XXXVII.—*On some Freshwater Amphipods: The Reduction of the Eye in a new Gammarid from Ireland.* By Prof. Dr. FR. VEJDOVSKÝ*.

[Plates XI. & XII.]

THE paper by W. F. de Vismes Kane (23) on the Amphipods of the Irish lake, Lough Mask, is worthy of attention in many ways. It records that the author collected there about 130 specimens of *Niphargus Kochianus*, among which there were three "which had well-developed pigmentation and a fourth which showed a cloudy shading in the optic region." As I had already stated (22) that in "*N. Kochianus*" rudiments of eyes without pigment are present, I was obliged to devote special attention to the work of de Vismes Kane, according to which pigment was still actually to be found in certain individuals.

Mr. de Vismes Kane, with the greatest kindness, placed at my disposal, for purposes of investigation, a portion of his collection of the above-mentioned Gammarids from Lough Mask, including examples of the wholly blind *Niphargus* and also the four individuals with the eye-flecks which had been preserved in formol. This valuable material, for which I here wish to thank Mr. de Vismes Kane, proved to be of great importance for several reasons, viz. :—

(1) Because it furnishes evidence as to the extent of the first stage in the reduction of the compound eye;

(2) Because by reason of this degeneration it is possible to explain the significance of the "pigment-veil" [Pigment-schleier] already known in *Crangonyx subterraneus*; and

(3) Because, lastly, it offers the possibility of deciding the relationship of the freshwater shrimp [Flohkrebs] found in the wells of Munich, usually alluded to as *Niphargus "Kochianus,"* with the similarly designated species from England and Ireland.

I. ON BATHYONYX, gen. nov.

In his paper de Vismes Kane refers all the Gammarids found in Lough Mask to a single species, viz., *Niphargus Kochianus*, Bate. I have been able to confirm this identification with the exception of those four individuals with eye-

* Translated by D. J. Scourfield from the 'Sitzungsberichte der königlichen böhmischen Gesellschaft der Wissenschaften,' No. 28. Prag, 1905.

pigment, which in no way possess the characters of the genus *Niphargus*, but are representatives of a new genus intermediate between *Crangonyx* and *Gammarus*, which I designate *Bathyonyx*. To the species I give the name of *B. de Vismesi*, gen. nov., sp. n., in honour of the discoverer.

Generic and specific characters:—*Bathyonyx* with both pairs of antennæ very short (the flagellum of the first usually 6-jointed, that of the second 4-jointed), with 2-jointed secondary branch on the first antennæ. Eyes consisting of crystalline cones diffusely distributed in the pigment. Gnathopoda with weakly developed hands; the hands of the anterior gnathopods broader than those of the second pair. Telson split for two-thirds of its length, consequently bilobed. Third pair of uropods with an outer 2-jointed, and a short inner 1-jointed branch, scantily furnished with setæ, as in *Crangonyx*. Segmental capsular epidermal sensory organs fusiform.

Bathyonyx de Vismesi, gen. et sp. nn.

The four specimens examined were all of equal length, namely 3 mm., and of similar form. Being preserved in formol they still showed traces of the original pale orange-red coloration which was especially noticed by de Vismes Kane in the living condition.

The antennæ are remarkably short, attaining about one-fourth of the body-length; there is no well-marked distinction between the joints of the peduncle and the flagellum, for the three basal joints pass gradually into those of the flagellum. In this way the total number of joints of the first antennæ amounts to nine in two specimens and eight in the third. (The fourth example was cut into serial sections.) The third joint carries the 2-jointed secondary branch, of the same form as in *Niphargus* for example, *i. e.* with an elongated and greatly swollen basal joint, and a short and slender distal joint (Pl. XI. fig. 2, *n*). The antennal setæ are weak, short, and scanty, from 1–4 on each joint as in *Niphargus*. The sensory setæ, which I have described from the antennæ of *Crangonyx* as sensory brushes [Sinnespinsel], are also present in *Bathyonyx*, but they are very feebly developed, so that they can be easily overlooked.

These remarkable sense-hairs are characteristic not only of these genera, but also of *Niphargus* and *Gammarus* (especially those of the first joint of the first antennæ), occurring, in fact, in the last-named genus in the greatest number.

Thus in *G. fluviatilis* from Herzegovina (collected by Dr. Thon) I invariably found seven sensory brushes on the

distal outer edge of the first joint in the space between the large ordinary setæ. In addition, there are in the middle of the same joint two further sensory brushes, accompanied by a thicker ordinary seta, exactly as in *Crangonyx*.

