

# MORPHOLOGY OF THE NERVOUS SYSTEM OF CYPRIS.

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*With Plates III—VIII.*

## Introduction.

About three years ago, on publishing a "Preliminary Note on the Nervous System of the Genus *Cypris*," I promised to publish, in the near future, a histological monograph on the Ostracoda. This paper is intended as the first installment of such a monograph. In this communication it is intended to give a detailed discussion of the central and peripheral nervous systems of the *Cypridæ*.

Owing to its large size, *Cypris herricki* Turner has been selected as the type to study. To eliminate all mere size-variations, *Cyprinotus incongruens* Ramdohr has been used as a check. For the study of the central nervous system, these two species have been considered representative types of the *Cypridæ*; but, in studying the peripheral sense organs, use has been made of all accessible genera. These genera are: *Candona*, *Cyclocypris*, *Cypria*, *Cypris*, *Cyprinotus*, and *Cypridopsis*.

This paper being the embodiment of neurological investigations, any prolonged discussion of extra-neural systems would be out of place; yet, in order to facilitate a comprehensive discussion of the nervous system, a few terse histological statements upon the associated systems have been made.

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#### HISTORICAL RESUME.

Among the legions of histological monographs that recent instruments and improved technique have called forth, those on the neurology of the *Ostracoda* form an all but insignificant part. To the best of my knowledge the first to write on this subject was Leydig. He described the peculiar seta found on the second joint of the antenna and called it a sensory seta.

Then followed Dr. Carl Claus, who, in 1860 (1) discussed these same setæ and called them "*blasse Kolben und Cylinder*" or "*Leydische organe*." In 1865 (2) the same author discussed the eyes of *Cypridina*, laying special stress upon a simple eye

which occurs in front of the paired eyes, because he thought that the presence of that eye renders quite probable the hypothesis that the compound eyes of the *Cypridæ* are analogous to those of the *Cladocera*. According to Dr. Claus this median simple eye consists of three layers; 1st, an outer transparent lens; 2nd, an inner nervous layer; 3rd, an intermediate pigment layer. Both in form and position the outer portion of this eye resembles the lens of the *Heteropod* eye. The non-pigmented striated portion, into the substance of which nerve fibres penetrate, contains elongated cells. Later Dr. Claus (5) showed that in *Cypridina* the size and position of the paired eyes serve to differentiate the sexes. In the males, the paired eyes are almost in the middle of the shell, while the much larger, unpaired, median eye is imbedded in a swelling of the forehead. In 1891, Dr. C. Claus (6) stated a theory concerning the compound eyes of the *Ostracoda*.

Dr. Rehberg (9) also has contributed something to further this cause. Among other things he has minutely and accurately described the tip of the second foot of *Cypris*. In his eyes, this member is something more than a leg functioning as an ovipositor, for in its tip it bears a sensory organ which is probably auditory in function. In addition to this he has described, in the following manner, the sensory seta found on the third joint of the antenna. This sensory seta consists of: 1st, a chitin-surrounded proximal portion; 2nd, a short transparent middle-piece; 3rd, a granular knob-like distal portion. Its nerve enters through a hole in the chitinous exoskeleton.

Later Dr. Lang (8) summarized the accessible literature on the central nervous system of the *Ostracoda* in the following words: "The ventral chain of *Cythere*, which follows the brain and circum-oesophageal commissures, is said to consist of an infra-oesophageal ganglion and four subsequent ventral ganglia. The infra-oesophageal ganglion is said to show its composition out of two ganglia and to innervate the jaws, while the three subsequent ganglia give off nerves to the limbs, and the last ganglion, nerves to the most posterior divisions of the body and the genital apparatus. In contrast with the above, the ventral chain of *Halo-*

*cypris* appears much concentrated. It consists of an infra-oesophageal ganglion, with nerves to the jaws and maxillipeds, and a small ventral ganglion. Out of the latter arise two pairs of nerves, which probably innervate the musculature of the limbs and the abdomen.

Finally comes Wenzel Vávra who, in his late work (11), has devoted three pages to the discussion of the nervous system of the *Ostracoda*. In that work he makes the following statements: 1st, the central nervous system consists of a brain and a five-ganglionic ventral chain; 2nd, the optic and antennular nerves arise in the brain, but the antennary nerve arises in the pharyngeal collar; 3rd, in the five-ganglionic ventral chain which extends to the genital apparatus, the anterior three ganglia are closely approximated; 4th, from each ganglion a nerve passes to a pair of limbs and from the last ganglion a nerve passes to the genital apparatus; 5th, what Dr. Claus says about the structure of the eye is correct; 6th, in *Cypria* and *Cyclocypris* the eye is large and the pigment black, in *Candona* the eye is inconspicuous and the pigment reddish; 7th, in *Typhlocypris*, although the eye of the embryo is pigmented yet the eye of the adult is a degenerated, non-pigmented, sense organ; 8th, in *Notodromas* the three eyes are separated, but each of the paired eyes is connected, by means of a stalk, with the median eye, and each of these three large eyes receives a distinct nerve from the brain; 9th, the sensory seta of the second antenna, which is longest in *Typhlocypris*, *Candonopsis* and *Cyclocypris*, is an olfactory organ; 10th, the "blasse kolben" on the last segment of both the antennules and antennae are composed of two segments; 11th, on the fifth segment of the antenna of male and female specimens of *Notodromas* there occurs a special sensory seta; 12th, in *Candona*, *Candonopsis*, and *Cypria* the distal extremity of the fourth segment of the male antennae bears a characteristic seta.

#### TECHNIQUE.

For hardening and fixing *Ostracodes* alcoholic picro-sul-

phuric has proven the best fluid. This fluid is compounded in the following way :

70 per cent. alcohol,	. . . . .	100 vols.
Sulphuric acid, conc.	. . . . .	2 vols.
Picric acid, as much as will dissolve.		

