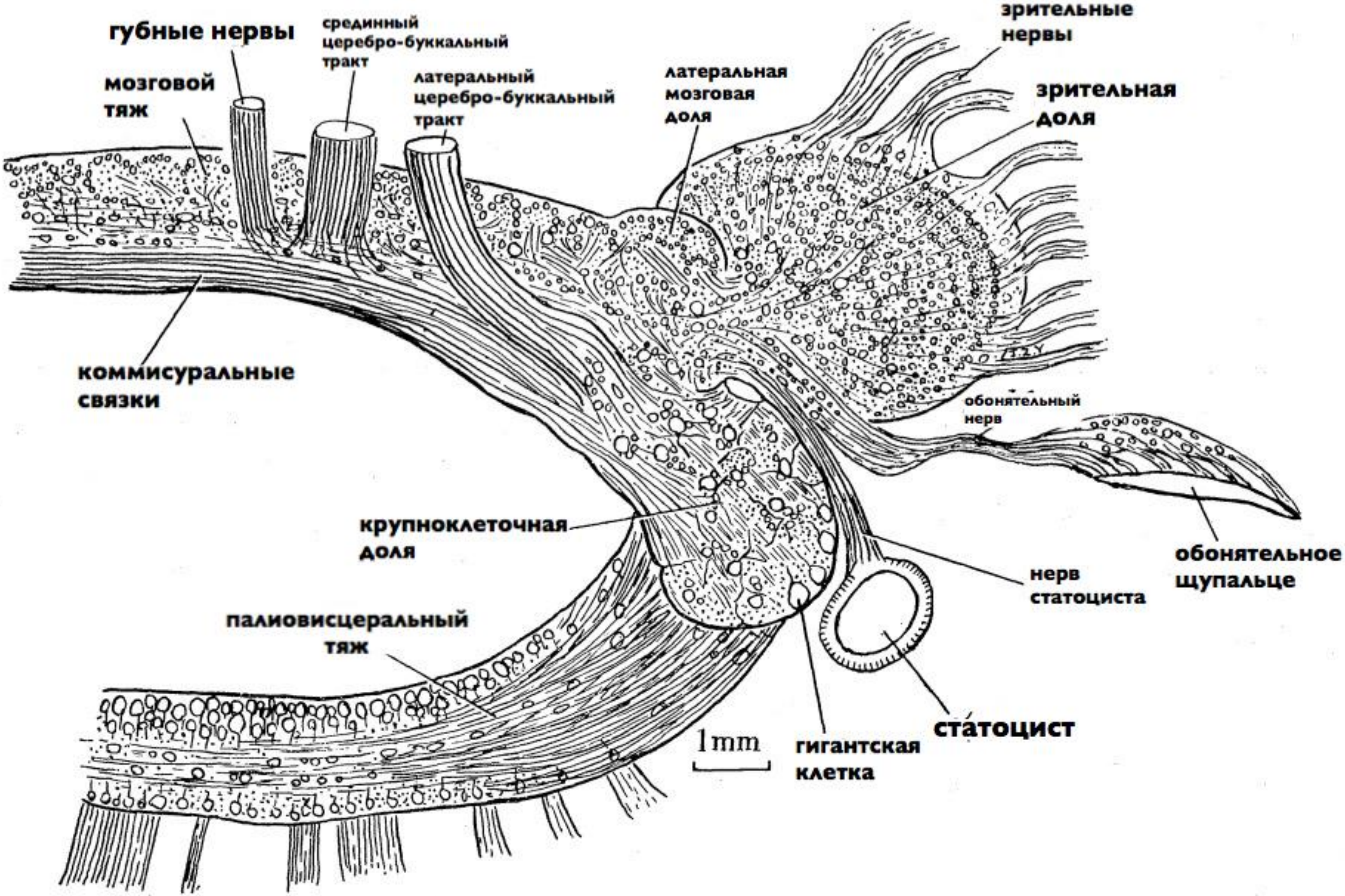
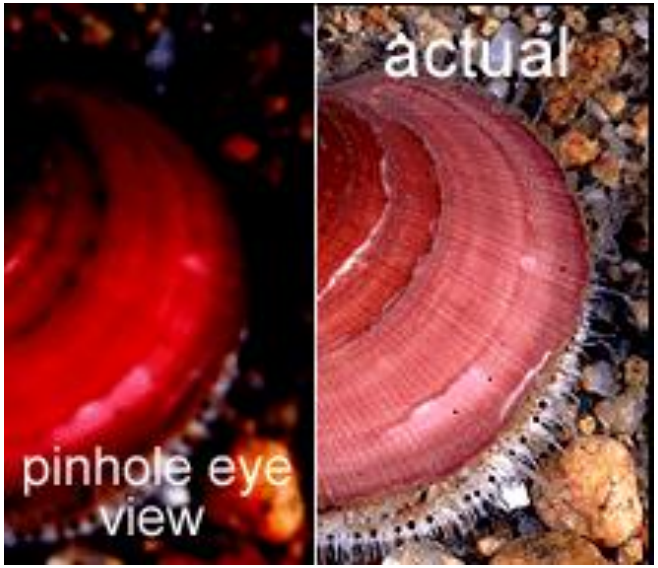


