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Anomalie i zniekształcenia narządów rozrodczych u *Helicigona (Arianta) arbustorum* (L.) oraz próby wyjaśnienia mechanizmu ich powstania.

Anomalies and deformations of the genital organs in *Helicigona (Arianta) arbustorum* (L.), with an attempt to explain the mechanism of their origin.

[Pl. XI—XVI, 6 Text-figures and 1 Table]

INTRODUCTION

The classification of Molluscs is being based more and more on a comprehensive knowledge of the soft parts of the body, and particularly of the internal organs, extending sometimes even to an investigation into the sets of chromosomes. This is of great importance, especially when the shell, the radula and the jaw fail as by establishing the degree of relationship of various species. All three are conchiolin excretion of the membrane of ectodermical origin. When comparing the appearance of particular organs, it is necessary to take into account not only their variability considering also different factors from the sphere of ethology, which have a modifying influence, such as the physiological state of the organ dependent upon the season of the year, the long-continuing contraction of the body during the period of hibernation; as well as the age of the organism, whether it be adolescent, mature, or senile. In many cases it is indispensable to work out the numerical particulars of the organs (or their parts) being compared, at the same time taking into consideration the proportion of the complexes of these organs. In these cases it is of importance to establish beforehand the point of departure from which these measurements are to be taken and the degree of elasticity of the organ itself, and also, if the animal dissected had previously been preserved, the chemical reagents more or less dehydrating the tissues.

Besides the normal variations, subject to Quetelet's law, different deviations are apparent, originating from the embryonic development. Many deviations come into existence in post-embryonic development, through imperfection of the appearance of organ characteristic with the full-grown organism, and also in the mature age. In order to elucidate the causes of their origin, we are obliged to enter into the topology of organs, this topology being dynamically conceived in connection with the development, activity and motion of separate organs.

With regard to snails, especially those belonging to *Stylommatophora*, the movements and consequent involutions of the internal organs are particularly remarkable. In *Stylommatophora* the temporary changes in the arrangement of the organs are very prominent e. g. during the retraction of the head, mostly connected with the retraction of the whole body within the shell, the peri-oesophageal nervous ring is excessively stretched and assumes a pre-oral position instead

of its former place behind the pharynx [Pl. XVI]. This movement, normal for *Stylommatophora*, can easily be observed by cutting the body of the creeping snail just at the moment of the withdrawing of the head. We must therefore often resort to vivisection in investigations of this kind. The best thing, however, would be to use in vitro methods — chemical as well as physical — of x-raying of the living organism and would permit examination of the arrangement and behaviour of the internal organs during different stages of the animal's life.

The analysis of the behaviour of the organs and their mutual interaction. taking into consideration also the membranous connective tissue which to a certain degree fixes the position of the organs, enters the sphere of dynamic topology or the ethology of organs. This analysis can explain to us, sometimes even without the use of experimental means, the reason for the different appearance of any organ which may exceed the normal range of mutability.

Many deviations in the appearance of organs, apart from those due to pathological causes, may be only of a temporary nature, due to pressure from adjoining organs (impressions, flexions, which have arisen during hibernation, etc.) or they may be due to influences of a physiological nature (self-caused or caused by the organs of the partner during copulation).

The entanglement of internal organs, especially in the case of snails of the order of *Stylommatophora*, may give rise to some permanent „correlative" anomalies, with simultaneous changes in both the entangled organs concerned. When trying to elucidate the causes of their origin, certain morphological, evolutionary, and topographical circumstances should be taken into account, as well as factors of a physiological and mechanical nature which exert an influence on the correlated organs.

Below, I attempt an elucidation of the mechanism giving rise to anomalies and deformations of the genital organs in *Helicigona (Arianta) arbustorum* (L.) During my investigations on the variability of this snail, I came across 22 cases in which different parts of the genital organs appeared abnormal [1]).

The snails were collected at different times of the year from the Pharmaceutical Gardens of the University of Warsaw, on a high terrace covered with old trees overlooking the Vistula.

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[1]) I noted deviations from the normal appearance in 17 out of 170 dissected specimens, i. e. 10%.

They were to be found in great numbers, togother with *Trichia (Trichia) hispida* (L.) [1]), hiding in the earth, under the walls, and among the fallen leaves and grass.

CORRELATIVE ANOMALY OF THE FLAGELLUM AND THE NERVUS PALLIALIS DEXTER

Description. The most complicated anomaly was found in the flagellum of a mature specimen caught on November 25th, 1930. It was preserved in formalin; its body was considerably detached from the shell, in the same state as when freely creeping [2]).

After dissecting the dorsal side of the snail and laying bare the distal parts of the genital organs, a vesicular form could be observed adhering springlike to the penis, a little darker in colour than this, while the mantle nerve (nervus pallialis dexter) was entangled just after its exit from the ganglion (ganglion parietale dextrum) in a mass of vesicles [Pl. XI, fig. 1].

Only after pulling the vesicles aside in the direction of the vagina was it possible to realize that we were dealing with an anomaly of the flagellum [Pl. XI, fig. 2].

In order to understand more easily the course of development of the specific segments of the gland which has undergone such considerable change, the drawings are successively numbered from the bottom upwards [Pl. XI, XII, figs. 3—4].

From the epiphallus the first segment emerges unchanged [1], though greatly stretched and twice twisted, its length being 1.25 mm. Further on it flattens out into a hard, thickened, cylindrical form [2] like a beak consisting of two accreted vesicles [3—4]. This first group of vesicles — there are four such groups — is connected with the next [5—6] by means of a soft, tape-like, flattened membrane of the gland, forming a ear-like, loosely hanging fold on the abdominal side. Further on, the beaks of the neighbouring groups of vesicles are joined together by means of the slightly-changed segments of the gland [7, 9]; these segments resemble the bottom one [1], being however shorter (0.25—0.5 mm.) and twisted only once.

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[1]) Less numerous: *Cochlicopa lubrica* (O. F. MÜLL.), *Pupilla muscorum* (L.) *Vallonia pulchella* (O. F. MÜLL.), *V. pulchella* v. *costata* (O. F. MÜLL.), and *Zonitoides nitidus* (O. F. MÜLL.).

[2]) The shell had five whorls and the following measurements: height 15 mm., breadth 17.5 mm., aperture 10×9.25 mm.

The flagellum, after its exit from the last vesicle [11], looks quite normal. It forms a loop [12] 5.5 mm. long, narrowing towards the centre. This loop embraces the bottom of the flagellum and the upper part of the epiphallus so strongly that it causes the posterior part of the spermiduct also to be pressed up against them [Pl. XI, fig. 2]. The loop is closed by accretion to the vesicle [11] along a length of 0.75 mm. [13] and afterwards the somewhat widened end of the flagellum projects rather stiffly for 2 mm. [14].

The combined length of the whole flagellum — this length being the sum of all the vesicles concerned, their beaks, the links between them, and the distal unchanged part of the gland — amounts to 23,5 mm., corresponding more or less to the average length for all adult individuals taken from that environment [1]).

On examination of the internal structure we are confirmed in our view that all these deformations are closely connected with the flagellum itself, because they are to be found within the limits of its walls.

From cuttings of those parts which had undergone the greatest changes, such as the vesicles and their beaks, the eccentric arrangement of the dark layers completely filling the lumen of the gland is visible [Fig. 1]. The outer layers are found directly under the tightly stretched membrane of the gland, while the inner ones are arranged nearer the spiral fold (raphis), running along the shorter surface and directed towards the inner side of the whole chain of vesicles. In the most deeply situated layers the spiral structure characteristic for the cauda of the spermatophore becomes more pronounced.

Fig. 1. Medial section through vesicle — 8. Spiral raphe visible; walls of spermatophore blackened. x 35.

