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CYTO-TOPOGRAPHICAL STUDIES ON THE CENTRAL NERVOUS SYSTEM OF LYMNAEA STAGNALIS L.

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The first anatomical description of the central nervous system of *Lymnaea stagnalis* L. was written by DE LACAZE DUTHIERS in 1872. Later works (PELSENEER, 1901; ELO, 1938; CARRIKER, 1946; MOUSSA, 1950; HEKSTRA and LEVER, 1960; JOOSSE, 1964) have furnished further valuable data on the anatomy and histology of the nervous system of the pond snail *Lymnaea stagnalis* L. There are, however, unclarified question in this field such as the denomination of the different ganglia, which is not uniform even in most recent works (JAZMIZINA et al., 1968; KARNAUKOV et al., 1968). The nervous nature of the cells of the mediodorsal bodies first described about 70 years ago (PELSENEER, 1901) has been the subject of ample discussions (CARRIKER, 1946; MOUSSA, 1950; JOOSSE, 1964) but the role of these cells has remained unelucidated up to the present (BOER, 1965; BULLOCK and HORRIDGE, 1965; TAUC, 1966).

The purpose of the present work was to perform a cytological study on the central nervous system of *Lymnaea stagnalis* L. with special regard to the location of large neurons within the ganglia.

Material and method

For the investigations medium-sized specimens of *Lymnaea stagnalis* L. weighing 14—16 g were used. After dissection the central nervous system was fixed in CARNOY solution and in 8% formol. Embedding in paraffin was preceded by a careful orientation of the ganglia. Serial sections were cut at 7—8 μ thickness. Sectioning was made in the parallel plane of the caudal surface of the central nervous system. For staining a mixture of pyronine (GT Gurr, England) and malachite green (Edard Gurr, No 315) was employed, according to the method of BAKER and WILLIAMS (1965). From the serial sections light micrographs were made on which the largest diameter of each neuron was measured. According to their size the nerve cells were classified in five groups:

1. Neurons smaller than 50 μ
2. ,, from 50 to 100 μ
3. ,, from 100 to 150 μ
4. ,, from 150 to 200 μ
5. ,, larger than 200 μ

The nerve cells of various sizes were counted and determined. Determination of cells over 50 μ was made with precision while small cells were determined with a deviation of $\pm 5\%$. The micrographs made from serial sections of a ganglion were divided in 3 equal zones:

Caudal third of the ganglion (zone I)
Median third ,, ,, ,, (zone II)
Oral third ,, ,, ,, (zone III)

By this division the demonstration of the neurons in three zones of depth was rendered possible.

For the investigations we have used the central nervous systems of three medium-sized specimens of *Lymnaea stagnalis* L. for cell counts and 5—7 ganglia from each ganglion type for the determination of the distribution within the ganglion of cells exceeding 100 μ in diameter.

Results

The number of neurons found in the central nervous system of *Lymnaea stagnalis* L. and their distribution according to size are shown in *Tables 1—3.* As can be seen from the *Tables*, the central nervous systems of snails of about the same size and weight differ as regards the number of cells they contain. The distribution of nerve cells in the different ganglia displayed a certain regularity. The proportion of cells of different sizes was more or less similar in all the three central nervous systems.

Buccal ganglion

Of all paired ganglia of the central nervous system of *Lymnaea stagnalis* L. the buccal ganglia are the smallest in size connected by the longest connectives (cerebro-buccal connective) to the cerebral ganglia and at the same time they contain the smallest number of nerve cells. Most neurons larger than 100 μ in diameter were found in zone I and no cells over 150 μ were present in zone III. Cells over 200 μ in size were not seen in any of the three zones. Most neurons over 100 μ in size were located in the part of the ganglion facing the cerebral ganglion, in the area between the issue of the cerebro-buccal connective and bucco-buccal commissure *(Fig. 1)*. The number of neurons comprised in the right and left ganglia was nearly identical *(Tables 1—3)*. The n. gastricus anterior was found to be surrounded in a ring-like manner by 60—80 small nerve cells forming a marked bulging *(Fig. 2)* in the ganglion. The picture is similar to that displayed by the group of bag cells in *Aplysia* (Toevs and Brackenbury, 1969).