For the above formula I am indebted to Dr. J. Playfair McMurrich, now of Ann Arbor. Since this fluid sometimes causes thin shells to curl, it is not so good for museum specimens as 70 per cent. alcohol ; but for histological work it is excellent. It does not injure the tissues, it penetrates chitin easily, and it fixes the cell structure. The living specimens were placed in this fluid and allowed to remain for at least twenty-four hours. Then after being washed in 70 per cent. alcohol until all the picric acid had been removed, they were either transferred to the stain or else, after being hardened and sectioned in the usual way, they were stained on the slide.

Among the numerous stains tried were: Kleinenberg's hæmatoxylin, Delafield's hæmatoxylin, Czokor's alum cochineal, borax carmine, eosin, etc., but none of these gave satisfactory results. Finally Ehrlich's hæmatoxylin and tincture of alum cochineal were tried. Both of these stains gave good results. In using both of these stains the specimens were stained in toto. When Ehrlich's hæmatoxylin was used, the specimens were overstained and then washed out with acidulated 70 per cent. alcohol ; but when the tincture of cochineal was used, after remaining in the stain for about twenty-four hours, the specimens were washed in 70 per cent. alcohol and then hardened and sectioned in the usual manner.

#### PRELIMINARY.

Although a lengthy discussion of the histology of extra-neural systems would be foreign to the purpose of this paper, yet, in order to facilitate a comprehensive description of the nervous system, it is thought best to give a brief description of the internal parts of the *Ostracoda*.

All previous writers to the contrary notwithstanding, the shell of the *Ostracoda* consists of three layers : an ectal layer,

which has been hardened by the deposition in it of calcium carbonate; an ental, thin, flexible layer; and an intermediate layer of connective tissue [fig. 1]. Where the shell is united to the body the ental layer is absent [fig. 1, 6]. The connective tissue in the shell is a continuation of the connective tissue of the body. Most of the space between the ental and ectal layers not occupied by the connective tissue, is filled by the gonads and lateral evaginations of the mid-gut.

The body proper consists of two regions, a broad cephalothorax and a narrower abdomen. The abdomen is movable on the cephalothorax [fig. 9]. Seven of the eight pairs of appendages arise from the cephalothorax, while the remaining pair (the abdominal rami) arises from the caudal extremity of the abdomen.

From near the dorsal extremity of the cephalic margin of this creature arise the antennules and from a little below the middle of the same margin arise the antennae. Passing caudad, from the ventral margin arise, in quick succession, the mandibles, 1st maxillae, 2nd maxillae, 1st leg, 2nd leg.

The mouth, which lies between the mandibles, is bordered by an unpaired upper and by paired lower lips. These, together with the mandibles, not only triturate the food, but serve also as the locus of three pairs of sense organs [fig. 16]. The short oesophagus, which is bordered with large cells [fig. 9c], extends almost vertically dorsad into the fore-stomach [fig. 9]. In the walls of this grinding apparatus cells can be seen. Now follows the stomach, from the walls of which lateral evaginations project into the shell. The wall of this stomach is composed of a single layer of columnar cells [fig. 37, 41]. The dorsal portion of the stomach is quite large, extending from the cephalic extremity of the cephalothorax to the beginning of the abdomen [fig. 9, 16]. The intestine extends through the abdomen to the dorsally located anus, which is situated near the abdominal rami [fig. 9].

The ovaries lie between the shell layers. After entering the body on the dorsal side just caudad of the abdomen and thence passing ventrad into the abdomen, the sexual ducts pass

ventro-meso-caudad to the median unpaired vagina, which lies on the ventral side near the abdominal rami. The walls of the abdominal portions of the sexual ducts are quite glandular. They secrete the chorion of the egg.

Near the ventral side of the body there is a broad chitinous exoskeleton [fig. 1, 5], to which the muscles of the extremities are attached.

Surrounding all the organs of the body (nervous system included) we find a mesenchyme-like connective tissue. This connective tissue consists of membranous and fibrous cells, among which are scattered larger and denser irregularly shaped cells [fig. 1, 11].

It is important that no one should suppose that the above description is intended as an exhaustive histological study of the *Ostracoda*. Although it contains some points that have not yet been brought out by other investigators, nevertheless, it is given merely to facilitate an intelligent description of the nervous system and its relation to the extra-neural systems.

#### **The Central Nervous System.**

The central nervous system of *Cypris*, like that of the higher crustacea (*Malacostraca*) is composed of a supra-oesophageal ganglion which is united by a pharyngeal collar to a multi-ganglionic ventral chain. This is true, not only of *Cypris*, but also of *Cypridopsis*, *Cyclocypris* and *Candona*. When we recall that Dr. Lang states that in *Cythere* and *Halocypris* this is also the case, we have grounds for believing that in all *Ostracoda* the central nervous system consists of a supra-oesophageal ganglion which is united to a ventral chain by a pharyngeal collar.

*Supra-oesophageal ganglion.*—This ganglion lies about half way between the dorsal and ventral surfaces of the body and between the oesophagus and the cephalic border of the body. It lies just below the place where the oesophagus enters the mid-gut. In my preliminary paper the statement was made that this ganglion was much nearer to the dorsal than to the ventral surface. This was a misprint; the ganglion usually lies nearer the ventral than the dorsal surface. This is a compound gan-

glion. Although small, yet this supra-oesophageal ganglion is probably compounded out of seven distinct ganglia. These problematic ganglia are: three ganglia that have fused to form the unpaired optic ganglion, two antennular ganglia, and two antennary ganglia.

The optic ganglion is located in the roof (dorso-cephalic portion) of the supra-oesophageal ganglion. Although in the adult it is a median unpaired structure, yet its histology seems to indicate that it is a triune structure. The optic nerve arises from the apex of this ganglion. In *Cypris* and the allied forms examined by me, the optic nerve is a single unpaired nerve; but in *Notodromas*, according to Wenzel Vávra, three optic nerves arise from the brain. The fact that in *Notodromas* three nerves arise from the optic ganglion lends support to the view that this is a triune ganglion. However, we must look to embryology for a final settlement of this question, and the necessary data are not at hand. Wenzel Vávra has called this portion of the supraoesophageal ganglion from which the optic nerve arises the fore-brain.