These layers, or more properly laminae, easily separable from one another, are formed of a homogeneous substance, corresponding to the inner structure of the walls of the spermatophore (8).

In the first group of vesicles [3 and 4], in longitudinal section [Pl. XII, fig. 5], instead of one, two sets of eccentric spiral laminae are seen adhering to each other. The concentric set visible under the membrane of the gland is a secondary formation, as will be shown below.

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[1]) The length of the flagellum, measured in 114 adult specimens, varies within the limits of 12.5 mm. to 28.25 mm.; the average is 21 mm.

The contents of the last vesicle have a different appearance [11]. On dissection the wall of the flagellum is seen, with complete atrophy of the spiral fold. Part of the cauda of the spermatophore, however, with a normal spiral structure, lies freely in the greatly extended interior of the flagellum [Pl. XI, fig. 3].

All the vesicles together with the beaks are hard on account of their contents, with the single exception of the last.

The whole is entangled, as observed above, with a plexus of the mantle-nerve [Pl. XII, fig. 4]. Freed however from the bands of the nerve it is gathered together into a ringshaped cluster, ad-hering firmly to the epiphallus and penis [Pl. XI, fig. 1]. The in-dividual parts of this cluster adhere closely to one another, adjusting themselves as if in a common endeavour to form a spherical mass. The inter-vesicular connections adherent to the bottom part of the flagellum [1] are similar to it, very elastic, with the lumen con-tracted [7, 9]. In this way this part of the flagellum is surrounded on two sides by the beaks of the vesicle lying on it [8]. If we also take into consideration the loop of the normal, distal segment of the gland entwining it, we shall then have a picture of scarcely a part of the peculiar system of constriction [Pl. XI, fig. 2]. The points of constriction, six of which may be distinguished [Pl. XI, fig. 3; I—VI], will be mentioned again in the discussion of the course of the mantle-nerve.

On the abdominal side can be seen three twists of the mantle-nerve, nervus pallialis dexter [Pl. XI, fig. 2]. The first, running from the ganglion, constricts in turn points VI, IV, and V, then passing in the dorsal side, forms a loop round the upper part of the epiphallus and the base of the flagellum (point of constriction - I) [Pl. XI, fig. 3; Pl. XII, fig. 4]. The two remaining twists form the sides of a loop thrust in between the epiphallus and the adjacent spermiduct, and constricting the points I, VI, IV, VI, and 1. The further course again results in the constriction of the points 1, IV, and V. The part of the nerve (c) running towards the mantle gives off a branch (b) entangling the inter-vesicular connection [7] and ending in a vesicle (v. n.) [Pl. XII, figs. 4, 7]. This vesicle is pro-vided with an arch round the base of the flagellum [1] and also the above-mentioned inter-vesicular connection. In this way there occur two additional points of constriction, II and III, indirectly connected with the previous ones [Pl. XI, fig. 3; Pl. XII, fig. 4].

The whole nerve, without counting the branch (b), is 15 mm. long — 11 mm. up to the point of bifurcation (a) and 4 mm. beyond it (c). This last part of the nerve, running towards the mantle, was probably a little longer (its exact measurement was not practicable owing to the damage sustained in its preparation).

The structure of the first section of the nerve (a) is normal only for the length of 5.5 mm., beginning from its exit from the ganglion. Here its width is 0.4 mm. In the second half, however, numerous narrowing points composed solely of fibrils are visible as well as flat frayed bands of cellular formation, corresponding to the sheath of the nerve [Pl. XII, fig. 6].

The branch of the nerve also deviates from its normal appearance [Pl. XII, fig. 7, b]. In between its two fibrous parts (each 1 mm. long), of which one forms a closed circle, lies a vesicle (v. n.) like a small sac 2 mm. in width. On the dorsal side, the tip of the vesicle, which is free, has a concave caused by the beak [2] of the first two vesicles of the flagellum [Pl. XI, figs. 1, 2; Pl. XII, fig. 7]. The interior of the vesicle is empty, and its walls have a cellular structure. Hence it corresponds to the frayed segments of the part of the nerve already mentioned (a), one of which also assumes a vesicular appearance.

Origin of the anomaly. In the course of the above analysis the supposition arises that the anomaly of the flagellum and mantlenerve under discussion originated when the flagellum first became entangled with the nerve. The conditions enabling such a coincidence must be sought for in the actual structure of the elements subject to the anomaly and in their mutual arrangement (topography) among the connective membranes in the region of the cavity of the body.

In *Arianta arbustorum* the flagellum is usually well developed; most often spirally twisted at the base, it is also apt to become folded in its further course. In only one case was a flagellum met with which lacked the spiral at the base or the folds [Pl. XIII, fig. 8], its length being scarcely 13.5 mm. [1]).

[1]) The typical spiral base is distinguished rather late in the development, only in individuals with 4.6 whorls of the shell, although indications of spiral twisting may be traced fairly early, even in a flagellum of scarcely 0,3 mm. in length (the dimensions of a shell with 3.6 whorls are 6.25×8.75 mm. with an aperture of 5.25×4.6 mm.) [Fig. 2].

The spiral part, turning to the right, may reąch a length of 5.75 mm. [Pl. XIII, fig. 9]. The number of turns varies from one to five. The cauda of the spermatophore arising in the flagellum assumes a similar form.

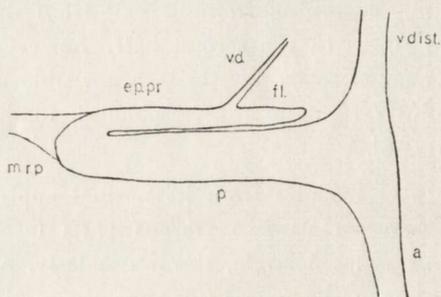The nervus pallialis dexter is about 12 mm. long. It emerges from the ganglion parietale dextrum in the sub-oesophageal part of the ring. It passes under the musculus retractor penis, adherent to the centre of the diaphragm where the latter comes into contact with the membrana intestinalis, and then proceeds on the dorsal side, passing over the female genital organs [Pl. XV, figs. 28, 29]. Hence it passes between the male and female parts of the genitals. In the

Fig. 2. Distal part of immature genitals. The tendency of the flagellum to twist is evident. x 30.

neighbourhood of the base of the mantle collar it divides into two bands, disappearing in the tissues near the aperture of the pulmonary cavity. There are strictly speaking two nerves, internus and externus, enclosed in a common sheath; they innerve the right half of the mantle (17).

The mutual positions of the nerve and the flagellum change according to the degree of contraction of the whole body, as well as during copulation.

At the time of the maximal expansion of the body, appearing while freely creeping, the nerve retreats under the retractor muscle of the penis. During the average contraction of the body, however, the nerve usually runs under the caput penis and over the region of the bursa hastae.

During the maximal retraction of the body into the interior of the shell, a vigorous compression of almost all the most important organs occurs in the region of one whorle, causing changes in their topographical arrangement [Pl. XVI, fig. 30]. This phenomenon is intensified still further by the ability to invaginate the head, characteristic of the *Stylommatophora*. The pharynx is pressed backwards by the effect of the contraction of its retractor, and forces its way through the perioesophageal ring, which assumes a pre-oral position

[Pl. XVI, fig. 30 and text-fig. 3] [1]). The mucous glands (glandulae mucosae) from the base up to half their length are adherent to the vagina distalis [Pl. XVI, fig. 30 and text-fig. 3].

In two cases the entanglement of the nerve in the mucous glands was observed during such a maximal contraction; in one case the nerve passed between the left mucous gland and the bursa hastae [2]), in the other it passed between the bursa hastae and the right mucous gland.

As a rule, all the distal genital organs, the apexes of which are detached and protrude freely from the surrounding membrane can become entangled with the unobstructed mantle-nerve [Pl. XV, fig. 29].