Cerebral ganglion

The small cells of the mediodorsal and laterodorsal bodies were not counted among the cells of the cerebral ganglion as they differ from the cells of the central nervous system in their morphology and physiology. The cerebral ganglion was found to contain 1700—2200 nerve cells. According to our data there is no essential difference between the right and left cerebral ganglia as

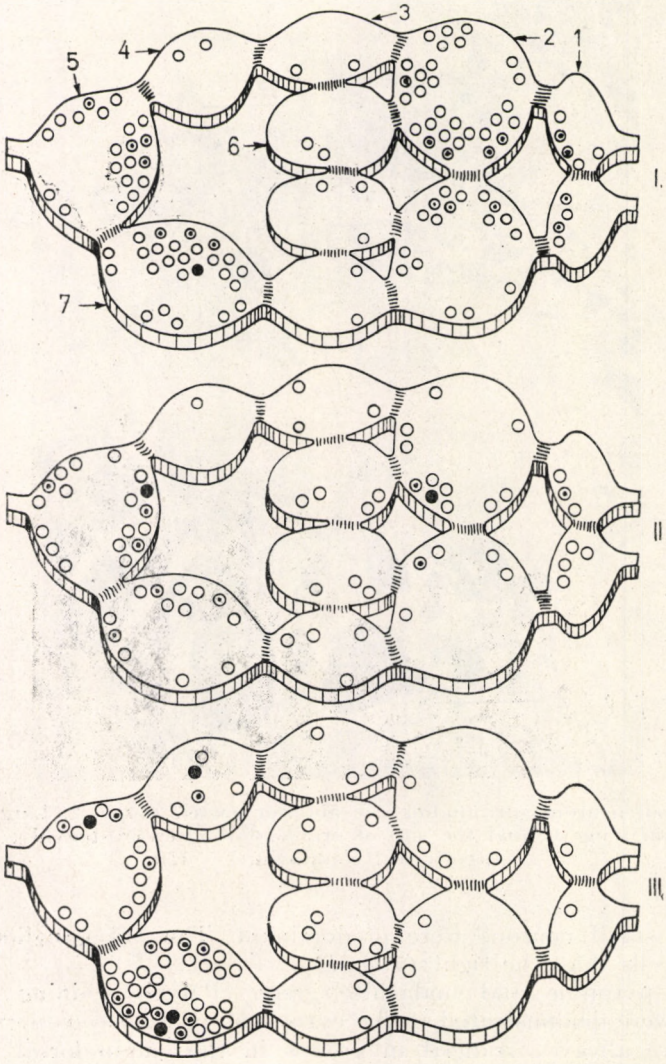

Fig. 1. Distribution of large (exceeding 100 μ in diameter) neurons in the central nervous system of *Lymnaea stagnalis* L.
zone I = caudal third; zone II = median third; zone III = oral third (basal part)
1. Left buccal ganglion; 2. Left cerebral g.; 3. Left pleural g.; 4. Left parietal g.; 5. abdominal g.; 6. left pedal g.; 7. right parietal g. (parieto-abdominal ganglion)
⊙ = neurons 100—150 μ in diameter; ○ = neurons 150—200 μ in diameter;
● = neurons larger than 200 μ in diameter

regards the number of cells. Neurons over 200 μ in diameter were rarely observed. The majority of neurons over 100 μ in diameter were localized, similarly to those in the buccal ganglion, in the caudal part (zone I), while in zone III only 3—4 such neurons were found. Large cells occurred mainly around the cerebro-cerebral commissure (Ccc) and in the anterior lobe. In the