The paired antennular ganglia occupy the lateral portion of the supra-oesophageal ganglion [fig. 10]. Wenzel Vávra has called this portion of this ganglion the mid-brain. From the dorsal portion of each side of this ganglion, arises a nerve.

Further ventrad, but nearer the meson, in the lateral portion of the supra-oesophageal ganglion lie the paired antennary ganglia [fig. 10]. A portion of this ganglion lies in the pharyngeal collar. Wenzel Vávra has called this portion of the ganglion the hind brain.

The supra-oesophageal ganglion is connected, by means of a pair of circum-oesophageal commissures, with a sub-oesophageal ganglion [fig. 16, 42]. These commissures pass obliquely backwards and downwards (ventro-caudad) from the lateral portion of the supra-oesophageal ganglion to the corresponding portions of the sub-oesophageal ganglion. These two commissures constitute the pharyngeal collar. This collar is not merely a commissure but it is also the locus of a nerve centre. All along



its front (cephalic) border extends a chain of ganglionic cells. The chain of cells is a portion of the antennary ganglion [fig. 3].

As in all invertebrate nervous systems, so here, the central nervous system is composed of two things: nerve cells and neuroglia ("Punksubstanz" of Leydig, "Marksubstanz" of Dietels and Rawitz, "central Nervenetz" of Bellonci and Haller). In the supra-oesophageal ganglia of *Cypris* the nerve cells are aggregated in the dorsal, cephalic, ventral and lateral portions of the periphery, while the neuroglia is central.

*Ventral Nerve Cord.*—In his comparative anatomy, Professor Lang has said: "The ventral cord of *Cythere* which follows the brain and oesophageal commissures is said to consist of an infra-oesophageal ganglion and four subsequent ventral ganglia. The infra-oesophageal ganglion is said to show its composition out of two ganglia and to innervate the jaws, while the three subsequent ganglia give off nerves to the limbs, and the last ganglion nerves to the most posterior division of the body and genital apparatus. In contrast with the above, the ventral chain of *Halocypris* appears much concentrated. It consists of an infra-oesophageal ganglion, with nerves to the jaws and maxillipeds, and a small ventral ganglion. Out of the latter arise two pairs of nerves, which probably innervate the musculature of the limbs and abdomen."

Morphologically the ventral chain of *Cypris* is intermediate between these two extremes. It is more concentrated than that of *Cythere* but not quite so compact as that of *Halocypris*. In this case the ventral chain consists of an infra-oesophageal ganglion and two subsequent ventral ganglia. All of these nerve ganglia are connected, not only by two longitudinal commissures, but also by straggling chains of nerve cells [fig. 32, 42]. To repeat, the ventral chain of *Cypris* is composed of three pairs of ganglia, which are united by commissural fibres and nerve cells.

Now Wenzel Vávra has recently stated that the ventral chain of *Cypris* is composed of five ganglia. At first blush these two views seem to be irreconcilable. However, when critically compared, the two views are not so antagonistic as they

seem. Dr. Wenzel Vávra confesses that “*Die ersten drei Ganglien stehen sehr gedrängt.*” Although in the adult the sub-oesophageal ganglion of *Cypris* is an indivisible unit, yet my investigations lead me to believe that it has been compounded out of at least three pairs of distinct ganglia. Now if by saying that the first three ganglia are closely compacted Wenzel Vávra means that they are compacted sufficiently to form a triune ganglion then our views harmonize.

From this compound ganglion arise the following five pairs of nerves: nerve of the upper lip, mandibular nerve, nerve of the lower lip, thoracic nerve.

The two halves of this ganglion are connected by three transverse commissures.

The first pair of ganglia behind (caudad of) the sub-oesophageal ganglion gives off a pair of nerves to the second maxillae.

From the last ganglion arise two pairs of leg nerves and one unpaired abdominal nerve.

In the region of the sub-oesophageal ganglion the ventral chain lies above (dorsad of) the endoskeleton, while back of that region it lies below (ventrad of) the endoskeleton.

In the region of the sub-oesophageal ganglion the nerve cells are confined to the ventral and lateral surfaces of the ganglion, while in the rest of the chain, the nerve cells occupy all of the periphery and also the mesal plane.

*Root ganglia.*—At the origin of certain nerves there is a mass of ganglion cells. The ganglion is often quite intimately united with the central nerve chain.

#### NERVES.

The principal nerves of *Cypris* are: the optic, the antennular, the antennary, the labial, the mandibular, the labral, the two maxillary nerves, the thoracic, the two leg nerves and the abdominal nerve.

*Optic Nerve.*—The optic nerve arises from the apex of the optic ganglion, which is also the apex of the brain. In *Cypris*, *Cyprinotus* and allied forms examined by me, this is a median unpaired nerve. At a distance from the brain which varies

in different species, this nerve splits into three branches—one for each of the divisions of the median tripartite eye. Passing upwards (dorsad) between the mid-gut and the cephalic border of the body these branches pass to the compound eye, which lies near the dorsal surface of the body. Indeed, this median eye lies against the shell, vertically above the supra-oesophageal ganglion [fig. 2, 9, 10 o, 42 o].

In *Notodromas*, according to Wenzel Vávra, there are three optic nerves arising from the apex of the brain [fig. 30]. Here also we find that the three parts of the eye are widely separated [fig. 30]. It does not require a very active imagination to conclude that simultaneously with the divarication of the component parts of the triune eye there went a longitudinal tripartite splitting of the entire optic nerve.

*Antennulary Nerves.*—The paired antennulary nerves arise one from near each lateral surface of the apex of the supra-oesophageal ganglion [fig. 10, 42]. After leaving this ganglion the nerve passes in a caudally convex curve upwards (dorsad), between the mid-gut and the cephalic border of the body, to the corresponding ganglion. There is no root ganglion at the base of this nerve.

*Antennary Nerves.*—Where each circum-oesophageal commissure leaves the supra-oesophageal ganglion arises an antennary nerve [fig. 3]. This nerve receives its fibres, not only from the brain, but also from a ganglion that extends in a straggling manner along the pharyngeal collar [fig. 2, 8].