The flagellum is very much more likely to become entangled with the nerve, as it is a long gland, rather elastic owing to its spiral form, and apt to form plexuses as it winds among the organs. In one specimen the whole flagellum, in which the plexuses were laid flat and the basal spiral was lacking, was squeezed

Fig. 3. Characteristic movement of the copulatory organs and of the peri-oesophageal ring during maximal contraction of the body. x 2.5.

deep into the fissure between the genital organs and the pharynx [Pl. XIII, fig. 10]. Usually the plexuses are situated in the fissure between the male and female part of the genital apparatus, the top segment leaning towards the dorsal side [Pl. XI, fig. 1 and Pl. XV, fig. 29]. The topmost plexuses sometimes embrace the salivary duct, or are thrown over the pharynx, passing under it on the left side [Pl. XIII, fig. 11].

During copulation, the erect flagellum is strongly pressed forward in the direction of the atrium genitale, following the invaginating of the male organ.

Also during copulation, and similarly at the time of the maximal contraction of the body, the flagellum, considerably detached in a backward direction from the spermiduct, might pass beneath the

[1]) The penetration of the pharynx through the peri-oesophageal ring occurs with each invagination of the head, oven when creeping, which can be confirmed by section of the trunk of the snail in the region of the fore-mantle at the most contracted point.

[2]) In one specimen from Bielany near Warsaw the course of the nerve was similar, and has been marked on Pl. XVI, fig. 30 by a dotted line.
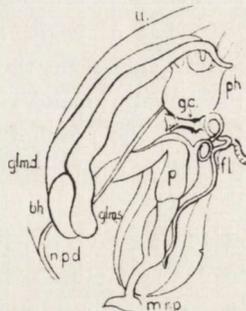
mantle-nerve and become entangled with it during the reciprocal movement of the internal organs.

In the case in question this was shown in all its possibilities. The loops of nerve which arose round the different segments of the flagellum were tightened more and more by each contraction and expansion of the body.

Let us begin first of all with the explanation of the origin of what would seem the most complicated loop, thrown round the apex of the flagellum and also passing between the penis and the spermiduct. It must be remembered that the spermiduct runs in a curve along the vagina and penis, its development being connected with theirs.

Here two possibilities must be considered: 1) an entanglement of the apex of the flagellum with a simple loop of the nerve, thrust in between the spermiduct and the penis, might occur [Pl. XIII, fig. 12]; this might later be crossed by the turning of the apex through an arc of 180⁰ [Pl. XIII, figs. 13, 14]. 2) The same effect might also be obtained by the entry of the apex of the flagellum between the penis and the spermiduct; but then after the entanglement with the nerve it should return by the same way along the dorsal side. A thrusting of the apex of the flagellum between the spermiduct and the penis was observed in one specimen.

The explanation of the way in which the other loops were formed would be comparatively easy. It would only be necessary to assume that the nerve, becoming entangled on account of the strong tension or for other reasons, split in mid-course into two parallel bands (possibly lapsing into internus and externus) already playing independent roles in the entanglement of the flagellum [1].

The excessive stretching of the nerve might eventually lead to the breaking of one of the bands (b). The end of the band when released then sprang back from the part of the nerve entering (a) and was pressed to the shred of the first whorl of its own spiral, which arose after becoming entangled with the flagellum. After accretion with this shred, a crook was formed in the ensuing sac, v. n. On the vesicle v. n., which is merely a prominent protuberance of the epineurium, a small fibrous band is visible from the dorsal side on the prolongation of the crook, establishing the accretion of these parts [Pl. XII, fig. 7].

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[1] On a model it is easy to untangle this „Gordian knot" by the free manipulation of the detached end of the flagellum round the nerve stretched taut.

Eventually the six points of constriction already mentioned resulted. The plexuses of the flagellum, tightly adherent to one another, formed a conglomerate. The distal part of the flagellum then formed a loop, embracing the base of the gland as well as the apex of the epiphallus and the spermiduct [Pl. XI, figs. 2. 3; Pl. XII, fig. 4].

The process of accretion of the walls began from the contacts between the plexuses: 1) with the preservation of the separateness of the lumen at the place of the accidental adhesion [13], visible at the apex of the flagellum [Pl. XI, figs. 1—3; Pl. XII, fig. 4]; 2) when carried further, it is connected with a slow atrophy of the actual membranes along the surface of the tighter adhesion, as was established in the region of the basal spiral [3, 4 in Pl. XI, fig. 3; Pl. XII, fig. 5].

The gland in its free segments, between the constricted points, continues the accumulation of the spermatophorous substance, but without the possibility of emitting it into the epiphallus. The activation of the gland, as usual, might have ensued in the period of excitement preceding copulation. There is however no certainty as to whether this went so far as actual copulation with the outlets of the spermiduct and flagellum closed, hence in the absence of spermatozoa and proper spermatophore [1]).

Normally the glandular activity of the flagellum causes the production of material for the anterior ridged part of the spermatophore, then for the middle part, forming the sheath proper for the spermatozoa; both parts are themselves formed within the lumen of the epiphallus. Only at the end, already inside the flagellum itself, is the cauda of the spermatophore definitively formed.

In the case under discussion, as a result of the periodical activity of the gland. fresh quantities of a gelatinous substance were constantly emitted inwards towards the unconstricted segments of the gland, and after hardening took on the conformation of the structure of only the cauda of the spermatophore,

The layers accumulated in this way caused a considerable extension of the walls of the gland, finally leading to the formation of vesicles with characteristic sections [Fig. 1].

The most complicated of these sections [Pl. XII, fig. 5] was that through a double vesicle, 3 and 4 [Pl. XI—XII, figs. 1—4].

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[1]) In any case neither spermatophore nor spermatozoa were found in either the epiphallus or penis.

The origin of this is explained by the accretion of the interior walls with the last whorl of the basal spiral (the first whorls became drawn out like tape) [1 in Pl. XI, fig. 3]. The lowest branch of the last whorl, starting a beak [2], functioned intensively. The topmost branch, however, became almost atrophied, having become accreted to the beak already mentioned. Part of it became very weak, and flattening out into a wide band, formed as it were the neck of the vesicle [5]. The convex outer walls of the whorl closed in this way by the constant accumulation of new layers of spermatophorous substance, began to stretch much more than the inner, concave ones. These last, adhering to one another more and more tightly and becoming flatter and flatter, finally accreted. Then the longitudinal spiral folds (raphes) became situated in the centre beside each other, separated by only the common membrane of the accreted glandular parts. In this way two sets of eccentric layers were formed. The gradual atrophy of the partition finally enabled the functioning of only the exterior surrounding membrane, accumulating layers which were more and more correctly concentric [Pl. XII, fig. 5].

The topmost vesicle [11] arose in a different manner from that described above. It also originated here in the vigorous stretching of the membrane, but only under the influence of the weight of those portions of the cauda of the spermatophore lying freely beside each other, produced by the unchanged segment of the flagellum.

It is interesting that the tendency to form vesicles in places free from pressure, and also the tendency to accrete, appear also in the region of the nerve itself [Pl. XII, figs. 6, 7].

On the other hand, it can be shown that in the constricted places, both in the flagellum and in the nerve, there is a tendency to form elastic threads of great resilience.

The resilience of the springy little bridges lying between the hard, inactive parts of the flagellum, is due to their spiral twist.

Owing to this resilience, the separate parts adhere tightly to one another on different planes, forming a strong grape-like growth which can be detached from the penis only by force [Pl. XI, fig. 1-2].