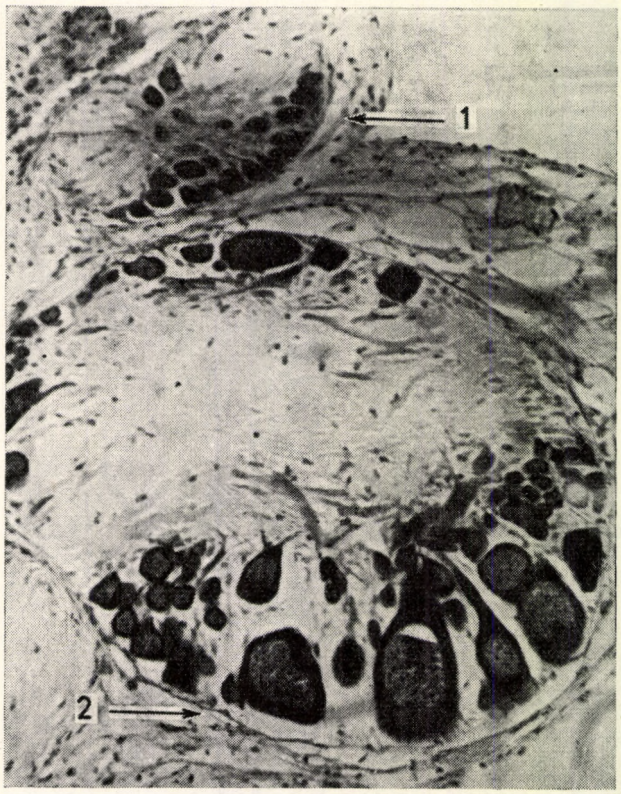

Fig. 2. 1. Small neurons surrounding the anterior gastric nerve. 2. Large cells of the buccal ganglion lying around the site of origin of the cerebro-buccal connective and bucco-buccal commissure. ×150

lateral lobe small neurons were predominant. The left ganglion contained more large cells than the right *(Fig. 1)*.

Using pyronine and malachite green (PMaG) staining disk-shaped formations were demonstrated in the cytoplasm of numerous nerve cells. The neurons were always arranged in groups in the caudo-dorsal area of the ganglion around the site of origin of the cerebro-cerebral commissure. Their number varied from 25 to 70. In the right cerebral ganglion the number of such cells was always higher (50—70 cells). The largest diameter of cells ranged from 70 to 140 μ.

Pleural ganglion

About 90—93 per cent of the neurons are small, under 50 μ in diameter. No cells larger than 150 μ occurred in any of the ganglia examined. The number of cells ranged from 800 to 1000. In all the specimens of *Lymnaea stagnalis* the cells of the right ganglion numbered about 100 more than those

TABLE 1

Cell number and size distribution of neurons in the different ganglia of Lymnaea stagnalis L. *weighing 14 g*

Ganglion	under 50 μ		50—100 μ		100—150 μ		150—200 μ		over 200 μ		Total number
	number	%	number	%	number	%	number	%	number	%	
Buccal (left)	470	87.2	59	10.9	7	1.3	3	0.6	—	—	539
Buccal (right)	432	85.5	60	11.9	11	2.2	2	0.4	—	—	505
Cerebral (left)	1512	90.5	111	6.7	35	2.1	12	0.7	—	—	1670
Crebral (right)	1460	88.0	180	10.8	18	1.1	2	0.1	—	—	1660
Pleural (left)	650	91.9	48	6.8	9	1.3	—	—	—	—	707
Pleural (right)	711	89.9	69	8.7	11	1.4	—	—	—	—	791
Parietal (left)	457	93.1	26	5.3	3	0.6	1	0.2	4	0.8	491
Parietal (right)	1265	83.2	189	13.3	49	3.5	12	0.8	5	0.4	1520
Pedal (left)	1775	89.4	202	10.2	9	0.4	—	—	—	—	1986
Pedal (right)	1893	88.8	225	10.5	12	0.6	1	0.05	—	—	2131
Abdominal	840	78.9	176	16.5	39	3.7	8	0.7	2	0.2	1065
Total number of cells in the central nervous system	11465	87.7	1345	10.3	203	1.6	41	0.3	11	0.08	13065

TABLE 2

Cell number and size distribution of neurons in the different ganglia of Lymnaea stagnalis L. *weighing 16 g*