In *Bathyonyx* also there are always two sensory brushes in the middle of the first joint and four on the distal edge. Their structure is the same as in *Crangonyx*, *Niphargus*, and *Gammarus*. Each sensory brush consists of a basal cup or urn sunk into the fibrous inner cuticle. (This fibrous inner cuticle is covered with a thin homogeneous outer cuticle, Pl. XI. fig. 14, c).

From the cup there arises the stem of the seta, which, at its distal end, is furnished with two lateral rows of fine hairs (Pl. XI. fig. 14). I have designated these sense-hairs in *Crangonyx* as "quaking-hairs" [Zitterhaare], because in the living state they are found to be subject to periodical vibratory movements, which points to some definite sensory action. The quaking movement of these hairs of Amphipods is certainly worthy of remark, especially as it resembles ciliary action, although produced in a different manner from the latter. The quaking of the sense-hairs reminds one rather of the flame-cells [Zitterorgane] of the Rotatoria, or of the tufted hairs [Büschelhaare] which I have described in *Bothrioplana bohemica* *.

By the examination in profile of the transparent first antenna it is easy to demonstrate that the sensory brushes are supplied with nerves from the antennal ganglion. Long and fine processes from the ganglion-cells are connected with special club-shaped cells, the short process from each of which is spread out like a dish at the base of the cup from which the seta arises (Pl. XI. fig. 14, ne). The structure of the ganglia in the antennæ of the Gammarids is, according to what I have so far been able to demonstrate in *Gammarus pulex*, &c., very characteristic and deserves special attention from comparative nerve histologists.

On the lower antennæ the sensory brushes only occur singly; thus I have observed two on the second joint and one each on the third and last joints of the same form and size as on the first antennæ.

I only found the hyaline clubs, so-called olfactory clubs, on one specimen (Pl. XI. fig. 3); they are very short, not attaining the length of the joints, and therefore very difficult to observe.

* "Zur vergleich. Anatomie der Turbellarien," Zeit. f. wiss. Zool. Bd. lx. (1905).

Sensory brushes are present on the telson * as well as on the antennæ, as has already been shown in many Amphipods. Their position upon the surface of the telson appears to be characteristic of the species of *Niphargus* and *Gammarus*. In *Bathynonyx* the telson is split for two-thirds of its length, thus being bilobed posteriorly, the lobes gradually narrowing and each being furnished at the point with a long and a short simple seta (Pl. XI. fig. 13).

In addition there is always present here a short sensory brush. Somewhat anterior to this group of hairs and towards the exterior edge there are always two longer sensory brushes of the same form and size as on the antennæ. The innervation of all the sensory brushes on the telson evidently proceeds from the lateral nerves of the last ventral nerve-cord ganglion, as I have been able to demonstrate, for example, on the telson of the New Zealand species *Crangonyx compactus*, Chilton.

Quite different in structure from the sensory brushes are the segmental sensory capsules, which, among different Gammarids, exhibit a form typical for the genus. By means of these sense-organs the genera *Niphargus*, *Crangonyx*, and *Gammarus* can be determined with perfect safety. But they are somewhat difficult to find, especially when only a few occur on the segment, as they are characterized by their extremely minute dimensions. It is only on this account that I have not made an earlier reference to their occurrence in *Crangonyx*. I refer to the capsules as segmental sense-organs because they are distributed partly on the body-segments and partly on the epimera. The form, number, and distribution of the capsules can be seen without much difficulty in preparations of the second epimera, where they appear regularly disposed in a semicircle on the margin, and, in consequence of the sharply contoured cuticular walls, they stand out as plainly in the living animal as in preparations. The sense-hairs, too, which are connected with the capsules, make the recognition of the latter easier.

Among the species of the genera already mentioned I have made out the following forms of sensory capsules:—

In *Niphargus* they are mostly flask-shaped, gradually narrowing towards the exterior, where they pass into the little sense-hair. The sense-hairs are mostly plumose, or like a paint-brush, rarely simple and pointed.

I have examined the sensory capsules of various species of

* Chilton has also observed them on the penultimate joint of the fourth pereopods in *Gammarus fragilis*.

Niphargus as regards shape and have been able to determine the following forms:—

Niphargus puteanus from Prague (Pl. XII. figs. 23 & 24). Sensory capsules $12\ \mu$ long and $4\ \mu$ broad, with usually a short sense-hair ending in a tuft. Less frequently the sense-hairs are simple, not branched.