*Labial Nerves.*—The labial nerve or nerve of the upper lip arises in the cephalic portion of the sub-oesophageal ganglion. Instead of leaving the central nerve chain immediately, this nerve passes upwards (cephalo-dorsad) into the pharyngeal collar and thence forward (cephalad) to the upper lip [fig. 3, 16, 42]. There is a large root ganglion at the origin of this nerve [fig. 3]. The labial nerve has two main branches. One branch innervates a pear-shaped sense organ situated in the front part of the body below [ventrad of] the base of the antenna, while the other innervates a harp-shaped sense organ located in the lower [ventral] portion of the upper lip [fig. 16].

*Mandibular Nerves.*—From each lateral portion of the sub-oesophageal ganglion, just below (ventro-caudad of) the place of fusion of the pharyngeal collar with this ganglion, a mandibular nerve leaves the nervous chain. Just after entering the mandible this nerve branches, one branch passing upwards (cephalo-dorsad) to the mandibular muscles, while the other passes downward (cephalo-ventrad) to a sense organ at the base of the mandibular teeth [fig. 7 *mx*, 40 *md*]. There is no root ganglion to this nerve.

*Labral Nerves.*—From each lateral portion of the ventral aspect of this same ganglion, a short distance behind (caudad of) the origin of the mandibular nerve, arises a labral nerve. Thence the nerve passes, in a caudally convex curve, downward (ventrad) to the lower lips [fig. 32, 42]. The chief function of this nerve is to innervate a harp-shaped sense organ located in the lower lip [fig. 16 *D*]. This nerve has a root ganglion.

*First Maxillary Nerves.*—A short distance caudad of the origin of the mandibular nerve, a maxillary nerve leaves each side of this same ganglion. This is the first maxillary nerve. It passes latero-caudad to the first maxilla [fig. 7 *mx*<sup>2</sup>, 42].

*Thoracic Nerves.*—All of the four pairs of nerves just described arise from the ventral side of the sub-oesophageal ganglion. We now come to a pair of nerves that arise from the dorsal aspect of the same ganglion. These are what I beg permission to call the thoracic nerves. These nerves arise from the lateral portion of the dorsal aspect of this ganglion just back of (caudad of) the origin of the first maxillary nerve. Arising as it does from the dorsal aspect of the ventral chain, the root of this nerve lies immediately beneath the endoskeleton. This nerve passes obliquely upwards and backwards (dorso-latero-caudad), and, after branching, innervates the abductor muscles of the shell [fig. 32 *T*, 42 *T*].

To the best of the writer's knowledge, neither this nerve nor the labial nor the labral nerves have been described by any previous writer on the *Ostracoda*.

From the cephalic extremity of the ventral nerve chain to the roots of the thoracic nerve the nerve cells are confined to

the ventral and ventro-lateral surfaces of the cord. Behind (caudad of) the roots the nerve cells entirely surround the ganglia and occupy the mesal plane as well.

Within the ventral chain, beneath the origin of the thoracic nerves, there is a pair of ellipsoidal cavities. These might properly be called thoracic ventricles.

*Second Maxillary Nerves.*—This nerve arises from the lateral aspect of the first ganglion behind (caudad of) the suboesophageal ganglion.

*Leg Nerves.*—From the last ventral ganglion of *Cypris* arise two paired nerves and one unpaired nerve. The paired nerves innervate the legs, while the unpaired nerve passes into the abdomen. The nerve of the first leg passes immediately latero-ventrad to the first leg; but the nerve of the second leg passes backwards (caudad) along with the abdominal nerve, a short distance before passing to the second leg [fig. 42].

*Abdominal Nerve.*—As has been stated, from the caudal portion of the last ventral ganglion a large unpaired median nerve passes upwards and backward (dorso-caudad) into the abdomen. This is the abdominal nerve. After entering the abdomen, this nerve becomes more and more attenuated, owing to the fact that it gives off fibres to the reproductive system [fig. 32 an, 42 Ab].

The above descriptions of the principal nerves of *Cypris* do not agree either with the descriptions of the few men who have written on this subjects or with the statements made in my preliminary paper. I cannot answer for the other men, but my error was in mistaking the labial nerve for the mandibular nerve. If you but recall the compactness of the anterior (cephalic) region of the body of *Cypris*, you can see how easy it would be to make such a mistake. However, I now have at hand several series which demonstrate, beyond the shadow of a doubt, that the nerves arise as stated in this paper.

No doubt it is this same compactness of the cephalic portion of the body of *Cypris* which is responsible for the non-discovery of the labial, labral, and thoracic nerves by other observers.

Careful search has not yet revealed a sympathetic nervous system.

#### **Sense Organs.**

*Compound Eye.*—The most conspicuous sense organ of the genus *Cypris* is the compound eye. When viewed from above, this eye usually resembles a quadrilateral pigment spot [fig. 36]. In *Cyclocypris* and *Cypria*, this eye is quite large and the pigment is intensely black; in *Cypris* and *Cyprinotus*, the eye is of medium size; in *Candona*, the eye is inconspicuous and the pigment is reddish; while in *Typhlocypris*, according to Wenzel Vavra, there is no eye in the adult. The eye of the embryonic *Typhlocypris*, according to the same author, becomes metamorphosed into an inconspicuous non-optical sense organ.

This eye is a triune structure. It consists of a median and two lateral portions, each of which is supplied with a lens [fig. 2]. The lens of the median portion is on the front aspect [fig. 36], while the lenses of the lateral portions are on the sides [fig. 2, 36]. This median compound eye, which lies in about the same vertical transverse plane as the supra-oesophageal ganglion, is located where the dorsal border of the animal is united to the dorsal portion of the shell. Hence there are two planes, at right angles to each other, that pass through both the compound eye and the supra-oesophageal ganglion. These two planes are the mesal and a transverse plane.

