DATA TO THE KNOWLEDGE OF INNERVATION OF THE BIRD'S DIGESTIVE TRACT

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(Received February 10, 1968.)

The problem of innervation of the intestinal tube and that of the origin of the automatic intestinal motions belong to he highly important and interesting fields of the neuro-histological investigations. Dogiel had studied, already in 1896—97, the plexuses in the wall of the gastro-intestinal system, and classified the nerve cells into different types. Later on, the examinations have been extended to nearly every group of vertebrates, thus there were investigated the single parts of the digestive organs, resp. inside them the nerve connections of the different layers, in fish (Kolossow et al., 1930; Ábrahám, 1933a; 1933b; Milochin, 1963), *Amphibia* (Horváth, 1959; 1962), *Reptilia* (Kolossow, 1929), *Mammalia* and men (Esveld, 1928; Harting, 1934; Botár, 1942; Bargman, 1943; Greving, 1952; 1954; Iwanowa, 1957; Jabonero, 1958). The results of the comparative neuro-histological investigations concerning the innervation of the digestive tract appeared in the papers of Okamura (1966), Oshima (1929), Sotelo (1954), Stőhr (1949; 1957) and Temesrékási (1955).

The data concerning the structure of the nervous system in the digestive system of birds are to be found in the works of Ábrahám (1934; 1935; 1935/36; 1936; 1938), Iwanow (1930), Kolossow, Sabussow and Iwanow (1932). The nerve plexuses of the bird's intestinal tube are compared with that of other vertebrates by Kolossow (1959), Kolossow and Iwanow (1930), Okamura (1934) and Temesrékási (1955). The researchers have usually studied the structure of ganglia in the plexuses, the types of nerve cells in the ganglia, and their distribution.

Appearance and pattern of the receptors in the field of the system were investigated by Ábrahám (1966; 1967), Kolossow, Sabussow and Iwanow (1932), Milochin (1963), Stőhr (1949), Temesrékási (1955).

In the enumerated works there can be found a lot of data corresponding to one another, although in several questions the opinions of researchers are contradictory. We have found the most problems and contradictions in the interpretation of receptors and effectors in the field of the system.

My comparative investigations, carried out in different species, would like to amplify our knowledge concerning the innervation of the bird's intestinal tract. My observations are affecting the structure of intramural plexuses, the types of cells in the ganglia, their occurrence as well the form and structure of receptors appearing here and there.

Material and methods

I have used the intestinal tract of sixteen species of birds to my investigations. The collected material, on the basis of Dudich's system, belongs into the following orders.

Gulls *(Lariformes)*. Black-headed gull *(Larus ridibundus* L.), herring guu *(Larus fuscus* L.), silver gull *(Larus argentatus* B.).

Ducks *(Anseriformes)*. Poachard *(Anas platyrhyncha* L.), small duck *(Anas crecca* L.), domestic duck *(Anas domesticus* L.).

Water-rails *(Ralliformes)*. Common coot *(Fulica atra* L.).

Herons *(Ardeiformes)*. Black stork *(Ciconia nigra* L.), glossy ibis *(Plegadis falcinellus* L.).

Pigeons *(Columbiformes)*. Turtle-dove *(Streptopelia turtur* L.), Stock-dove *(Streptopelia decaocto* Friv.), pigeon *(Columba domestica* L.).

Hens *(Galliformes)*. Hen *(Gallus domesticus* L.), guinea-fowl *(Numida meleagris* L.), turkey *(Meleagris gallopavo* L.).

Sparrows *(Passeriformes)*. Sparrow *(Passer domesticus* L.).

After dissection, the intestinal canal has been conserved in neutral formalin of ten percent. The sections made with a freezing microtome were silvered with the procedures of Ábrahám, Bielschowsky-Ábrahám, Bielschowsky-Gros-Cauna, and Jabonero.

In the following I am going to discuss the conditions found in some parts of the intestinal tube, taking into consideration the points of view suitable for being compared and the establishments published in literature so far. First of all I review the nerve connections of oesophagus, then those of the glandular portion of ventricle *(proventriculus)* and, the gizzard *(ventriculus)*, intestine *(intestinum)*, and *cloaca*.

Oesophagus

Meissner's *plexus* takes place in the *lamina propria* in the *oesophagus*. In its structure some fibres myelinated and non-myelinated are participating, forming wavy trunks of different sizes. Beside them there occur smaller and bigger nerve cells that are always bigger in the lower third part of the *oesophagus* and in the area of crop than in the upper parts of *oesophagus*. The nerve cells are mostly multipolar though also unipolar ones can be observed among them. The multipolar nerve cells are of type Dogiel I. and rarely of type Dogiel II. The cell body is spherical, rarely elliptic, in them the nucleus and sometimes the neurofibrils, can be distinguished very well.