Niphargus elegans from Modena (Pl. XII. fig. 22). Sensory capsules of the same form as in *N. puteanus* from Prague, but the sense-hairs have forked ends with a long tuft on one side.

Niphargus tatrensis (Switzerland, fig. 26), more strongly swollen, with a simple sense-hair ending in a thread.

A *Niphargus* from Lille has very small sensory capsules with sense-hairs of the paint-brush type (fig. 27).

In *Niphargus Caspary*, from Munich, the sensory capsules are very pale, thin-walled, and short. They give rise to a simple short sense-hair (fig. 28).

Niphargus Kochianus (Lough Mask in Ireland) is provided with nearly spherical sensory capsules narrowed towards the exterior and tufted sense-hairs (fig. 29).

In *Crangonyx subterraneus*, great numbers of which I have been able to examine recently from the point of view of the sense-organs now in question, the capsules are almost cylindrical, longer than broad, the sense-hairs long, not plumose; sensory capsules $4\text{--}5\ \mu$ long, sense-hairs $20\ \mu$ long (fig. 30).

In *Crangonyx compactus*, from New Zealand, the sensory capsules are very slender, terminating with a simple hair (fig. 25).

In all the species of *Gammarus* the capsules are, in the main, spindle-shaped, slender, pointed exteriorly, not infrequently constricted in the middle, the sense-hairs short, not plumose. The length of the capsules varies, according to the species, from $16\text{--}22\ \mu$ (figs. 20 & 21). The same details of the form of the capsules apply, in general, to *Bathynonyx* also, but the structures are much smaller and difficult to find (figs. 17, 18, *spo*, *spo'*).

The internal structure of the sensory capsules differs from that of the sensory brushes, but is the same in all genera, as can be demonstrated with the greatest precision on the larger forms occurring in the Gammarids. The proximal portion of the cuticular wall of the capsule turns inwards and forms a hollow axial stalk, to which the sensory seta is attached. In some species of *Gammarus* and in *Crangonyx* the distal end of the stalk, *i. e.* where the sensory seta arises, is thickened into a little head. It is not difficult to make out that the

capsules are innervated from the cutaneous nerves, for a pale but sharply contoured nerve-thread approaches the base of each capsule and then clearly passes along the stalk to be joined to the sensory seta. The nerve-fibre always originates from one ganglion-cell, as is accurately shown by Hamann.

The sensory capsules are found on all the segments. On the cephalic segment of *Bathynonyx*, close behind the diffuse eye, there are 4-5 capsules arranged in a curved line (fig. 17, *spo*), and not far behind there is a second row of 3-4 capsules (fig. 17, *spo'*). On the following segments the number may be less, but they occur more or less regularly also on the hinder segments.

In *Crangonyx* I always found, in the hinder region of the body, four capsules on each segment, two anterior and two posterior, while on the anterior segments they were rarer and less regularly distributed, although one must take into account the circumstance that the structures can easily escape observation by reason of their minuteness and their usually small refractive power.

The attention of earlier investigators was very often given to the sensory capsules. Thus La Valette observed them on the back and therefore referred to them as "capilli in corporis dorso siti." Humbert recognized them as sense-organs and designated them accurately as "capsules sensitives." As Hamann justly remarks, Leydig combatted the correctness of this expression, "for it is not a question of capsules but of modified cuticular canals. But from his description it is evident that he classed these organs with the similarly formed hair-structures of the antennæ and only examined the latter." Vom Rath and more recently Hamann have correctly described and figured the sensory capsules (referred to by Hamann as sensory clubs). Della Valle calls the organs "peli," but his figures are reproduced on a small scale, so that the structure of the capsules, nerve-endings, and sensory setæ do not clearly appear.

The most remarkable organs of *Bathynonyx* are undoubtedly the EYES, and for this reason I propose to describe them in detail. Not one of the four above-mentioned specimens has normal compound eyes such as are found in *Gammarus*, but visual organs with scattered components on both sides of the head. Unfortunately, owing to the fixing agent, the pigment was not perfectly preserved, so that it is impossible to state exactly the number of the pigment-cells.

One example was cut into a complete set of serial sections, principally with the object of showing more precisely the relation of the nerves and optic ganglia to the external visual

apparatus. Unfortunately the preservation in formalin had so much damaged the internal nervous structure and the brain that nothing definite can be said in this connection. It is only possible to refer to the superficial appearance of the eye, and in addition at most to the position of the dioptric elements under the hypodermis as observed in preparations of the entire animals under moderate and high-power magnification. But even in this way interesting results are obtained.