Ganglion	under 50 μ		50—100 μ		100—150		150—200 μ		over 200 μ		Total number
	number	%	number	%	number	%	number	%	number	%	
Buccal (left)	438	89.8	42	8.6	8	1.6	—	—	—	—	488
Buccal (right)	432	89.6	43	8.9	6	1.3	1	0.2	—	—	482
Cerebral (left)	1514	84.8	241	13.5	28	1.5	3	0.2	—	—	1786
Cerebral (right)	1455	85.3	214	12.5	33	1.9	5	0.3	—	—	1707
Pleural (left)	899	90.6	81	8.3	11	1.1	—	—	—	—	981
Pleural (right)	965	92.6	71	6.8	5	0.5	1	0.1	—	—	1042
Parietal (left)	465	87.8	58	10.9	9	1.7	2	0.3	—	—	534
Parietal (right)	1510	78.0	335	17.3	67	3.4	23	1.2	1	0.05	1936
Pedal (left)	1866	87.0	267	12.4	13	0.6	—	—	—	—	2146
Pedal (right)	1974	88.3	249	11.1	11	0.5	1	0.04	—	—	2235
Abdominal	836	76.2	197	18.0	45	4.1	16	1.4	3	0.3	1097
Total number of cells of the central nervous system	12344	85.5	1798	12.4	236	1.6	52	0.4	4	0.03	14434

of the left ganglion *(Tables 1—3)*. Cells larger than 100 μ in size were few in number and scattered in the ganglion. Two or three of such cells were localized in each of the three zones *(Fig. 1)*.

Parietal ganglion

The number of cells in the two ganglia is not identic, the right ganglion containing about three times more nerve cells than the left *(Tables 1—3)*.

About 90—93% of the neurons in the left parietal ganglion are small (under 50 μ in diameter). Nearly all large cells are located in zone III. While

TABLE 3

Cell number and size distribution of neurons is the different ganglia of Lymnaea stagnalis L. *weighing 16 g*

Ganglion	under 50 μ		50—10 μ		100—150 μ		150—200 μ		over 200 μ		Total number
	number	%	number	%	number	%	number	%	number	%	
Buccal (left)	509	91.2	45	8.1	4	0.7	—	—	—	—	558
Buccal (right)	544	92.0	43	7.3	4	0.7	—	—	—	—	591
Cerebral (left)	2056	91.3	189	8.3	8	0.4	—	—	—	—	2253
Cerebral (right)	2107	90.9	205	8.8	5	0.2	1	0.05	—	—	2318
Pleural (left)	916	94.7	47	4.8	5	0.5	—	—	—	—	967
Pleural (right)	1015	92.8	74	6.7	5	0.5	—	—	—	—	1094
Parietal (left)	597	94.5	32	5.1	2	0.3	1	0.1	—	—	632
Parietal (right)	1425	83.6	225	12.5	43	2.4	9	0.5	2	0.1	1704
Pedal (left)	2086	88.1	274	11.6	8	0.3	—	—	—	—	2368
Pedal (right)	2127	87.8	289	11.9	6	0.2	1	0.04	—	—	2423
Abdominal	810	78.2	183	17.6	36	3.5	4	0.4	3	0.3	1036
Total number of cells in the central nervous system	14192	89.0	1605	10.0	126	0.8	16	0.1	5	0.03	15944