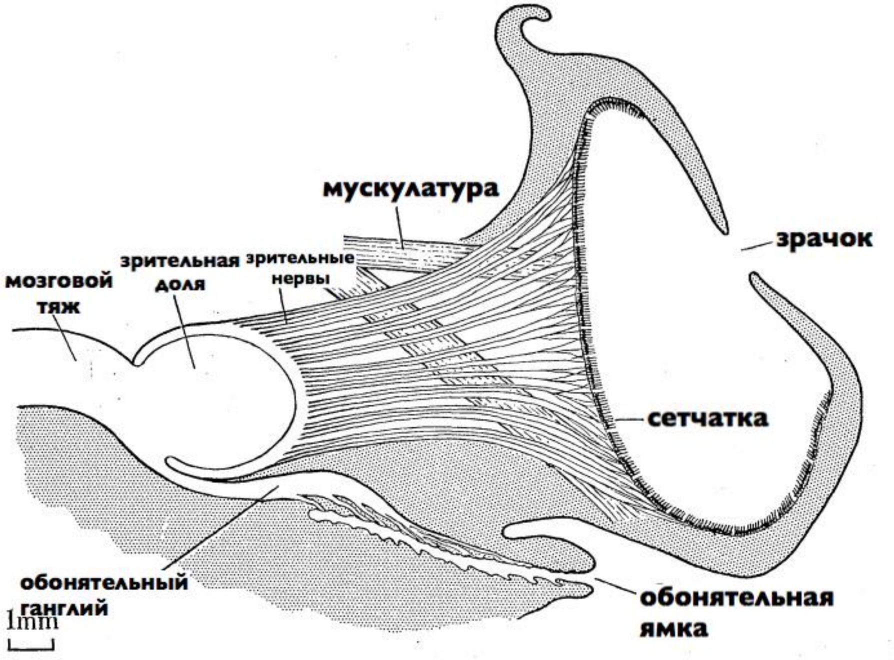
FIGURE 4. Reconstruction of central nervous system from tracings of serial transverse sections. As seen from the front.

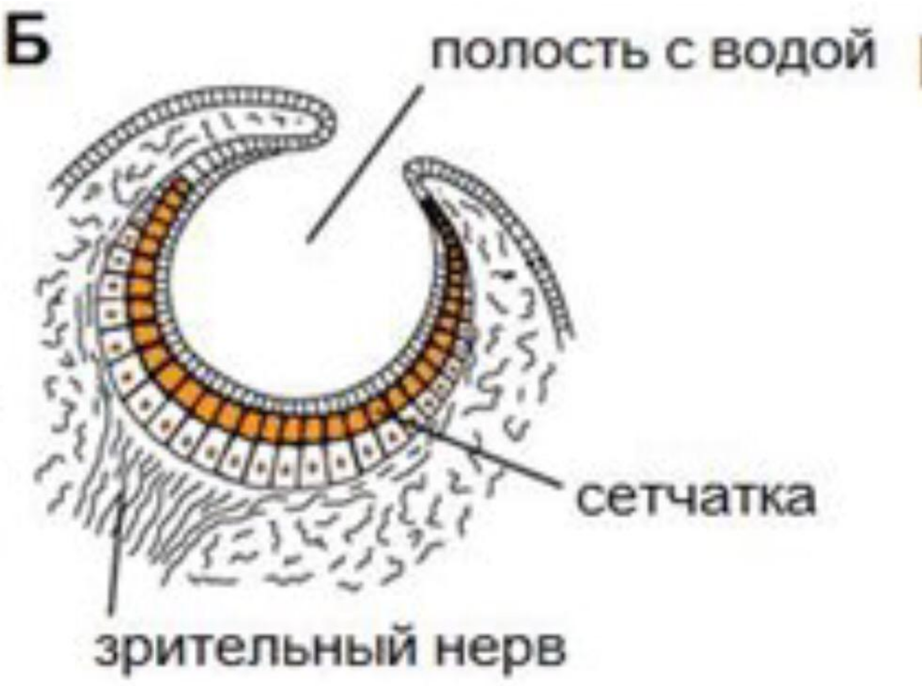

латеральная мозговая доля
зрительная доля
обонятельная доля
плечевая доля передней подпищеводной массы
крупноклеточная доля
гигантская клетка
нервы статоциста
статоцист
педальная доля
1mm
передняя подпищеводная комиссура
нервы воронки