The *epithelium* and the glands of *oesophagus* possess a lot of nerve-fibre bundles, divided into several branches especially under the glands, sometimes run over from the *lamina propria* to the stratified squamous *epithelium* (Iwanow, 1930). I have observed such intraepithelial nerve fibres in the stratified squamous *epithelium* of *oesophagus* of the black stork where the fibre is showing a mildly wavy course among the epithelial cells, running more or less parallel with the internal surface (Table I, fig. 1).

Between the two layers of the *tunica muscularis*, A u e r b a c h's *plexus* takes place. Its nerve trunks and ganglia are bigger than those of M e i s s n e r's *plexus*. At *Columbiformes*, at glossy ibis the ganglia are massive, the cells are generally located in the middle of ganglia, while at guineafowls, hens and gulls the location of cells is more scatterred (Table I, fig. 2). The most part of nerve cells are representing type D o g i e l I. though, in the ganglia of the crop, some cells of type D o g i e l II. occur, as well (Á b r a h á m, 1935; 1936; I w a n o w, 1930). There are solitary nerve cells, too, their number and appearance isn't showing, however, any regularity. At gallinaceans we could, anyway, observe that the ganglia and solitary cells of A u e r b a c h's *plexus* may get down even to the border of the *tunica muscularis* and *tunica adventitia*, either. The outer lamina of the muscle layer is namely very weakly developed there.

Some peculiar thick-fibre branchings were visible in the connective-tissue *septum*, separating the two *laminae* of the *tunica muscularis externa*. They are probably receptors. Their fibres tear apart all at once or successively into several branches. I could not observe the termination forms of the end fibres starting from the branches (Table I, figs. 3, 4).

Glandular portion of ventricle *(proventriculus)*

The plexuses of glandular ventricle differ in many aspects from the plexuses of *oesophagus*. The *plexus submucosus Meissneri* is poorer in ganglia. Besides the ganglia, the solitary cells of uni- and bipolar forms are very characteristic. However, the most frequent cells in this *plexus* are the multipolar type D o g i e l II. The nerve fibres of the *plexus* are isolated or they form small nerve trunks and may be observed mainly in the interglandular connective tissue. One part of the fibres go into the gland *parenchyma*, forming fine plexuses there in the substance of connective tissue. The latter ones are left by varicose fibres that can be followed until the bases of the gland cells.

The ganglia of A u e r b a c h's *plexus* are extremely varied concerning their sizes and structures. They are of highly large extension at guinea-fowls, domestic ducks, and pigeons while at other species they are much smaller. This may particularly be observed in A u e r b a c h,s *plexus* of the glandular ventricle of black storks. The multipolar cells of the *plexus* are considered by I w a n o w (1930) to be mainly of type D o g i e l I., but by Á b r a h á m (1935) of type D o g i e l II. I myself consider the second opinion as verified.

In the connective tissue joint to the inner layer of *tunica muscularis*, in the black storks, black-headed gulls, herring gulls, hens, pigeons and stock-doves, I have observed peculiar nerve-fibre endings. The termination systems of largest extension may be found in the black storks and headed gulls. It is characteristic that a thick fibre is torn into many branches seemingly with anastomoses. Judged from their structure, they may be considered receptors. The most usual ones of them are of cornered and round formations (Table II, figs 1, 2). There are peculiar coil-like terminations in the muscle layer of the *proventriculus* of glossy ibis, resp.

in the connective-tissue between the muscular layers (Table II, fig. 3). All these endings can be considered as pressoreceptors (Á b r a h á m, 1966; 1967) receiving the *stimulus* of pressure exerted on the stomach wall.

Gizzard (ventriculus)

The nerve supply of muscular ventricle is assured, as well, by the two nerve plexuses. It is characteristic of the structure of plexuses that in M e i s s n e r's *plexus* there cannot be observed any ganglia of a major extent. We could find here either solitary nerve cells or small ganglia containing quite few cells. In A u e r b a c h's *plexus*, apart from the solitary cells, also larger ganglia can be observed. Their multipolar nerve cells belong to type D o g i e l II. In the muscular ventricle I could not see any receptory nerve-ending.