In general the eye of *Bathynonyx* is not a compact organ, such as we are accustomed to picture the compound eye of Arthropods, but forms a large irregularly defined fleck of unequal size with a variable number of crystalline cones in each of the available specimens. I figure such eyes in figs. 16-18.

In fig. 16, which is drawn under a low magnification, there are twenty-four cones. They occur in a dark (brown to brownish black) fine-grained pigment which appears to be most thickly developed in the centre of the eye.

Here was evidently situated the original eye, as, for example, in *Gammarus*. In this central pigment most of the crystalline cones are collected, without, however, forming a compact organ.

They are as irregularly distributed in the pigment, without any definite position, as the peripheral crystalline cones, which mostly lie under the ordinary hypodermis without any pigment. All the crystalline cones are commonly composed of two segments or simply constricted, the hemispheres being sometimes equal and sometimes unequal in size. Now and again at the periphery small wholly isolated cones are also found. The crystalline cones consist of a strongly refractive homogeneous brownish substance, and therefore stand out clearly in the preparations.

In this condition the individual cones appeared in all four specimens. Another eye, as seen under strong magnification (as with Hom. Imm. Apochr. Obj. 2 mm., Oc. 4) and showing interesting details in the structure of the cones, is reproduced in fig. 17.

Here the scattered components of the eye are still more striking; in the centre of the eye-fleck one finds large, simple, rarely double, hexagonal or irregularly branched pigment-cells in the midst of whose granular substance a small rounded nucleus can be detected (*p*). The whole system formed by the cones and the central pigment-cells retains in the main a reniform shape, as is also typical of the compound eyes of *Gammarus*. In *Bathynonyx*, however, there exists no

connection between the individual cones; they are isolated and mostly situated at the periphery of the pigment-cells. The total number of the cones in the specimen represented amounts to only fourteen, and the variable form and size of the components can be well seen in the drawing.

The number, form, and size of the crystalline cones vary, however, not only in different individuals, but also in the right and left eyes of one and the same animal. The eye just described belongs to the left side of the head (fig. 17). In fig. 18 is shown the eye from the right side of the same animal. In the centre of the pigment-cells there is only one crystalline cone; the others are situated at the periphery of the pigment-cells, irregularly scattered, and two even lying not far from the frontal margin of the head. In this case there are only eleven crystalline cones of the most diverse size and form.

The structure of the crystalline cones here reproduced is certainly very peculiar and difficult to correlate with the details of an ordinary compound eye of *Gammarus*. In each cone there is a dark, finely granular, sharply defined matrix, at whose margin, when in a favourable position, a little body can be seen which I am inclined to consider as a nucleus. In this matrix an irregular number of smaller rounded bodies are present. In the simplest case there is a large central sphere and with it one or more little spheres. There can, however, be such an increase of both kinds that the matrix appears to be filled with vacuoles. These inner vacuolar spherical bodies are filled with a homogeneous slightly refractive substance which is only stained by carmine in a very feeble and diffuse way.

In the above-mentioned serial sections into which one specimen was cut, I have unfortunately found little explaining the connection of the appearance in side view of the crystalline cones, as described, with the nervous organization. In fig. 19 one such section is reproduced. Nothing is here to be seen of the nerves. The cuticle of the head (*c*) stands off a long way from the eye. The hypodermis (*hp*) forms a thin layer which contains only the regularly placed nuclei. Underneath there are three groups of large pigment-masses without nuclei, between which occur rounded vacuolar bodies. These are the rudiments of the crystalline cones, and they are not nearly so refractive in these sections of 5 μ in thickness as in the preparations showing the animals from the side. A direct connection between the outer larger pigment-masses and the deeper layer of smaller pigment-cells (*rt*) does not exist in the serial sections.

Between the two layers there is a hollow space, whether artificially produced or not I am unable to decide. But according to the known structure of the eye in *Gammarus* we should be dealing, in the lower pigmented layer of cells arranged almost like epithelium, with retinula-cells, to which also the outer pigment-masses belong, they being certainly only separated by the unsatisfactory method of fixing. From this it would seem that in *Bathynonyx* the retinula apparatus was still retained, although the dioptric elements were gradually destroyed. For the crystalline cones described above must be considered as being in process of degeneration: firstly, because they do not form a single compact eye, but are only loosely scattered under the hypodermis, and, secondly, because the actual substance of the normal crystalline cone is gradually degenerating.