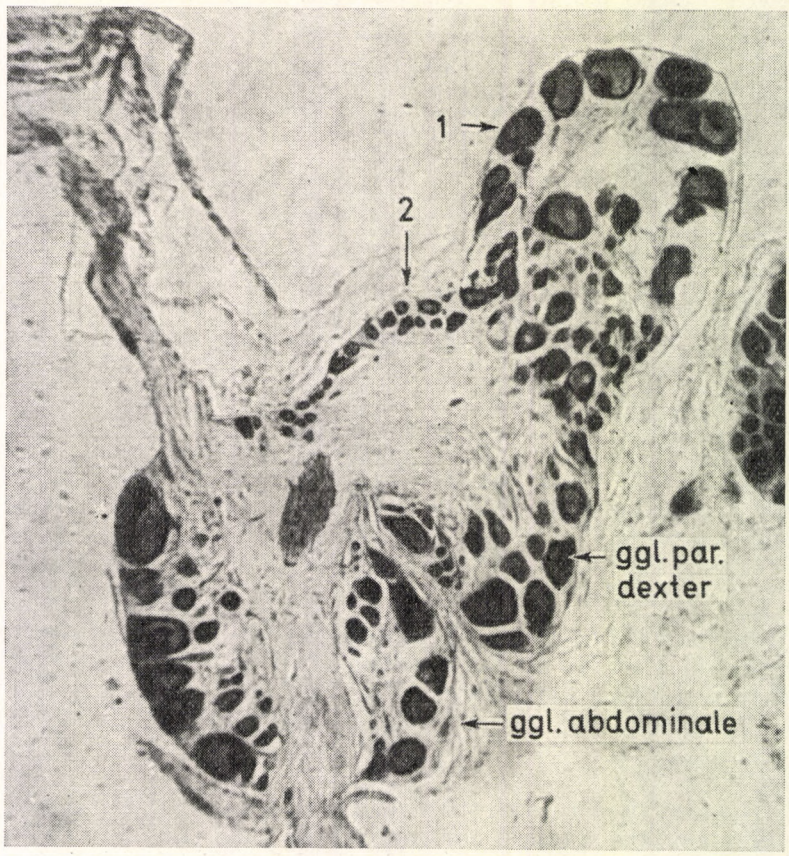

Fig. 3. Micrograph of the oral part of the right parietal ganglion. 1. Lateral part; 2. Medial part ×40

in zone I and II there are but one or two large cells, their number rises to 4—8 in zone III, some of them exceeding 200 μ in size. In our material consisting of 6 left parietal ganglia we have invariably found two neurons over 150 μ in the basal part (zone III) of the ganglion.

In addition to the difference in cell number between the two ganglia, the right parietal ganglion differs from the left also in structure and distribu-

Fig. 4. Large cells in the basal part (zone III) of the right parietal ganglion not surrounded by small cells. ×200

tion of cells of various sizes. It may be divided into a medial and a lateral part. In the latter area of the ganglion a marked protuberance is present which is even more conspicuous in histologic section *(Fig. 3)*. Such a protuberance is always absent in the left ganglion. A further difference between the two ganglia is the strikingly high number of large cells (among them one or two exceeding 200 μ in size) in the caudal part of the right parietal ganglion. The median part (zone II) consists mainly of small cells. The large cells present in this zone are usually surrounded by numerous small cells under 50 μ in diameter. Similarly to the left ganglion, the oral part (zone III) of the right one contains many large cells, most of them located in the lateral part of the ganglion. The large cells in this zone are rarely surrounded by small cells *(Fig. 4)*. In some specimens the examination disclosed nerve cells outside the ganglion, in the immediate vicinity of the connective tissue. In one case the larger part of the neuron was lying in the connective tissue between the abdominal and the right parietal ganglion, while its minor part was within the ganglion *(Fig. 5)*.

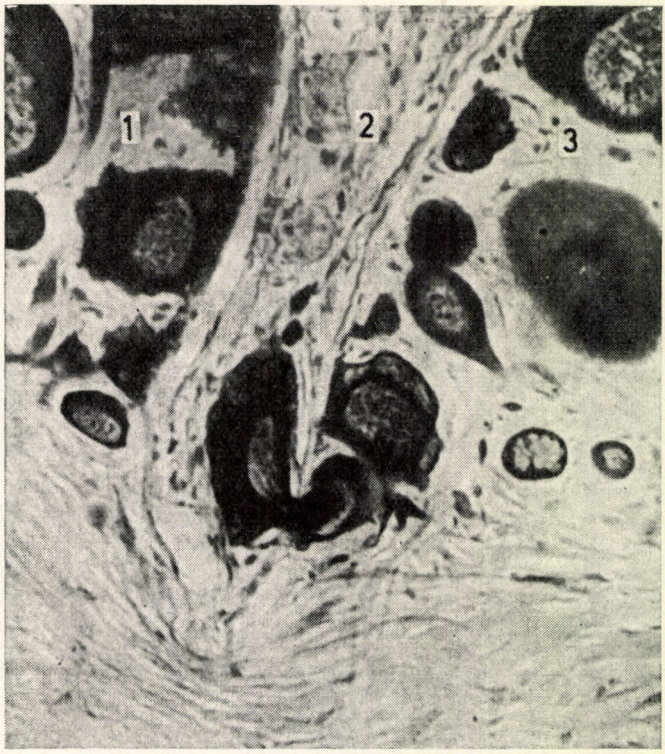

Fig. 5. Neuron lying in the connective tissue between the abdominal and right parietal ganglion. A minor part of the cell is located in the right parietal ganglion.
1. abdominal ganglion; 2. connective tissue between the ganglia; 3. parieto-abdominal ganglion. ×200