ANALYSIS OF OTHER ANOMALIES AND DEFORMATIONS
DEPENDING ON VARIOUS PHYSIOLOGICAL STATES
OF THE ORGANISM

In this section, anomalies of a teratological character observed in the glandula mucosa or in the receptaculum seminis and also such deformations as are normally connected with various physiological states of the organism will be discussed.

It was sometimes difficult to decide on the basis of the prepared material to what category a given deformation belonged. For this reason, all deviations from the normal have been given, i. e. from the appearance most frequently met with in the organs.

The most definitive observation would certainly be that of the organs in the living organism.

Glandulae mucosae. The mucous glands in *Arianta arbustorum* are paired organs entering the vagina at the beginning of its distal part. The left gland is usually a little longer than the right one; this is already distinct fairly early in the development, for it is seen in specimens with shells twice as small as those of adults
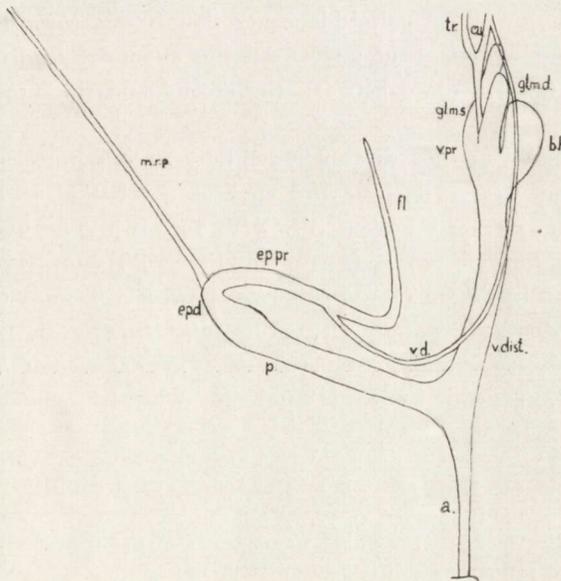

Fig. 4. Distal part of genital organs in youth. The assymetry
of the glandula mucosa is visible. x 16.

[Fig. 4] [1]). This comparatively small difference in the length of the two glands might be explained by their different positions in the interior of the body. The left gland, being pushed towards the dorsal side of the body, and at the same time most of all on the periphery of the last convolution, has more room for growth than the right [Pl. XV, fig. 29; Pl. XVI, fig. 30].

Two cases of anomaly were observed in the mucous glands.

In one specimen [2]), in which the lip of the shell was not yet formed, appeared a bifurcation of the apex of the right gland [Pl. XIV, fig. 15]. Here are found two regular, cylindrical branches of different dimensions: 3.25×0.5 mm., and 1×0.35 mm. Apart from this, the gland presents a quite normal appearance along its remaining length 10.25 mm. It is 0.7 mm. thick at the base. The left gland is markedly larger, 17×0.75 mm.

HOFMANN (8) gives three cases of a similar anomaly (Fig. 15, Taf. 11), from among a large number of specimens of *Arianta arbustorum*. In one specimen from Jena a small branch („Anhang‟) is found near the centre of the gland, in another from Siegmündung there is one near the apex [3]), and in a third, also from Siegmündung, the tip of the gland is divided dichotomically. In each case the remaining gland was normal. It is a pity that in his paper HOFMANN does not state which gland underwent the anomaly. The case observed by me takes a place between the second and third cases of this author.

Again, in another specimen, withdrawn into the depths of its shell for the winter sleep [4]), the apex of the left gland is strongly bent downwards, as if broken [Pl. XIV, fig. 16]. The basal part of the gland is normal for its entire length, 20.25 mm.; it is 2 mm. thick at the base. In the upper part however, from the point of flexion, a violent diminution in thickness appears in two places (respective measurements, 4×0.75 and 4.75×0.5 mm.). This is accompanied, as can be seen from the whitish contents shining

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[1]) The measurements of a shell with 4.1 convolutions are: $8\,25 \times 11.25$ mm.; the opening measures 6.75×5.75 mm. The length of the left gland is 0.9 mm., and that of the right 0 75 mm.

[2]) Caught on 23 : X : 1929. The dimensions of the five-whorled shell are 13.5×15.5 mm.; the aperture is 9.25×8.25 mm.

[3]) The length of this branch is 2 mm.

[4]) Caught on 6 : XII : 1929; the dimensions of the shell, with 5.25 convolutions, are 16.75×21 mm., and the aperture is 11.25×10.25 mm.

through the walls, by a simultaneous narrowing of the duct. The inclusive length of the gland thus changed is therefore 29 mm.

The right mucous gland, 24.75 mm. long by 1.75 mm. thick, presents a normal appearance, although its apex is rather narrow and not too well filled by the contents.

From these observations the supposition arises that the apex of the gland, considerably bent and narrowed, may finally fall off, and so establish a base for the arising of a dichotomic regeneration [1]. This falling off may be caused also by the mantle-nerve, discussed in connection with the anomaly of the flagellum.

HOFMANN is inclined to see in the dichotomy of the mucous gland a small reminiscence of the relations prevailing among species of the family *Helicidae*, in which as a rule this gland is dichotomically divided.

Receptaculum seminis. Normally the spermatheca in *Arianta arbustorum* is spherical or pear-shaped.

In two adult specimens in structure was assymetrical; it was more strongly developed on one side, as if under the influence of the pressure exerted by the upper side [Pl. XIV, fig. 17].

The receptaculum seminis is found already in the region of the visceral sac, beyond the membrana transversa (9), transversally dividing the body cavity. This membrane is accreted to the oviduct, as well as to the base of the spermatheca, which in this way becomes immobile and may lead to deformation during the prolonged contraction of the body, in contact with the strongly compressed parts of the alimentary canal and the liver, or with the initial segments of the genital organs. The stomach and, nearer the columella, the musculus columellaris [Pl. XVI, fig. 30] move freely through the opening in the membrane.

In both cases the diverticulum was also strongly folded in its upper part [Pl. XIV, fig. 18].

A similarly modified vesicle was also observed by the author in a specimen caught on 8 : IX : 1929 by POLIŃSKI on Mount Sinai in Roumania at a height of 1150 m. (over 3500 feet) [Pl. XIV, fig. 19].

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[1]) In the given case however the tissue of the bifurcated part of the gland does not outwardly differ from the normal. The immaturity of the specimen moreover compels us to look for the cause rather in some disturbance during development.

All three snails were preserved in the contracted state.

In one case the receptaculum seminis deviated markedly from the normal appearance [Pl. XIV, fig. 20]. Its duct in the distal part, very much widened and arched, is gradually transformed into a sac-like vesicle, slightly spirally twisted at the base. The longitudinal striation appearing usually in the duct of the receptaculum is seen on the walls of the vesicle. In the duct itself the striae run only as far as 8 mm. from the base [1]).

The abnormal receptaculum seminis just discussed recalls by its shape the same organ in species of the sub-family *Hygromiinae* (10, 19, 20, 23).

Glandula albuminalis. The albuminous gland lies near the axis of the shell under the transparent membrane of the visceral sac. It marks out a fairly long impression, covered by the very delicate membrane, membrana hepatica (9), among the three lower lobes of the liver, which are divided by the loops of the intestine.

A marked flattening of this gland appeared in two specimens in a state of maximal contraction inside the shell caught one in winter and one in summer.

In two other cases, in individuals caught in December during hibernation, and so with the body strongly retracted within the depths of the shell, the author observed a lateral flexion halfway along the length of the gland. The curved walls were tightly adherent to each other along the edge of the vesicula ovo-seminalis. In one gland the base was 4.75 mm. in length, but the flexed apex was 5.25 mm. In the second gland the two branches of the flexions were equal, being 7 mm. long [Pl. XIV, fig. 21]. The author considers that here the adhesion had attained a constant character, since there was a simultaneous topographical adaptation of the oviduct. Its initial segment, much swollen on one side, formed a support for the bent upper part of the albuminous gland, the concave surface of which was precisely adjusted to the convex walls of the oviduct. Owing to this the whole gland is seen at the first glance to have changed its shape, becoming thicker and shorter.