Special investigation of the mouth-organs of *Bathynonyx* shows that they resemble in form those of *Crangonyx*, except that they are much more feebly developed, thus corresponding to the general organization of *Bathynonyx*. The drawings of the mandibles and their palps (fig. 4), of the maxillæ of the first (figs. 5 & 6) and second pairs (fig. 7), and, lastly, of the maxillipedes (fig. 8) entirely support this conception. The palpi of the maxillipedes are almost as long as the gnathopods, which are also very weakly developed, especially the hands, which, under low magnification, can scarcely be distinguished from the almost equally broad or even broader proximal joints (carpopodites). The form of the hands of the gnathopods of both pairs reminds one of *Crangonyx*, but in general in this case, as in *Crangonyx*, there is some variability. In order to show this I give in figs. 9-11 camera drawings of the hands of three specimens. Figures 10 and 11 are shown under the same and fig. 9 under a slightly higher magnification. From a comparison of the three it is apparent that the only character common to all is that the hands of the first pair are obviously broader and shorter than those of the second pair. It can also be seen from the drawings that the oblique outer edge of both hands is finely toothed and that the armature of strong setæ which is characteristic of the hands of *Gammarus*, *Crangonyx*, and in part *Niphargus* (as I have specially remarked in connection with *Crangonyx*) is entirely absent in *Bathynonyx*. In other respects a slight variability in the form of the hands is to be observed in all three cases, which is also true of *Crangonyx*. A comparison of the form of the gnathopod hands of the last-named genus, as I have figured them in my paper (21, figs. 12-14), with those figured

by Chilton (7, fig. 4, *gn*, *gn*²) might easily lead to the view that the *Crangonyx* found in Bohemia in a certain measure represented a different species to that found in English wells. Indeed Stebbing, on the ground of my representation and his own experience, has considered that the *Crangonyx* found at Radotin near Prague belongs to a distinct genus and species "*Eucrangonyx Vejdovskyi*." Only after comparison of the original specimens from Bohemia and England, which we made in Prague with Chilton, was it demonstrated, beyond all doubt, that we were dealing with one and the same species, in which the form of the gnathopod hands in different individuals is subject to a noticeable variability.

I have been able recently to convince myself that this is actually the case by an examination of numerous specimens of *Crangonyx* which were collected in the course of last year in great quantities in wells at Podbaba, near Prague, by my energetic pupil Herr Niessner.

I have not specially investigated the other feet, as, in the main, they resemble in form the corresponding extremities of *Crangonyx*. The little double hooks on the thighs of the first and second pleopods also differ only in a small degree from the same structures in other Gammarids, especially *Gammarus* (fig. 15). Further, the last pair of uropods correspond with those of *Crangonyx*; they are rather short, the basal joint almost as high as broad; the outer branch consists of a long proximal and a short thin distal joint (fig. 12).

The proximal joint bears on its side only one or two setæ, and differs essentially in this respect from the corresponding joint of the *Niphargi* and Gammarids, which is armed with tufts of strong setæ.

The inner branch is 1-jointed and reaches more than half the length of the outer branch. Moreover, it is comparatively longer than in *Niphargus* and shorter than in *Gammarus*. I must, however, remark that I have only examined these uropods in two specimens.

From the point of view of general biology the discovery of *Bathynonyx* is very important. So far as its systematic position is concerned, the genus comes between *Gammarus* and *Crangonyx*, as it agrees with the former in its capsular segmental sense-organs and with the latter in the rest of its organization. Only the absence of the so-called secondary gills, which are so characteristic of *Crangonyx* (and *Boruta*), and the two-lobed telson separate *Bathynonyx* from the genera

mentioned and bring it in some respects near to *Gammarus* and in others to *Niphargus*.

According to de Vismes Kane, *Bathynonyx* was obtained from a depth of from 130 to 150 feet in Lough Mask. From the general habitus of its body and most of the details of its organization it may be regarded as a degenerate form, a conception which is strongly supported by the sense-organs, especially the eyes. All the above-mentioned cuticular sense-organs, as the sensory brushes and capsules, are present in all species of *Gammarus* living in ordinary fresh waters, but in much greater number and development than in *Bathynonyx*, where they are subject in both directions to a reduction corresponding to that of the eyes, and cannot therefore be considered as compensatory organs. The ancestors of *Bathynonyx* evidently possessed the same sense-organs as, for example, the common *Gammarus*, and in the same number and development, but they degenerated in the course of time in the depths of Lough Mask. There is no reason for supposing that these crustaceans reached the lake in the water from the springs; their organization strengthens us rather in the opinion that the progenitors are to be sought perhaps only in a species of *Crangonyx* or *Gammarus* which gradually adapted themselves to life at the bottom of Lough Mask. Although species of *Crangonyx* possessing eyes are known, among which especially *C. recurvus*, according to Grube, lives in Lake Vrana, on the island of Cherso, unfortunately its organization has not been hitherto carefully studied*. From what has been said it appears that we must attach the greatest importance to the eyes.