Abdominal ganglion

The percentage ratio of small cells is only about 76—78 in this ganglion. In the central nervous system the abdominal ganglion is the richest in cells exceeding 100 μ in diameter. Cells over 150 μ in size were also found to be relatively numerous and large cells over 200 μ in size were found in all the specimens examined. Numerical distribution of large cells was nearly identic in all three zones. Most of them were located in the area facing the cerebral ganglion, between the sites of origin of the two parieto-abdominal connectives *(Fig. 1)*. The large cells located here were usually close to each other and in most cases they were not surrounded by small cells.

Pedal ganglion

Of all the ganglia the pedal ganglion contains the highest number of neurons, about 4500—5000, which is about 30—31% of all the cells of the central nervous system. About 88—89% of the cells are small in size (under 50 μ). Cells exceeding 150 μ in diameter were only observed occasionally, and cells over 200 μ were never encountered in the specimens examined. While

1.4% of all the cells of the central nervous system are about 100—150 μ in diameter, this percentage ratio in the pedal ganglion is but 0.4—0.5 *(Tables 1—3)*.

Neurons larger than 100 μ in size are scattered in the ganglion, each zone containing about 3—5 such cells *(Fig. 1)*.

Discussion

From our results it appears that the central nervous system of *Lymnaea stagnalis* L. weighing 14—16 g contains about 13000—16000 nerve cells. The differences between certain specimens are so great that they cannot be attributed to errors due to calculation. The data shown in *Table 1* refer to specimens weighing 14 g and those shown in *Tables 2* and *3* to snails weighing 16 g. The difference in cell number is probably due to individual variations. According to KUNZE (1917) there is an individual difference in size in the large cells of the central nervous system of *Helix pomatia* L.

The various ganglia within the central nervous system contain different numbers of nerve cells. The fewest neurons are in the buccal and the most numerous in the pedal ganglion. No appreciable difference was found in the number of cells between the left and right ganglion of the paired buccal, cerebral and pedal ganglia. In the case of the buccal and pedal ganglia this may be explained by the fact that the ganglia situated on the left and right side have a common area of innervation. The right and the left cerebral ganglia have different number of main nerve branches. The single nervus penis arises from the right cerebral ganglion. As according to our data, the two cerebral ganglia contain identic number of nerve cells, it seems probable that in the innervation of the nervus penis the left cerebral ganglion is likewise involved.

The right pleural ganglion contains by 60—100 neurons more than the left one. At present we cannot give a satisfactory explanation of this finding.

As regards the number of neurons the greatest difference can be found between the two parietal ganglia, the right containing about three times more cells than the left. It should be noted that KUNZE (1917) found but a slight difference in the number of neurons between the right and left parietal ganglia of *Helix pomatia* L. About 88—89% of the cells of the central nervous system of *Lymnaea stagnalis* are smaller than 50 μ in diameter, whereas the number of large cells (over 200 μ) is insignificant. In the basal part of the parietal ganglion and in the abdominal ganglion of the specimens examined (5—7 pieces) one to three giant cells were nearly always present, while in the cerebral ganglia a giant cell was seldom encountered *(Fig. 1)*. As regards ganglionic distribution and localization of cells over 100 μ in diameter a certain regularity was noted.