Intestine (intestinum)

From the different parts of the bird's intestinal tube the largest nerve supply was found in the intestine and especially in the *duodenum*. Both plexuses are very rich in fibres and nerve cells. The location of the vegetative trunks demonstrate a high degree regularity by the fact that the thicker bundles are rent into smaller ones and farther on these are again united in larger ones. At the meeting place of nerve trunks there are mostly ganglia, here too. In the ganglia the fibres remain almost in the background beside the cells. The cells are generally of the same size, except in the *duodenum* of black storks where the cells are comparatively small (Table II, fig. 3); in the *ileum* fo the glossy ibis and turkey (Table III, fig. 1), however, the nerve cells, of the type D o g i e l II, occurring isolated, are conspicuously large. In the intestinal tract everywhere, and particulary in the intestines, the vegetative trunks become obviously thinner and thinner in the course of their repeated branchings. These trunks, as well the isolated fibres, permeate the smooth musculature densely, producing rich plexuses owing to the gradual branching among the smooth muscle cells.

Table I.

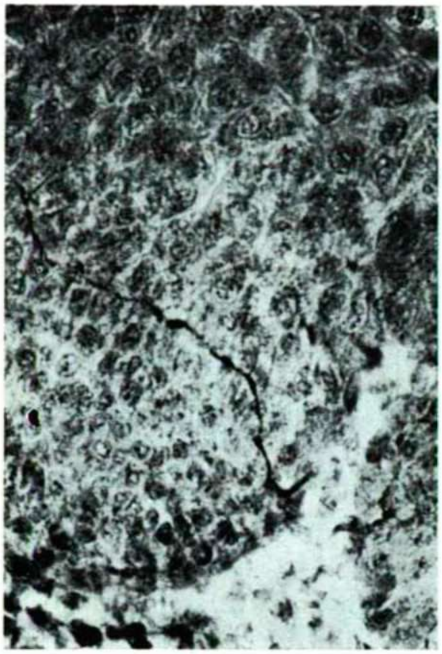
Fig. 1. *Ciconia nigra: Oesophagus.* Intraepithelial end-fibre. Á b r a h á m's method. Magn. x 300.

Fig. 2. *Larus ridibundus: Oesophagus.* Detail from the A u e r b a c h *plexus.* B i e l- s c h o w s k y - G r o s - C a u n a's method. Magn. x 300.

Fig. 3. *Ciconia nigra: Oesophagus.* Thick fibre ramification. Á b r a h á m's method. Magn. x 300.

Fig. 4. *Ciconia nigra: Oesophagus.* Sersory ending. Á b r a h á m's method. Magn. x 300.

TABLE I



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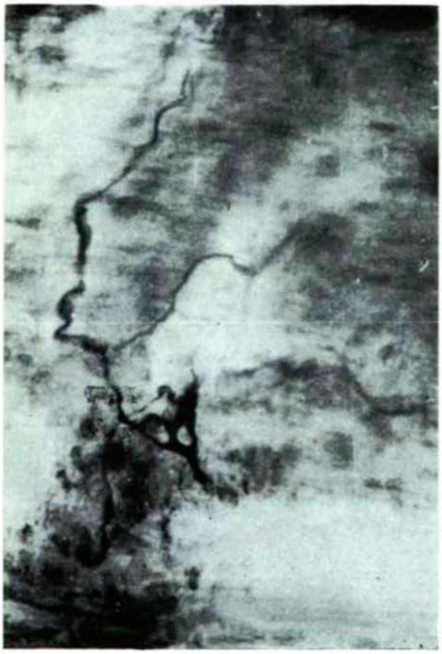

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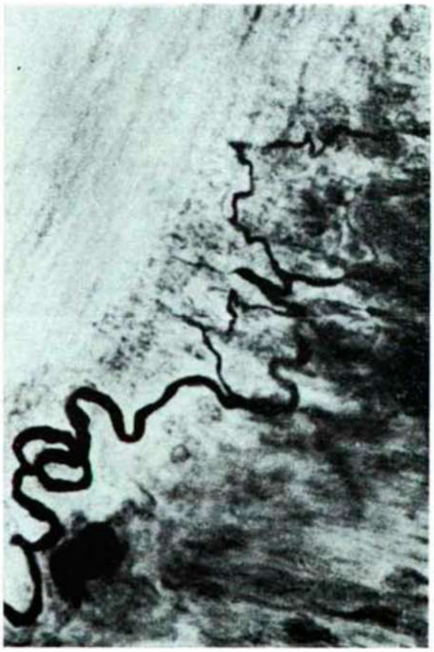