Histologically there are five parts to this compound eye: lens, retina, pigment, superficial epithelium, nerve [fig. 2]. Corresponding to each of the three divisions of the eye we have a retina and a lens [fig. 2] and a nerve. The pigment is deposited between and around the retina. The retinas are cellular structures, the cells being arranged with their longest axis perpendicular to the outer surface of the retina [fig. 2]. Each retina is supplied with a lens, and these are always on the outer surface. In the lateral portions these lenses are on the side, while in the median the lens is on the front aspect [fig. 36]. The median portion lies lower than the lateral. Excepting the central portions of the lenses, all of the surface of the eye, as well as the space between the retinas, is pigmented [fig. 2, 36].

In *Cypris herricki* Turner the nerve fibres are united to the outer (peripheral) ends of the retinal cells. This agrees with what Dr. Claus found to be the state of things in the eyes of the *Copepoda*, *Clodocera* and *Ostracoda* examined by him [7].

There is a striking resemblance between the triune eyes of the *Ostracoda* and those of the *Copepoda*. In describing the compound eye of *Calanella mediterranea*, Dr. Grenacher remarks "Each eye is composed of a pigment cup and a strongly refractive transparent 'lens' laid in and on it. The term lens is, however, not applicable. It is composed of several cells, each of which is connected, whether at its outer or inner side is not yet certain, with a fibre of the optic nerve, and must therefore be considered as a retinal cell." Since the superficial resemblance between the *Ostracod* eye and the *Copepod* eye is so great, one is apt to conclude that the above words of Dr. Grenacher might be applied to the *Ostracod* eye. Against such an assumption I desire to enter a most emphatic protest. As stated above, in the eye of *Cypris* we find both retinal cells and lenses, and the two structures are histologically quite distinct. On the outside of the eye, covering lens and all, there is a nucleated epithelial layer [fig. 2].

Since the publication of the paper<sup>1</sup> in which O. Bütschli attempts to show how the lateral eyes of the vertebrates may have been derived from the median tripartite eye of *Salpa*, this tripartite eye, which is of almost universal occurrence among the entomostraca, becomes enhanced in interest. One at once begins to speculate on the possibility of this median triune eye of the entomostraca becoming transformed into the lateral eyes of the higher crustacea. Indeed, in his late work, Dr. Claus<sup>2</sup> has already stated that the lateral eyes of the Corycæidæ are laterally rotated portions of the median eyes. In this connection it may be of interest to quote a portion of Dr. Giesbeck's

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<sup>1</sup> Einige Bemerkungen ueber die Augen der Salpen, *Zool. Anz.*, XV., Jahrg. 349.

<sup>2</sup> Ueber die feineren Bau des Medianauges der Crustaceen. *Anzeiger Akad. Wien*. 1891, pp. 124-127. Ref. in *Zool. Jahrsbericht* für 1891, Arthropoda, 29.

résumé of Dr. Claus' paper: "Die Sietenaugen der Corycæiden sind abgedrückte Theile des Medienauges, diejenigen der Pontelliden entsprechen dagegen dem zusammengesetzten Arthropodenaugen, während ihr ventrales Auge ein dreitheliges Medienauge dürfte ebenso wie die beiden frontalen Sinnesorgane der ersten anlage nach auf Zellengruppen der Scheitelplatte, vor der aus wir, . . . die obern Schlundganglien der Gliederthiere abzuleiten haben, zu beziehen sein; die drei Augentheile sind vielleicht mit den drei Punktaugen an der Scheitenplatte von Annelidenlarven phylogenetisch in Beziehung zu bringen; die Lage ihrer Pigmentzellen und ihre inverse Form werden auf eine convergent nach einem Punkte gerichtete Drehung zurückgeführt, welche mit dem Herabrücken des Organs in die Tiefe verbunden war; die Secret und Cornealinsen werden von Hypodermiszellen abgeschieden, ähnlich wie Krystallkegel und Corneafacette des zusammengesetzten auges; das Auge besitzt eine mesodermal Hülle, die sich in das neurilemm des Opticus fortsetzt; Die function des Medienauges war ursprünglich das Thier bezüglich der Richtung der Lichtquelle zu orientiren; bei compliciterem Bau, schon bei den Calaniden, hat es wahrscheinlich auch die Fähigkeit einer beschränkten Bildperception. Am Medianauge der Malakostraken-larven ist der ventral Becher bisher nicht beobachtet, aber wohl auch vorhanden."

A comparative study of the eyes of the *Ostracoda* lends support to the view held by Dr. Claus. In *Typhlocypris* there is practically no eye, in *Candona* the triune eye is small and inconspicuous, in *Cypris* it is somewhat larger, in *Cypria* and *Cyclocypris* it is large and conspicuous, while in *Notodromas* the paired portions of the compound eyes are so far separated that they look like a pair of simple eyes united to a median eye by means of a stalk [fig. 30].

*Pear-shaped Sense Organs.*—In the cephalic portion of the body, a short distance above (dorsad of) the upper lip, there is a pair of peculiar pear-shaped sense organs [fig. 16, P]. To the best of my knowledge this organ has been overlooked by all other writers on the histology of *Cypris*. When viewed



from the side, this is a pear-shaped organ, with its base directed outwards (ectad) and its apex inwards (entad).

In hæmatoxylin preparations, in the base of this pear-shaped organ, there is a densely stained circular disc. In *Cyprinotus incongruens* (Ramdohr) this disc is 12.92 micromillimeters in diameter [fig. 34].

The apex of this organ is surrounded by a ganglion of nerve cells [fig. 34].

The length of this organ varies in different species. In a general way, the larger the species the larger this sense organ. In *Cyprinotus incongruens* Ramdohr, which is about 1.35 millimeters in length, this organ is 35.53 micromillimeters long and 32.3 micromillimeters wide; while in *Cypris herricki* Turner, which is about three millimeters in length, this organ is 71.06 micromillimeters long and 48.45 micromillimeters wide. In other words, in *Cypris herricki*, which is about twice as long as *Cyprinotus incongruens*, the pear-shaped sense organ is about twice as long as the corresponding organ of *Cyprinotus incongruens*.