The large cells of the buccal ganglion were always found in the caudal part (zone I), around the sites of origin of the cerebro-buccal connective and bucco-buccal commissure. In the oral part of the ganglion (zone III), large cells were very rare. A similar distribution was noted in the large cells of the cerebral ganglia, as well. The left ganglion was always found to contain more large cells than the right one *(Fig. 1)*. The majority of the large cells are located around the site of origin of the cerebro-cerebral commissure, where

Nissl cells ranging from 70 to 140 μ in size are also present. According to BOER (1965) the Nissl cells are in relation with the small nerve cells of the medio-dorsal and medio-lateral bodies. Their number in the left ganglion is about 50—70 which is about the double of the Nissl cells found in the right ganglion.

In the pleural and pedal ganglia there are very few cells exceeding 100 μ in diameter. Their numerical distribution is about the same in all three zones of these ganglia. In the pleural ganglion of *Helix pomatia* the number of large cells is likewise low but in the pedal and parietal ganglia their number is much higher (KUNZE, 1917).

The abdominal ganglion is characterized by the presence of large cells. About 4—5% of all its cells are larger than 100 μ in size displaying an identic numerical distribution in all three zones, in particular in the area of the origin of the two parieto-abdominal commissures (PAC), as can be seen in *Fig. 1.*

As regards location of large cells, the left parietal ganglion differs from all the other ganglia, zones I and II containing but a few large cells, while zone III is relatively rich in them. Two large cells are always present in the basal part of the ganglion, one of them sending direct fibers to the nerve branch innervating the heart (GUBICZA and S.-RÓZSA, 1969), while the fibers emitted by other are directed towards the cerebral ganglion and left pallial nerve (JAZMIZINA, 1968).

There is a difference in location of the large cells between the right and left parietal ganglia. In the right ganglion their number is always high in zone I, relatively reduced in the median zone (II) and high again in zone III. The considerably higher number of cells over 100 μ in diameter and their different location in the right parietal ganglion raises the question whether these ganglia are an identic pair. The dissimilarity between them seems to be confirmed by the difference in their size, the right ganglion being much larger than the left, and by the presence of a well visible protuberance in its lateral part. Therefore, some authors (NABIAS, 1899; KARNAUKOV et al., 1968) suggested the right parietal ganglion to be termed as "large" and the left one as "small". Such a distinction between these ganglia does not seem to be entirely satisfactory as besides the difference in size, there are also other dissimilarities between them, e.g. the lateral protuberance differs in structure from the median part of the ganglion. A further difference is that two main nerves take origin from the right parietal ganglion, namely the right internal and the right external pallial nerves, while only one: the left pallial nerve arises from the left ganglion. Moreover, the innervation area of the right ganglion is larger than that of the left one (NABIAS, 1889; CARRIKER, 1946).

In a previous work (GUBICZA and S.-RÓZSA, 1970) we have reported that different results were obtained in the two parietal ganglia after trans-section of various nerve branches and connectives. The response of the right parietal ganglion to nerve trans-section was similar to that of the abdominal ganglion. As it has been demonstrated (SALÁNKI and KISS, 1969), some nerve cells of the abdominal and right parietal ganglion exhibit identic electro-physiological properties.

From our investigations it was concluded that the ganglion regarded as the right parietal one has come into being from the fusion of the right parietal and right abdominal ganglia, therefore; the term "parieto-abdominal ganglion" seems to be more appropriate for it. Correspondingly, for its connective to

the abdominal ganglion the term "parieto-abdomino-abdominal connective" (PAAC) and for its connective to the pleural ganglion the term "pleuro-parieto-abdominal connective (PPAC) are suggested.

Summary

From the results of cyto-topographic investigations performed on the central nervous system of *Lymnaea stagnalis* L. it was concluded that

1. The central nervous system of medium-sized specimens of *Lymnaea stagnalis* L. (weighing 14—16 g) contains about 13000—16000 neurons.

2. The pedal ganglion contains the highest and the buccal ganglion the lowest number of nerve cells.

3. The number of neurons in the right and left buccal, cerebral and pedal ganglia is nearly identic, whereas the right pleural ganglion in all the specimens examined contained more nerve cells than the left one.

In the right parietal ganglion the number of neurons was three times higher than in the left.

4. Most nerve cells exceeding 100 μ in diameter are comprised in the right parietal and the abdominal ganglia. No cells over 200 μ in diameter were found in the buccal, pleural and pedal paired ganglia.