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TABLE II

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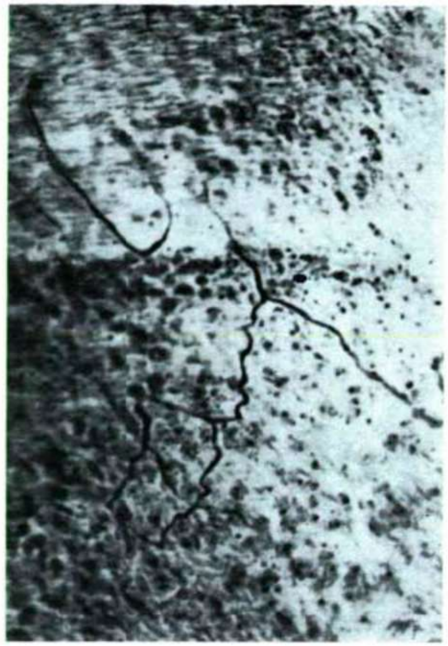

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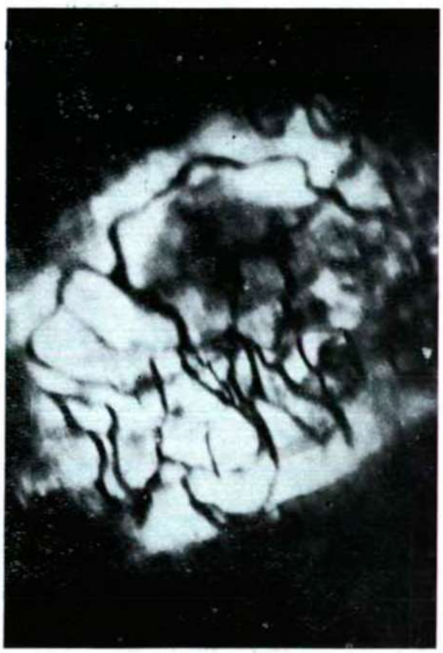

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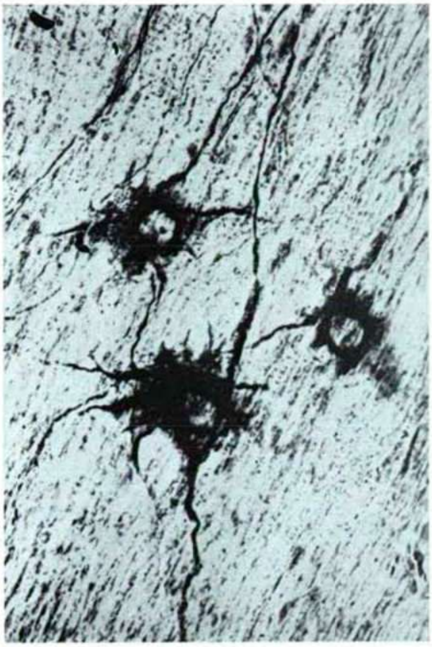
TABLE III



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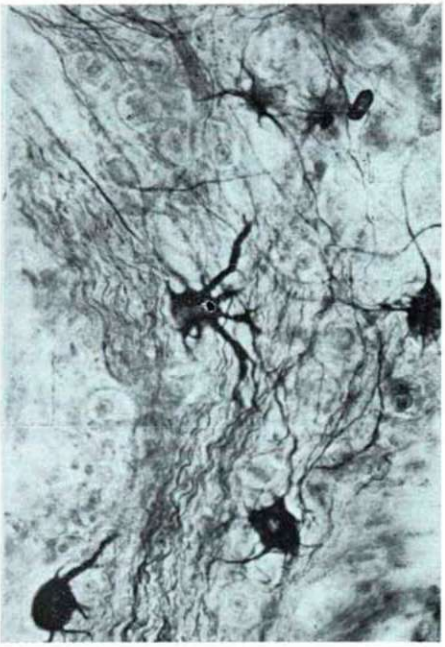

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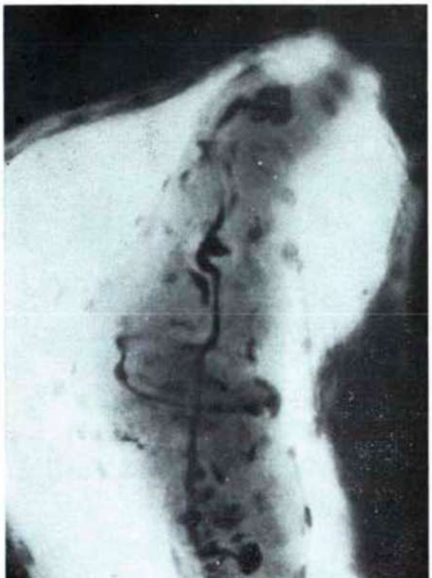