This organ is situated a short distance below the base of the antenna and close to the outer wall of the body. The broad base lies in contact with the body wall [fig. 16, P].

Since this organ is much larger in *Cypris herricki* Turner than in any other form known to me, the following histological study of the organ is based upon sections of that species.

From a histological standpoint, this pear-shaped organ is composed of a neuroglia-like matrix, in which are two transverse rows of nuclei. One of these rows of large nuclei is located about half way between the base and the apex, while the other row is situated near the apex. Near the base of this organ the matrix is denser than it is elsewhere [fig. 31]. The organ is surrounded by a nucleated epithelium.

This organ is innervated by a branch of the labial nerve [fig. 16].

There is a pair of these organs, but they are so closely approximated that a hasty glance might not reveal both members of the pair.

As to the function of this organ, I have no definite proof; but I am inclined to think that it functions as an eye. In *Cypridina*, besides the usual compound eye, Dr. Claus has described a median, unpaired simple eye. Now I am inclined to think that this pear-shaped organ of *Cypris* is homologous with the unpaired simple eye of *Cypridina*. At first blush, there are two facts that seem to militate against such an assumption 1st, the median eye described by Claus is unpaired, while this pear-shaped organ is distinctly paired; 2nd, the median eye described by Dr. Claus is near to the compound eye, while this pear-shaped organ is far removed from the compound eye. In spite of these opposing facts, there are several weighty considerations which lead me to hold to the statements made above. 1st, *Cypridina* is much less compact than *Cypris*; 2nd, in *Cypridina* the compound eye and the simple eye are situated near the centre of the shell; 3rd, in *Cypridina* the parts of the compound eye are widely separated, while in *Cypris* they are closely approximated. May it not be that in the ancestors of *Cypris* the compound and simple eyes lie near each other and near the middle of the shell, as it now is in *Cypridina*? May it not be that when the compound eye migrated towards the dorsal surface, the simple eye migrated towards the ventral? And when we remember that in histology this pear-shaped organ resembles the invertebrate simple eye, we have, I think, sufficient grounds for calling this a simple eye. To be sure this pear-shaped organ is one of a pair while the simple eye of *Cypridina* is unpaired; but in this day, the phenomena of transformations due to fission and to fusion are too well known for this difference to merit even a passing consideration. The settlement of this question, however, must be left to embryology.

*Sense Organs of the Mouth.*—In this same region of the body, there is another set of hitherto undescribed sense organs. From the caudal border of the upper lip, from the cephalic border of the lower lip, and from between the teeth of the mandible, arise numerous hairs [fig. 16]. These hairs are sometimes plumose [fig. 35]. At the base of each of these sets of hairs there is a similar sense organ [fig. 16, *B, C, D*]. Each

of these organs is composed of oblong nucleated cells, which are arranged with their longest axes perpendicular to the hirsute surface [fig. 4]. The organs in the upper lip are innervated by a branch of the labial nerve, those in the mandible by a branch of the mandibular nerve and those in the lower lip, by the labral nerve [fig. 16]. Thus we have, surrounding the mouth, three pairs of similar sense organs.

I have no definite proof as to the function of this set of organs; but, since they surround the mouth, they probably function as food discriminators. Whether this discriminating sense is one of touch or taste I am not prepared to state.

*Auditory Organ.*—After describing rather minutely what he considers to be a sense organ located at the tip of the second foot, Dr. Rehberg expresses his belief that that organ is an ear. Now I agree with Dr. Rehberg in believing that there is a sense organ located in the tip of the second foot; but I think that its function is not auditory but tactile. I do not think that the structure of the tip of the second foot warrants Dr. Rehberg's assumption. And beside, at the base each of the antennules I have found what I consider the auditory organ of *Cypris* [fig. 16, *E*]. This is an ellipsoidal body in the centre of which there is a sac. The space between the outer wall of the ellipsoid and the sac is occupied by a single layer of columnar cells. The nuclei of these cells are located near the periphery. These cells are best seen in transverse sections of the organ [fig. 33]. Often the cells contain large vacuoles [fig. 29]. Within the sac there is a small spherical body which I take to be an otolith [fig. 29]. Since in most of my preparations this sac has been filled with a deposit of the stain used [fig. 33] I am not sure that this spherical body that I find in other preparations is an otolith or merely a bit of stain.

As to the innervation of this organ, I have no definite knowledge. However, the antennary nerve is so intimately associated with this organ [fig. 29*a*], that I am inclined to believe that that nerve innervates the auditory organ.

There are two patent facts that lead me to hold that this is an auditory organ: 1st, in histology it resembles an otocyst;

2nd, in location it resembles the auditory organ of the higher crustacea (*Malacostraca*).

*Olfactory Organs.*—On the third joint of the antenna of all the fresh-water *Ostracoda*, there exists a peculiar seta which all writers have called an olfactory organ. As has been remarked by other writers on this subject, this organ consists of the following three segments: basal piece, middle piece, end piece [fig. 15]. In some cases the basal piece has been subdivided into two pieces [fig. 17], while in others no middle piece can be distinguished [fig. 14]. The nerve enters this organ through a perforation in its base. Thence it extends along the axis of this portion until it reaches the base of the middle-piece, where it terminates in a small knob [fig. 15, 17]. In *Cypris herricki* Turner this terminal knob is about three micromillimeters in diameter.

The usual width of this organ is about three micro-millimeters. However, in *Cypria exculpta* Fischer it is only about two micromillimeters wide, while in *Cypris herricki* Turner it is about eight eight micromillimeters wide. In length the organ varies from about 85 micromillimeters in *Cypris herricki* Turner to about 29 micromillimeters in *Cypria inequivalva* Turner. In the same genera the length of the organ varies directly with the length of the body of the specimen—the longer the body the longer the organ. In those genera in which the swimming setae of the antenna are greatly developed (*Cyclocypris*, *Cypria*) this olfactory organ is relatively larger than in those genera in which the natatory setæ of the antenna are more feebly developed (*Cypris*, *Candona*).