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[1]) The duct is slightly shortened. It is 14 mm in length, within however the limits of normal variation (11.5—24.5 mm.). The vesicle itself runs 2 mm. beyond the normal limits of variation, since it reaches the exceptional length of 6 mm.

In all these changes, it seems that, the decisive role was played by the exhaustion of the gland (11, 12, 13, 14) demonstrated by its weakening. The flexions themselves however appeared by chance, induced only by the facility of movement of the apex of the gland in the region of its impression during strong contraction of the body.

The **epiphallus, penis, truncus receptaculi** and **vagina** may also undergo temporary deformations in connection with the physiology of reproduction.

During the formation of the spermatophore, its widest medial part distends the epiphallus considerably. It is then thicker than the penis proper. which at the same time is considerably shortened, being as if pushed on to a further plane [Pl. XIV, fig. 22]. The ratio of the length of the epiphallus thus changed to that of the penis is 3 : 1 (8.25 : 2.75 mm.), which deviates markedly from the mean 1.27 : 1, observed in all mature specimens.

During copulation the truncus receptaculi may be greatly distended by the penis of the partner [Pl. XIV, fig. 23]. A head-like distension may also be visible at the beginning of the diverticulum.

Functionally, the truncus and diverticulum form a prolongation of the vagina. The canalis receptaculi would be merely their lateral branch. The spermatophore, directed to the diverticulum at the end of copulation, remains there in order to undergo dissolution later. In one specimen, in a diverticulum 41 mm. long, the initial segment, 8.5 mm., was occupied by the anterior part of the cauda of the spermatophore, of which 5 mm. was taken up by a spiral. The rest of the cauda was involved in the truncus and vagina proximalis. The shank of the spermatophore, 4 mm. long, caused a distinct thickennig of the diverticulum. Within the sheath of the shank, provided on the inner surface with small transverse edges, is found the charge of sperm, in characteristic lamelliform folds. The anterior part of the spermatophore, a few millimetres long, is longitudinally ribbed. In transverse section, more or less regular star-shaped forms are obtained, with four or five rays [Fig. 5], giving the shape of the very much folded interior of the epiphallus [1]).

Fig. 5. Section through the anterior part of spermatophore (head). Seen from the anterior, narrower side. x 80.

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[1]) The star-shaped folding appears most distinctly in the epiphallus distalis.

TABLE

Numbers of figs. in plates and text-figs.	Number of specimen	Age of individual	Organ	Deviation from normal state	Degree of permanence
			DESCRIPTION		
1—5 12—14, 1 in text	136	mature	flagellum	arising of vesicles with accretions within the spiral and plexuses	permanent
1, 2, 4, 6, 7 12—14	136	mature	nervus pallialis dexter	medial part bifurcated into two bands; one of them broken off; frayed; arising of a vesicle & accretion	permanent
8	39	mature	flagellum	erect; basal spiral lacking	permanent
15	16	young	glandula mucosa dextra	dichotomy of the apex	permanent
16	79	mature	glandula mucosa sinistra	curved with step-like narrowing tip	permanent?
17, 18	5, 74	mature	receptaculum seminis	lateral assymmetry	temporary?
18	5, 74	mature	diverticulum	folding of the apex	temporary
20	94	mature	receptaculum seminis and canalis receptaculi	sac-like extension	permanent
21	61	mature	glandula albuminalis	laterally curved with topographic adaptation of oviduct	permanent
	170	mature	glandula albuminalis	laterally curved	temporary?
	77 98	mature	glandula albuminalis	considerably flattened	temporary
22	139	mature	epiphallus and penis	changed in the ratio of their lengths	temporary
23	32	mature	truncus and diverticulum	excessive widening	temporary
24, 25	22, 35	mature	truncus	excessive widening	temporary
25	22	mature	vagina proximalis	excessive widening	temporary
26, 27	24, 106	mature	m. retractor penis	swelling at one end	temporary (repeatable?)

The positions in the table are arranged according to the description in of the University of Warsaw.

1.

C A U S A T I O N

No of cases	Consideration of the morphological, topographical and developmental dispositions and distinction of the physiological and mechanical factors acting in maturity	
1	secretion of the spermatophorous substance, without the possibility of excretion within the parts of the flagellum unconstricted by the mantle-nerve	After the mutual entanglement of the nerve and flagellum during strong contraction of the body or during copulation
1	excessive stretching of nervus pallialis dexter (internus and externus)	
1	case, considered by author to be within the limits of variability, of arrest of appearance of gland in youthful stage. Erect flagellum appears only in very young individuals; in mature *Helicidae* it occurs except in the genera *Campylaea* and *Helicigona*	
1	anomaly of teratologic character. Dichotomy of this gland appears regularly in various other species of *Helicidae* (*Campylaea*)	
1	state of exhaustion of the gland, connected with the pressure of organs during contraction of the body during the winter sleep	
2	probably the pressure of organs on receptaculum in a mature specimen during contraction of the body. Appearance of receptaculum recalls that of *Hygromiinae*	
2	influence of the pressure of organs during contraction of the body	
1	anomaly of teratologic character recalling in appearance the sac-like receptaculum in *Hygromiinae*	
1	influence of prolonged pressure of organs during contraction of the body on the weakened gland exhausted by starvation during the winter sleep. The possibility of movement of the apex of the gland in the region of its impression compressed among the lobes of the liver should be emphasized	
1		
2	exhaustion of the gland with simultaneous pressure of organs during contraction of the body	
1	spermatophore, being formed in epiphallus, caused: extension of that part of the copulatory organ and simultaneous contraction of the penis proper	
1	stretching by penis of the partner, remaining after copulation	
2	stretching caused in laying-period by eggs moved backwards during sudden contraction of the body	
1	stretching caused by the egg arrested during contraction of the body	
2	unequal tonus of the strongly contracted muscle during the maximal contraction of the body within the shell	

the text. They refer only to material collected in the Pharmaceutical Garden

The truncus may undergo temporary deformation also in the egg-laying period, which was verified in preserved snails in the contracted state. The egg then, instead of proceeding normally from the collum uteri to the vagina, becomes thrust into the truncus, the base of which it distends enormously [Pl. XIV, figs. 24, 25].

In the same way the vagina may be deformed [Pl. XIV, fig. 25]. The width of such a distended part amounts to about 2.75 mm., equivalent to the diameter of an egg.

Very great variations occur in the length of the **musculus retractor penis,** depending on the degree of contraction of the body [Pl. XV, fig. 29; Pl. XVI, fig. 30].

The author observed certain deformations of this muscle in two specimens. In one, at the period of the maximal contraction of the body, the proximal part of the muscle was excessively thick [Pl. XIV, fig. 26], in the other however it was the distal part [Pl. XIV, fig. 27] [1]). In all other specimens the retractor of the penis was of equal thickness independently of the degree of contraction.
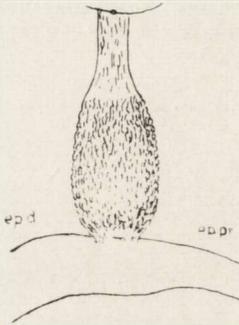

Fig. 6. Musculus retractor penis. Contraction of its proximal part in a living specimen from Bielany. x 10.

The deformation of the proximal part of the muscle also appeared in a living specimen from Bielany (caught on 13 : X : 1942). During the maximal contraction of the body the length of this muscle was 3 mm., of which 1 mm. was taken up by the flat, transparent distal part. The proximal part was considerably swollen and semi-transparent [Fig. 6]. After a brief exterior pressure by means of a laboratory needle, the muscle elongated, assuming a uniform thickness and transparency along its entire length.