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Cloaca

The anatomically separated parts of the *cloaca* are different concerning their innervation. The plexuses of *coprodaeum* and *urodaeum* appear differing from the previous sectors of the intestinal canal by their ganglia being scatterred, containing relatively few cells which belong mostly to the type Dogiel II. (Table III, fig. 2). In the *proctodaeum* there couldn't be observed any ganglia. Although the *cloaca* is poor in nerve cells, it is extremely rich in nerve fibres and, probably, in nerve terminations, as well. Its enormous trunks have a course being here and there more strongly, in other places more mildly wavy. Some of the nerve terminations take place in the connective tissue, others in the musculature. In the connective tissue two kinds of the sensory nerve terminations could be separated, namely Herbst's nerve terminations and the so-called "free coil-formations". Herbst's nerve terminations are by and large identical with the terminal form derived from the beak skin. It may be mentioned as a matter of curiosity that in sections made from the *proctodaeum* of a hen I have observed also Herbt's terminations where the nerve fibre entering the connective tissue capsule makes a loop at about the middle of it (Table III, fig. 3).

"Free coil-formations" can mostly be observed among the striated muscle fascicles of *tunica muscularis*. First Ábrahám (1935/36) described these coils which differ in their appearance from the typical free convolutions because here fibre fascicles and not isolated fibres occur. The nerve fibre fascicles always leave the coil after some milder bends.

In the connective tissue between the two smooth muscle layers of *tunica muscularis*, a loose coil was observed to be produced by thin fibres. The thin fibre takes several mild bends in a comparatively small territory, and then leaves it becoming a little thinner (Table III, fig. 4).

Table II.

Fig. 1. ***Larus ridibundus: Proventricle.*** Baroreceptoric ending Bielschowsky's method. Magn. x 600.

Fig. 2. ***Larus ridibundus:*** Proventricle. Sensory endsystem. Bielschowsky-Gros-Cauna's method. Magn. x 600.

Fig. 3. ***Plegadis falcinellus:*** Proventricle. Sensory coil. Ábrahám's method. Magn. x 600.

Fig. 4. ***Ciconia nigra: Duodenum.*** Ganglion from the Auerbach ***plexus.*** Ábrahám's method. Magn. x 300.

Table III.

Fig. 1. ***Plegadis falcinellus: Ileum.*** Nerve cells of the Auerbach ***plexus.*** Jabonero's method. Magn. x 600.

Fig. 2. ***Numida meleagris: Cloaca.*** Nerve cells in the Auerbach ***plexus.*** Ábrahám's method. Magn. x 300

Fig. 3. ***Gallus domesticus: Cloaca.*** Herbst body Jabonero's method. Magn. x 600.

Fig. 4. ***Ciconia nigra: Cloaca.*** Nerve coil from the connective tissue between the two muscular layers. Ábrahám's method. Magn. x 300.

The musculature of the lower third part of *cloaca* is constructed by striated muscle fibres. Among the muscle fibres there can be found bigger and smaller nerve-fibre bundles. There are here a great number of thin fibres of central origin running among the muscle fibres after having left the trunks. The fibres end in small terminal heads that can be observed very well in some rather thick sections.

Summary

I can summarize the results of my investigations carried out on the intestinal tract of sixteen bird species with different procedures of nerve impregnation.

1. The two nerve plexuses that are generally characteristic of the intestinal tube can be found in the whole length of the bird's intestinal tract. A difference can be observed but in the position of plexuses. In the *oesophagus* the *plexus submucosus Meissneri* lies in the *lamina propria,* while Auerbach's *plexus* descends, here and there, even till the border of *tunica adventitia,* resp. *tunica serosa.*

2. The cells of plexuses are uni-, bi- and multipolar. The multipolar nerve cells may be classed among types Dogiel I and II.

3. The myelinated nerve fibres with central origin are partly intra-epithelial fibres, partly free coils, and partly dendritic branches.

4. The nerve fibres of sympathic origin form a delicate *plexus* system in the smooth musculature, the terminal fibres of which are ending among the muscle cells, resp. on these cells.

5. The dendritic branches are to be considered as pressoreceptoric (baroreceptor) nerve terminations of the intestinal tube.

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