In the same species the tip of this organ may be either blunt or pointed. Indeed, on one antenna of a specimen the apex of this organ may be blunt, while on the other the tip may be pointed.

The shape of this organ varies in different species. A consultation of figures 12-15, 17-19 and 21-22 will give a better idea of these various shapes than could any number of words.

The following table has been compiled in order to facilitate a comparative study of this olfactory organ:

Table showing the relative size of Leydig's organ in a few Cypridæ.	MICROMILLIMETERS				
	Basal Piece	Middle Piece	End Piece	Total length of Leydig's organ	Length of Specimen
NAME OF SPECIMEN.					
<i>Candona acuminata</i> (Fischer) ♀	13	10	20	43	1250
<i>Candona crogmani</i> Turner ♀, type	19	6	23	48	1520
“ “ “ exception	16	—	19	35	
“ “ “ ♂	13	6	26	45	1520
<i>Candona delawarensis</i> Turner, ♀	10	3	23	36	950
“ “ “ ♂	14	5	20	39	
<i>Candona fabæformis</i> (Fischer) ♀	12	6	19	37	1030
<i>Cyclocypris levis</i> (O. F. Müller)	29	6	32	67	570
<i>Cypria exculpta</i> (Fischer)	23	3	16	42	640
<i>Cypria inequivalea</i> Turner, ♀	13	10	6	29	520
<i>Cypria ophthalmica</i> (Jurine)	10	10	16	36	580
<i>Cypridopsis vidua</i> (O. F. Müller)	19	—	16	35	700
<i>Cyprinotus burlingtonensis</i> , Turner, ♀	26	10	29	65	1600
<i>Cyprinotus crena</i> , Turner, ♀	19	8	23	40	1230
<i>Cyprinotus incongruens</i> (Ramdohr)	39	6	16	61	1350
<i>Cypris fuscata</i> (Fischer)	36	7	20	63	1500
<i>Cypris herricki</i> Turner ♀	32	4	49	85	3000

*Sensory Setæ*.—In addition to the sense organs already described there are several types of sensory setæ that deserve at least a passing notice. Not having been able to trace a nerve into any of these setæ, I have given but a brief notice of them.

At the tip of the antennules and antennae of all the *Cypridæ* there occurs a two-segmented sensory seta [fig. 20]. This seta is longest in *Taphlocypris*, where it is as long as the terminal claw. In *Condona fabæformis* Fischer this seta is 48 micromillimeters long. In this case, the terminal segment is ten micromillimeters long. Owing to its small size and to the number and size of the associated claws and filaments, this organ is a very difficult object to study.

At the extremity of the fourth segment of the antenna of *Notodromas* there is a peculiar seta with a funnel-shaped tip [fig. 28].

At the tip of the fourth segment of the antenna of the male members of the genera *Candona*, *Candonopsis* and *Cypris* there is a peculiar two-jointed seta [fig. 24-27]. Dr. Wenzel Vavra

considers this a rudimentary organ. Its morphology varies in different species. By Dr. Wenzel Vávra the variations that we meet with in this organ are considered to be of taxonomic value.

On the tip of the third and fourth segments of the mandibular palp of certain *Cypridæ*, there occurs a short dagger-shaped setose seta [fig. 23 D.S.]. This seta was first described in the "Entomostraca of Minnesota."<sup>1</sup> This seta occurs in: *Candona crogmani* Turner, *Candona delawarensis* Turner, *Cypridopsis vidua* O. F. Müller, *Cypris herricki* Turner, *Cyprinotus burlingtonensis* Turner.

#### Recapitulation.

1. The nervous system of *Cypris* consists of a supra-oesophageal ganglion, which is connected to a ventral chain by a pharyngeal collar.

2. The ventral chain consists of an infra-oesophageal and two subsequent ganglia. The infra-oesophageal ganglion has probably been compounded out of at least three pairs of ganglia.

3. From the supra-oesophageal ganglion arise one unpaired and two paired nerves. These nerves are: the optic, the antennular, the antennary. The antennary nerve receives a portion of its fibres from a ganglion that lies within the pharyngeal collar. The nerve itself arises from the point where the collar joins the supra-oesophageal ganglion.

4. From the infra-oesophageal ganglion arise five pairs of nerves. Four of these pairs arise from the ventral portion of the ganglion, while the other arises from the dorsal. The four that arise from the ventral half are: the labial, the mandibular, the labral, and the first maxillary. The one that arises from the dorsal portion is the thoracic nerve.

5. The labial nerve passes forward into the pharyngeal collar before leaving the central nerve chain.

6. The thoracic nerve innervates the shell muscles.

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<sup>1</sup> C. L. Herrick and C. H. Turner. Synopsis of the Entomostraca of Minnesota with descriptions of related species comprising all known forms from the United States included in the orders Copepoda, Cladocera, Ostracoda. *St. Paul, Minn.*, 1895.

7. The 2nd maxillary nerve arises from the first ganglion back of the infra-oesophageal ganglion.

8. From the last thoracic ganglion arise one unpaired and two paired nerves. The paired nerves are the leg nerves; the unpaired nerve is the abdominal nerve. The abdominal nerve innervates the genital apparatus.

9. There is a median compound triune eye. The eye is situated near the dorsal surface. Each of the three divisions of this eye is supplied with retinal cells and a lens. The nerve enters the outer ends of the retinal cells. In most of the fresh-water *Cypridæ* the component parts of this eye are closely approximated. In *Notodromas*, on the contrary, the three parts are widely separated.

10. In most of the fresh-water *Cypridæ* the optic nerve is a median unpaired structure, which splits into three branches. In *Notodromas*, however, there are three distinct optic nerves.

11. In the front part of the body, between the base of the antennae and the upper lip, there is a pair of pear-shaped sensory organs. These are probably simple eyes. This organ is innervated by a branch of the labial nerve.

12. At the base of the antennule there is an auditory organ.

13. Bordering the mouth there are three pairs of similar sense organs. These organs lie in the upper lip, at the base of the mandibular teeth, and in the lower lip. They are innervated by branches of the following nerves: labial, mandibular, and labral.