[1]) The lengths of the whole muscle in the two given cases are 2.75 mm. and 4.75 mm.

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EXPLANATION OF PLATES

Plates XI—XII, figs. 1—7.
Anomaly of flagellum and nervus pallialis dexter.

Plate XI.

Fig. 1. Distal part of genitals seen from the dorsal side; the peri-oesophageal nervous ring is visible on the left. x 4.2.

Fig. 2. Male copulatory organ from the abdominal side. x 5.6.

Fig. 3. Schematic appearance of deformed flagellum; its probable course before deformation is marked by a dotted line; the dotted area within the vesicle (11) shows part of the cauda of the spermatophore lying freely inside; the constricted points are marked with Roman numerals, I—VI; the particular segments discussed in the text are marked with Arabic numerals. x 10.5.

Plate XII.

Fig. 4. Schematic course of the flagellum and its entanglement with the mantle-nerve. That part of the nerve shown by a dotted contour was not investigated; x 12.

Fig. 5. Longitudinal section of the accreted vesicles (3+4). x 12.

Fig. 6. Nervus pallialis dexter; proximal part (a). x 16.

Fig. 7. Nervus pallialis dexter; distal part (c) with a branch (b), ending in a vesicle (v. n.). Dorsal view. x 16.

Plate XIII.

Fig. 8. Flagellum lacking spiral and folds. x 3.2.

Fig. 9. Flagellum with a five-whorled spiral. x 5.6.

Fig. 10. Flagellum lacking spiral, with flat folds involved between genitals and pharynx. x 4.8.

Fig. 11. Flagellum, considerably folded, its end entering under the pharynx from the left side. x 4.8.

Figs. 12—14. Hypothetical schemata explaining the origin of the nerve-loop entering between the spermiduct and penis.

Fig. 12. Flagellum caught in a simple nerve-loop. Sketch of probable situation. x 4.8.

Fig. 13. Loop crossed from the dorsal side.

Fig. 14. Loop crossed from the abdominal side.

Plate XIV.

Fig. 15. Right mucous gland dichotomically bifurcated. x 8.

Fig. 16. Apex of left mucous gland, considerably bent and narrowing step-like. x 3.2.

Figs. 17—19. Receptaculum seminis, deformed by pressure of internal organs strongly contracted during hibernation.

Fig. 17. Lateral and top depressions are visible. x 4.8.

Fig. 18. Assymetry of receptaculum with simultaneous folding of the diverticulum. x 1. 6.

Fig. 19. Assymetry of spermatheca in a specimen from Roumania. x 2.8.

Fig. 20. Receptaculum seminis and canalis receptaculi with teratological changes. x 2.4.

Fig. 21. Glandula albuminalis. Flexion of permanent character. Apex artificially retracted sideways. x 4.

Fig. 22. Epiphallus and penis modified by spermatophore. x 3.2.

Fig. 23. Truncus receptaculi and diverticulum. Postcopulative extension. x 4.

Fig. 24. Truncus receptaculi with a fixed egg. x 4.

Fig. 25. Truncus receptaculi and vagina proximalis extended by eggs contained in them. x 1.6.

Fig. 26. Musculus retractor penis. Contraction of proximal part. x 4.8.

Fig. 27. Musculus retractor penis. Contraction of distal part. x 1.6.

Plate XV.

Figs. 28—29. Expanded body of *Arianta arbustorum* after removal of shell.

Fig. 28. View of connective membranes after dissection of skin and diaphragm. x 2.

Fig. 29. Situs viscerum after dissection of visceral membrane (membrana circumintestinalis). Mantle-nerve embraced by lowest whorl of spiral of flagellum. x 3.

1. Integumentum regionis praepallialis. 2. Integumentum regionis pallialis s. pallium. 3. Integumentum regionis metapallialis s. sacci intestinalis. 4. Collar of mantle. 5. Cavum pulmonale. 6. Rectum. 7. Diaphragma. 8. Membrana circumintestinalis; large fenestrae visible. 9. Membrana capitocerebralis, passes over pharynx. 10. Membrana circumgenitalis. 11. Membrana uterina. 12. Ganglia cerebralia. 13. Nervus tentacularis. 14. Oesophagus. 15. Ventriculus. 16. Glandulae salivales. 17. Canalis glandulae salivalis. 18. Musculus retractor pharyngis.

Plate XVI.

Fig. 30. *Arianta arbustorum* during maximal physiological contraction. In order
to increase the transparency the mantle was removed, its margin
only is visible on the border. The compressed internal organs shine
through the diaphragm. x 4.

1. Contour of shell.
2. Lip of shell.
3. Umbilicus obtectus.
4. Foot, with sole visible.
5. Invaginated head.
6. Integumentum regionis praepallialis.
7. Integumentum regionis metapallialis.
8. Pallium.
9. Mantle-collar.
10. Mantle-groove.
11. Pulmonary cavity.
12. Pneumostom.
13. Rectum.
14. Ureter.
15. Diaphragma.
16. Membrana circumintestinalis.
17. Membrana capitocerebralis.
18. Membrana transversa.
19. Tentaculum majore sinistrum.
20. Oculus.
21. Tentaculum minore sinistrum.
22. Musculus retractor tentaculi majoris sinistri.
23. Musculus retractor tentaculi minoris sinistri.
24. Musculus retractor pedis.
25. Musculus retractor pharyngis.
26. Musculus columellaris sinister.
27. Ganglia cerebralia.
28. Nervus tentacularis.
29. Nervus pallialis sinister.
30. Nervus pallialis dexter bifurcated near pneumostom; a dotted
    line marks its course in another specimen.
31. Nervus analis.
32. Connectivum cerebrobuccale.
33. Ganglion buccale and nerves emerging from it.
34. Pharynx.
35. Oesophagus.
36. Glandulae salivales.
37. Canalis glandulae salivalis sinister.
38. Ventriculus.
39. Intestinum tenue.
40 Hepar.
41. Aorta.

42. Atrium genitale.
43. Penis.
44. Epiphallus distalis.
45. Epiphallus proximalis.
46. Musculus retractor penis.
47. Vas deferens.
48. Flagellum.
49. Vagina proximalis.
50. Collum uteri.
51. Uterus.
52. Truncus receptaculi.
53. Canalis receptaculi.
54. Receptaculum seminis.
55. Diverticulum.
56. Bursa hastae.
57. Glandula mucosa sinistra.
58. Glandula mucosa dextra.

Explanation of abbreviations used in drawings of plates and text.