5. In the distribution of large cells (over 100 μ in diameter) the following regularity was noted:

The majority of large cells are located in the caudal part (zone I) of the buccal and cerebral ganglia and in oral part (zone III) of the left parietal ganglion. In the other ganglia the number of large cells is nearly identic in all three zones.

6. On the basis of the anatomical and histological structure of the right parietal ganglion, cell number and distribution of large cells within it, and according to the data of earlier works, this ganglion should be regarded as one arisen from the fusion of the right parietal and right abdominal ganglia. Therefore, the term "parieto-abdominal ganglion" is suggested.

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A LYMNAEA STAGNALIS L. KÖZPONTI IDEGRENDSZERÉNEK CYTO-TOPOGRÁFIAI VIZSGÁLATA

Gubicza András

Összefoglalás

A *Lymnaea stagnalis* L. központi idegrendszerének cytotopográfiai vizsgálatainak adataiból az alábbi következtetések vonhatók le:

1. A közepes súlyú (14—16 gr-os) *Lymnaea stagnalis* L. központi idegrendszere 13—16 000 db idegsejtet tartalmaz.

2. A legtöbb idegsejt a ggl. pedalében, legkevesebb a ggl. buccalében van.

3. A ggl. buccale cerebrale és pedale jobb és bal dúcaiban közel azonos számú idegsejt van. A jobb ggl. pleurale minden vizsgált példánynál több idegsejtet tartalmazott, mint a bal. A ggl. parietale dexter háromszor annyi idegsejtet tartalmaz, mint a ggl. parietale sinister.

4. A központi idegrendszeren belül legtöbb 100 mikronnál nagyobb idegsejtet a ggl. parietale dexter és a ggl. abdominale tartalmaz. A ggl. buccale, ggl. pleurale és a ggl. pedale dúcpárban nincs 200 mikronnál nagyobb idegsejt.

5. A 100 mikronnál nagyobb idegsejtek dúcon belüli elhelyezkedésében az alábbi törvényszerűség tapasztalható:

A ggl. buccale és a ggl. cerebrale caudalis részében (I. zóna), a ggl. parietale sinister orális részében (III. zóna) találhatók a nagyméretű idegsejtek többsége, más dúcokban pedig mindhárom zónában közel azonos számban fordulnak elő *(1. ábra)*.

6. A jobb ggl. parietale-t az anatómiai szövettani szerkezete, sejtszáma s a nagyméretű idegsejtjeinek elhelyezkedése és a korábbi munkák eredményei alapján úgy kell tekinteni, mint két idegdúc — a ggl. parietale dexter és a ggl. abdominale dexter — összenövéséből létrejött ganglion. Ezért a ggl. parietale dexter helyett alkalmasabb a ganglion parieto-abdominale elnevezés.

ЦИТОТОПОГРАФИЧЕСКИЕ ИССЛЕДОВАНИЯ ЦЕНТРАЛЬНОЙ НЕРВНОЙ СИСТЕМЫ

А. Губица

Из данных цитотопографических исследований центральной нервной системы большого прудовика были сделаны следующие выводы:

1. Центральная нервная система больного прудовика, со средним весом (14—16 гр), содержит 13 000—16 000 нейронов.

2. Больше всего содержится нейронов в педальных ганглиях меньше всего в буккальных ганглиях.

3. В правых и левых половинах буккального, церебрального и педального ганглиев содержатся нейроны приблизительно в одинаковом количесиве. У всех исследованных особей в правом плевральном ганглии было больше нейронов, чем в левом. Правый париетальный ганглий содержит в три раза больше нейронов, чем левый.

4. Нейронов, размером выше 100 мк, больше всего содержится в правом париеталном и в абдоминальном ганглиях. В буккальных, плевральных и педальных ганглиях не найдено нейронов выше 200 мк.

5. В расположении нейронов размером выше 100 мк, внутри ганглиев наблюдаются следующие закономерности:

Большинство гигантских нейронов найдены в буккальном ганглии, в каудальной части церебрального (I. зона) и в оральной части левого париетального ганглиев (III. зона); в других ганглиях во всех трёх зонах число нейронов одинаковое.