14. On the third segment of the second antenna there is the so-called olfactory organ. This organ consists of three segments; the basal, the middle, and the end piece. The nerve enters the basal portion and extends to the base of the middle piece, where it terminates in a knob-like swelling.

15. In addition to the above sense organs there are several types of sensory setae.

## EXPLANATION OF PLATES.

Excepting where otherwise stated, the plates were all made from camera drawings made by the writer.

## PLATE III.

*Fig. 1.* *Cypris herricki* Turner, transverse section of body in the region of the posterior portion of the mid-gut. A, endoskeleton; n, nerve chain.

*Fig. 2.* *Do., do.*, transverse section of median eye.

*Fig. 3.* *Do., do.*, longitudinal section of circum-oesophageal commissure. a<sup>2</sup>, antennary nerve; md, mandibular nerve.

*Fig. 4.* *Do., do.*, transverse section of the sense organ of lower lip.

*Fig. 5.* Transverse section of the endoskeleton.

*Fig. 6.* *Do., do.*, transverse section of the body in the region of the lateral diverticles of the mid-gut.

## PLATE IV.

*Fig. 7.* *Cypris herricki* Turner, longitudinal section through the sub-oesophageal ganglion. Mx', mandibular nerve; mx'', 1st maxillary nerve.

*Fig. 8.* *Do., do.*, longitudinal section through the brain at the level of the origin of the circum-oesophageal commissures. A<sup>2</sup>, antennary nerve.

*Fig. 9.* *Do., do.*, median longitudinal section of the entire body. S.g., brain; A, harp-shaped sense organ of the lower lip; B, ventral nerve chain; C, cells in wall of oesophagus.

*Fig. 10.* *Do., do.*, transverse section through the brain, in the region of the optic and antennular nerves.

*Fig. 11.* *Do., do.*, longitudinal section of a portion of the ventral chain.

## PLATE V.

*Fig. 12.* *Candona delawarensis* Turner, olfactory seta from the third joint of the antenna.

*Fig. 13.* *Candona faebiformis* (Fischer), *do., do.*

*Fig. 14.* *Cypridopsis vidua* (O. F. Müller), *do., do.*

*Fig. 15.* *Cypris herricki*, Turner, *do., do.*

*Fig. 16.* *Cypris herricki* Turner, longitudinal section through the body. A.N., antennular nerve; B, harp-shaped sense organ of the upper lip; C, harp-shaped sense organ at the base of the mandibular teeth; D, harp-shaped sense organ in the lower lip; E, auditory organ; L.N., labial nerve; P, pear-shaped sense organ of the upper lip; S.G., supra-oesophageal ganglion.

*Fig. 17.* *Cypris fuscata* Jurine, olfactory seta from the third joint of the antenna.

*Fig. 18.* *Cyclocypris laevis* (O. F. Müller), *do.*

*Fig. 19.* *Cypria exculpta* (Fischer), *do.*

*Fig. 20.* *Candona fabæformis* (Fischer), sensory seta from tip of first antenna.

*Fig. 21.* *Cypria ophthalmica* (Jurine), sensory seta from third joint of antenna.

*Fig. 22.* *Cyclocypris laevis* (O. F. Müller), *do., do.*



## PLATE VI.

*Fig. 23.* *Cypris herricki* Turner, mandibular palp. D.S., dagger-shaped seta.

*Fig. 24.* *Candonopsis pubescens*, sensory seta from the four segments of the antenna of the male.

*Fig. 25.* *Candonopsis kingslei*, do.

*Fig. 26.* *Candona fabaeformis*, do.

*Fig. 27.* *Candona candida*, do.

*Fig. 28.* *Notodromas monacha*, Sensory seta from the fifth segment of the antenna.

Figures 24-28 have been copied from Wenzel Vávra.

## PLATE VII.

*Fig. 29.* *Cypris herricki* Turner, auditory organ from a longitudinal perpendicular section. A, antennular nerve; m, muscle.

*Fig. 30.* *Natodromas monacha*, eyes (after Vávra).

*Fig. 31.* *Cypris herricki* Turner, pear-shaped organ of the upper lip, sectional view.

*Fig. 32.* *Cyprinotus incongruens* (Ramdohr), ventral chain. A, antennary nerve; A N, abdominal nerve; L, labial nerve; L', branch of same to pear-shaped organ; L'', branch of same to harp-shaped organ; La, labrum.

*Fig. 33.* *Cypris herricki*, Turner, auditory organ, from a horizontal-longitudinal section.

*Fig. 34.* *Cyprinotus incongruens* (Ramdohr), pear-shaped sense organ of upper lip, surface view.

*Fig. 35.* *Cypris herricki* Turner, tip of mandible showing hairs that belong to the sensory organ found in the mandible.

*Fig. 36.* *Cypris pubera*, eye, surface view (after Wenzel Vávra).

## PLATE VIII.

*Fig. 37.* *Cypris herricki*, Turner, wall of mid-gut.

*Fig. 38.* *Cypris herricki*, Turner, tip of second foot.

*Fig. 39.* Do., do., wall of oesophagus.

*Fig. 40.* *Cyprinotus incongruens* (Ramdohr), transverse section through the mandibular nerve. S, sub-oesophageal ganglion; md, mandibular nerve.

*Fig. 41.* *Cypris herricki* Turner, surface view of wall of mid-gut.

*Fig. 42.* Diagram of the central nervous system of *Cypris*. A, antennular nerve; Ab, abdominal nerve; At, antennary nerve; L, labial nerve; L', branch of labial nerve passing to the pear-shaped sense organ; L'', branch of labial nerve passing to the harp-shaped sense organ; Lb, labral nerve; Lg', 1st leg nerve; Lg'', second leg nerve; Md, mandibular nerve; Mx', 1st maxillary nerve; Mx'', second maxillary nerve; T, thoracic nerve; T. V., thoracic ventricle.

*Fig. 43.* Nerve cell of *Cypris*.