a. — atrium genitale, ao. — aorta, b. h. — bursa hastae, c. r. — canalis receptaculi, c. u. — collum uteri, d. — diverticulum, d. h. — ductus hermaphroditicus, ep. d. — epiphallus distalis, ep. pr. — epiphallus proximalis, fl. — flagellum, g. c. — ganglia cerebralia, g. p. — ganglia parietalia, gl. m. d. — glandula mucosa dextra, gl. m. s. — glandula mucosa sinistra, m. r. p. — musculus retractor penis, m. r. t. m. d. — musculus retractor tentaculi majoris dextri, m. r. t. m. s. — musculus retractor tentaculi majoris sinistri, n. a. — nervus analis, n. i. — nervus intestinalis, n. p. d. — nervus pallialis dexter, n. p. s. — nervus pallialis sinister, p. — penis, ph. — pharynx, pr. — prostata. r. s. — receptaculum seminis, spo. — spermoviductus, tr. — truncus receptaculi, u. — uterus, v. d. — vas deferens, v. dist. — vagina distalis, v. os. — vesicula ovoseminales, v. pr. — vagina proximalis.
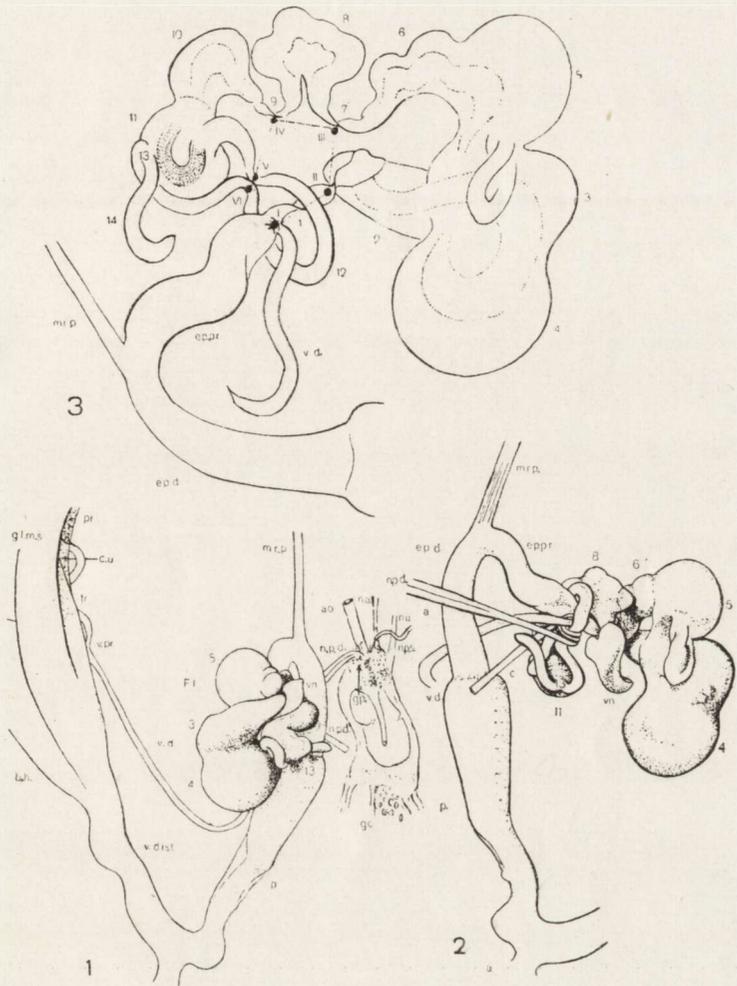

STRESZCZENIE

Autor omawia 22 przypadki anormalnego wyglądu różnych części narządów rozrodczych u *Helicigona (Arianta) arbustorum* L. z Warszawy, zastanawiając się nad przyczynami ich powstania.

Przychodzi do wniosku, że przeważająca liczba odchyleń od normy wystąpiła w okresie dojrzałości płciowej i to pod wpływem czynników: fizjologicznych, związanych z funkcją danych organów, jak również czysto mechanicznych. Odchylenia te mają raczej charakter przemijający, nie będąc tym samym właściwymi anomaliami.
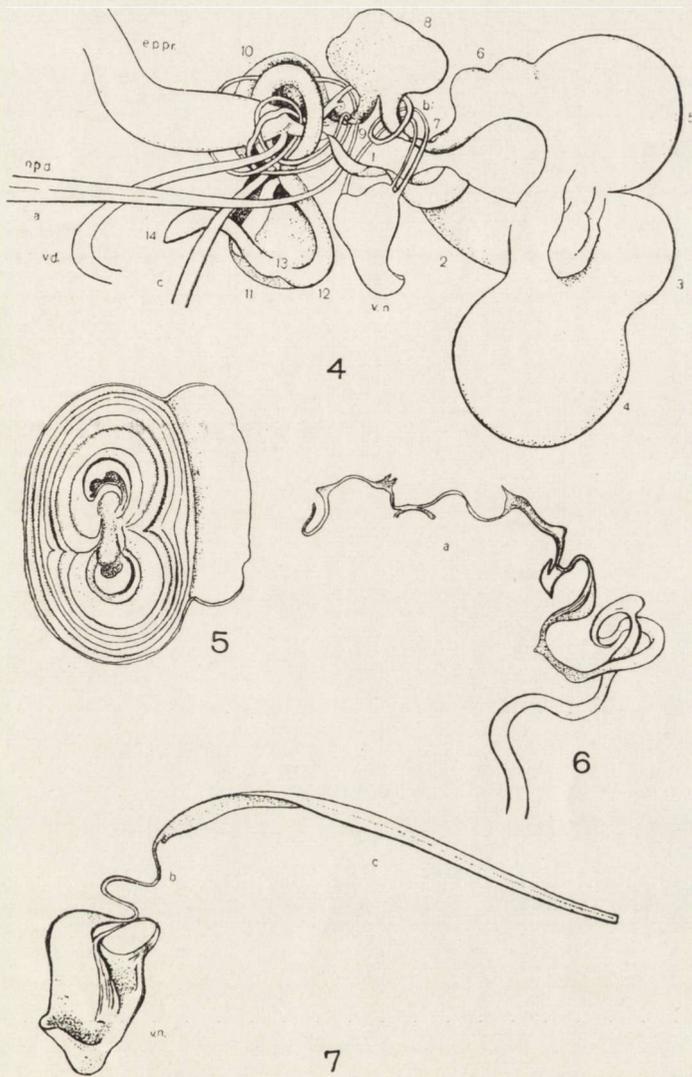
Niewielka część anomalii jedynie wystąpiła we wczesnym rozwoju: na drodze niezupełnego się ukształtowania organu, charakterystycznego dla osobników dorastających — w przypadku prostego flagellum, lub też na drodze pojawienia się nowego kształtu narządu, przypominającego napotykany normalnie u gatunków pokrewnych — w przypadku dichotomii glandula mucosa. Świadczyć by to mogło o pewnych skłonnościach rozwojowych, nie wiadomo tylko, czy anomalie te są dziedziczne, czy też są jedynie wynikiem zaburzeń o charakterze teratologicznym.