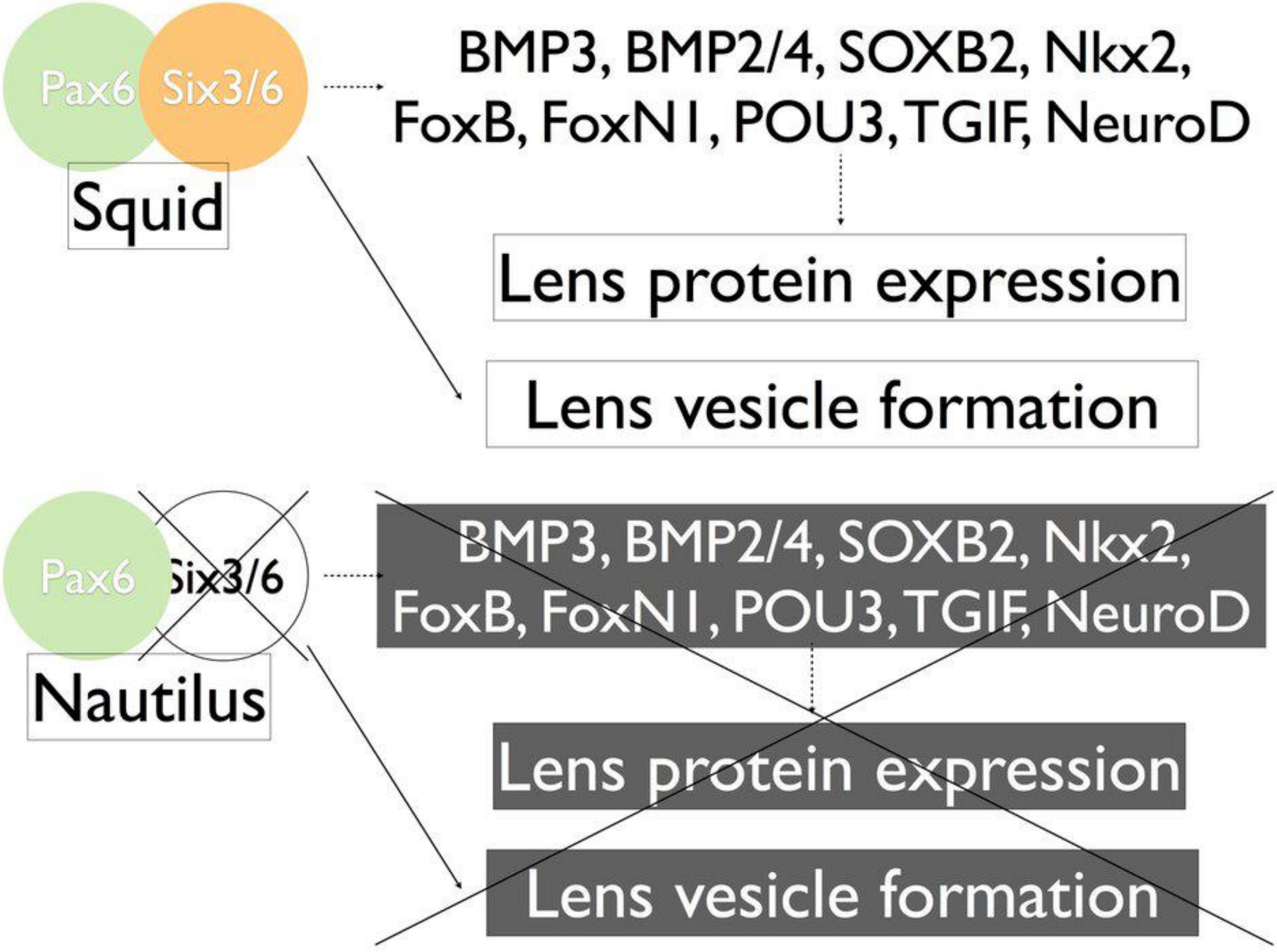

пластинчатая зона мозгового тяжа
переплетённая зона мозгового тяжа
церебро-буккальные коннективы
центральная зона мозгового тяжа
задняя буккальная доля
коммисуральные связки
0·5mm


губные нервы
срединный церебро-буккальный тракт
мозговой тяж
латеральный церебро-буккальный тракт
латеральная мозговая доля
зрительные нервы
зрительная доля
коммисуральные связки
обонятельный нерв
крупноклеточная доля
обонятельное щупальце
нерв статоциста
палиовисцеральный тяж
статоцист
1mm
гигантская клетка


pinhole eye view
actual


мускулатура
зрачок
зрительная доля
зрительные нервы
мозговой тяж
сетчатка
обонятельный ганглий
1mm
обонятельная ямка


Б
полость с водой
сетчатка
зрительный нерв



Pax6 Six3/6

Squid

BMP3, BMP2/4, SOXB2, Nkx2, FoxB, FoxN1, POU3, TGIF, NeuroD

Lens protein expression

Lens vesicle formation

Pax6 Six3/6

Nautilus

BMP3, BMP2/4, SOXB2, Nkx2, FoxB, FoxN1, POU3, TGIF, NeuroD

Lens protein expression

Lens vesicle formation

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