Najobszerniej omawiana jest anomalia sprzężona: flagellum i nervus pallialis dexter. Autor szczegółowo wyjaśnia mechanizm jej powstania. Uważa mianowicie, że u osobnika już dorosłego nastąpiło zaplątanie się flagellum w nerwie płaszczowym. Po zaciśnięciu się powstałych węzłów, gruczoł funkcjonował nadal bez możliwości usuwania substancji spermatoforowej poza odcinki międzyzaciskowe. W rezultacie powstał twór pęcherzykowaty o ściankach przylegających do siebie w różnych płaszczyznach, co doprowadziło znów w niektórych miejscach do zrostów. Napięty nerw rozszczepił się częściowo na dwa odcinki: internus i externus. Jeden z nich przy tym uległ przerwaniu, a końcowa jego pętla zamknęła się na drodze zrostu; jednocześnie powstał pęcherz z pozostałego strzępka otoczki nerwowej.
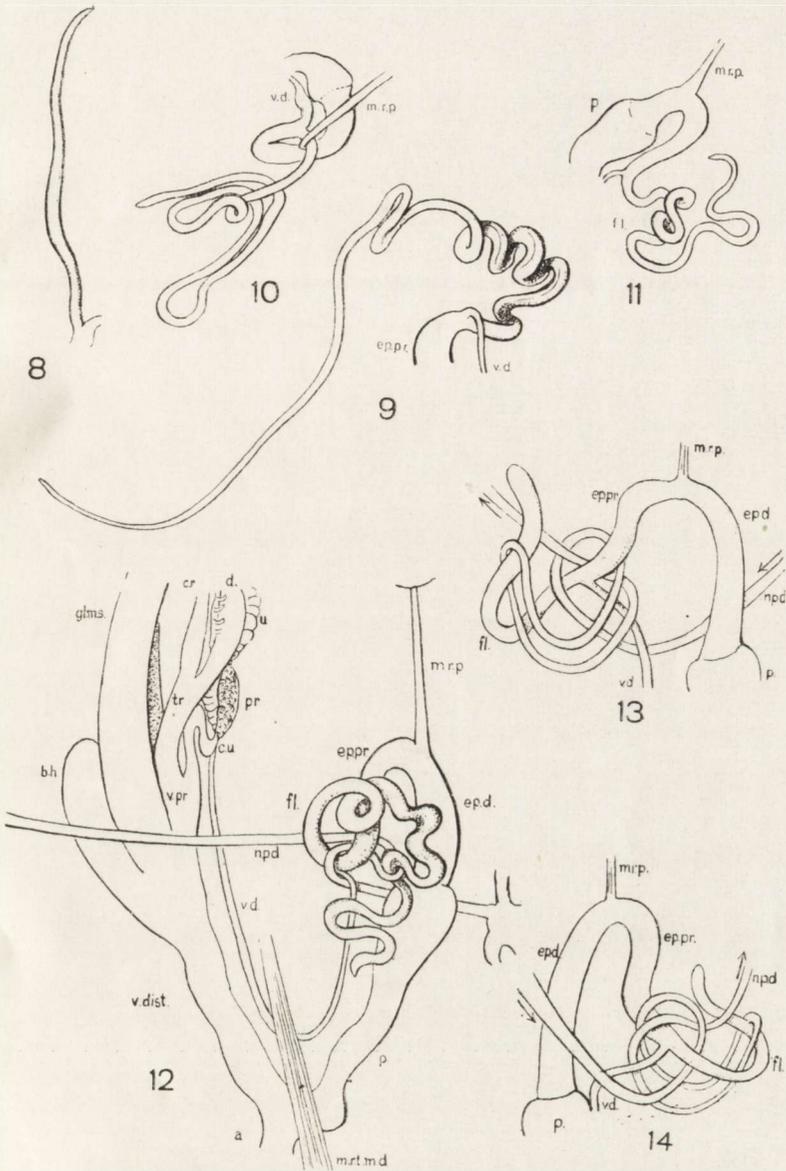
Podobne anomalie są możliwe przede wszystkim u ślimaków w związku z olbrzymią przesuwalnością narządów przy wciąganiu ciała w głąb muszli, dotyczy to zwłaszcza ślimaków trzonkoocznych (*Stylommatophora*). U tych ślimaków, w związku z wnicowalnością głowy, nawet pierścień nerwowy okołoprzełykowy zmienia swe położenie na przedustne. W celu wyświetlenia wielu anomalii konieczna jest analiza zachowania się narządów za życia, wzajemnego ich na siebie oddziaływania, co stanowiłoby temat topologii dynamicznej lub inaczej etologii narządów.
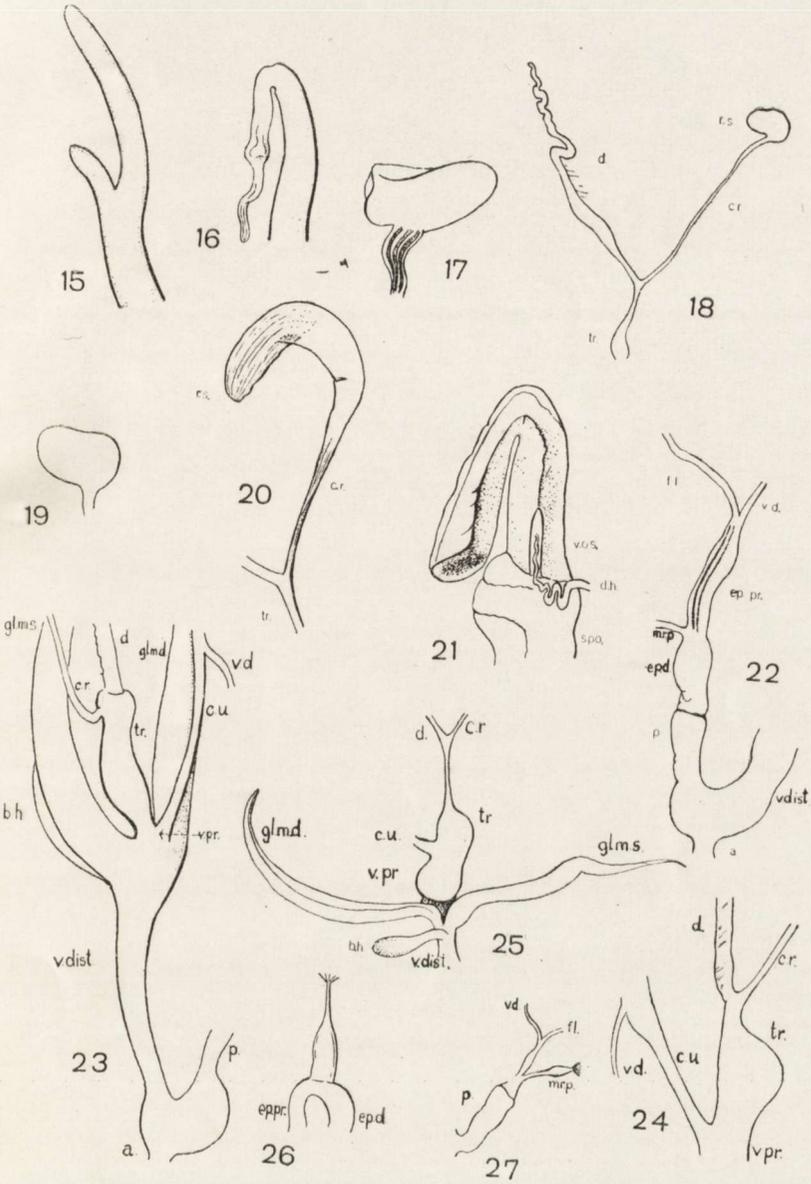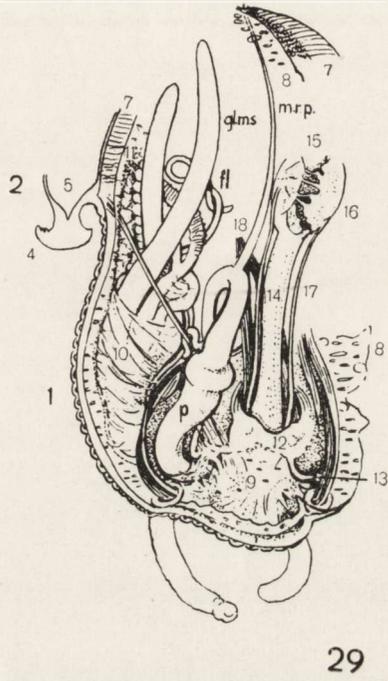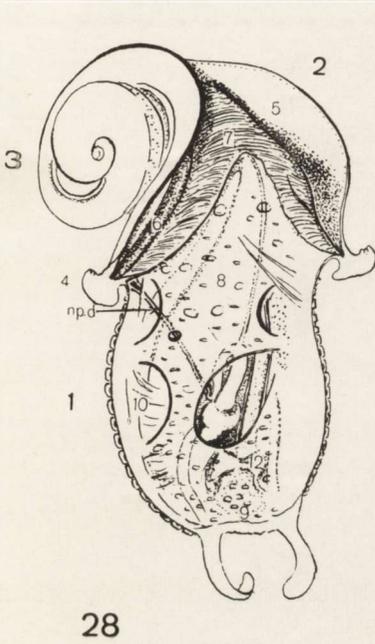

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Auctor del.
St. Feliksiak

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Auctor del.
St. Feliksiak

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