The gradual adaptation to life in the darkness of deep lakes and subterranean waters generally produces the result that the organs of sight are gradually, not suddenly, reduced, until at length the animal appears quite eyeless, and transmits its blindness to the following generations. So far as the freshwater Amphipoda are concerned, we now know a series of cases in which we must conclude that eyes were formerly present. Reference has often been made to the observation of Leydig that certain individuals of *Niphargus puteanus* were provided with eye-pigment just in that part of the head where the eyes are situated in such a form as the common *Gammarus*.

* From an interesting paper by M. Grochowski (11) I learn that he and Professor B. Dybowski found in 1895 a large number of *C. recurvus* in the lake mentioned. A special account of this species therefore may be expected.

Although in the course of thirty years I have investigated from this point of view hundreds of examples of the species mentioned, I have not been able to find anything of the pigment in question in a single individual, and I believe therefore that we are driven to the conclusion that Leydig only had *Crangonyx* before him. In this genus I have invariably found, not only in examples from Radotin, near Prague, but also recently among great numbers of individuals from the wells of Podbaba, near Prague, pigment-flecks on both sides of the head, consisting of large branched cells such as I have described in an earlier paper.

Very interesting is the further statement of Moniez (14), from which it appears that he observed a "*Gammarus fluviatilis*" in the drinking-water of Emmerin, near Lille, whose eyes appeared in the form of dark flecks.

They were not so compact as in the normal freshwater shrimps, but appeared to consist of single ommatidia surrounded by black pigment, and the crystalline cones were not so round as in the typical species. Moniez therefore described the form he had observed as *G. fluviatilis*, var. *d'Emmerin*. According to the description we should have here a case of rudimentary eyes exactly corresponding to what we have specially described in *Bathynonyx*, and it is to be hoped that the Emmerin variety may be subjected to an examination as to its other characters in order to see whether it may not represent a distinct species closely allied to *Bathynonyx de Vismesi*.

Not less important is the communication of R. Schneider (19) about the *Gammarus pulex* living in the underground waters of Claustal, in which the author found the eyes to be in a peculiar condition. They are of irregular form, without definite outline, with a little blackish pigment which is confined to the centre of the eye, disappearing towards the periphery. The crystalline cones are separated from one another, and the eye is therefore diffusely formed as in our *Bathynonyx*. R. Schneider designates the form as *G. pulex*, var. *subterraneus* *.

According to Garbini, the *G. fluviatilis* observed by him near Verona exhibits the same arrangement with regard to the eyes as Schneider's *G. pulex*, and he calls the form *G. fluviatilis*, var. *monophthalmus*. The same author mentions also *N. elegans*, var. *imperfectus*, with small brownish pigment-

* [The original description by Schneider is given by Prof. Vejdvský in a long footnote, but it has not been thought necessary to reproduce it in this translation.—*Translator's note.*]

flecks, like those I have referred to in connexion with the specimens from Modena.

The large pigment-flecks of *Crangonyx subterraneus*, which I have described as a pigment-veil ["Pigmentschleier"], suggest by their position the former presence of eyes; I have not, however, referred to them as rudiments of eyes so long as there was no definite proof that the pigment was directly connected on the one hand with the crystalline cones and on the other with the optic ganglia.

We know now, however, that on the one side there are species of *Crangonyx* with normal eyes, and on the other that the eyes of *C. compactus* from New Zealand are, according to Chilton, only represented by two or three little "lenses" without pigment. If we turn to *C. subterraneus*, we must regard the pigment-veil as a rudiment of an eye in which the crystalline cones have completely disappeared and only the pigment-cells remain. We find, therefore, that the genus *Crangonyx* is characterized by visual organs in all possible stages of reduction; and we might expect to find similar series of degenerating eyes in other genera. For *Gammarus* I have already mentioned the observations of Moniez and Schneider; a completely eyeless species *G. fragilis*, has been described from New Zealand by Chilton, and I myself know a large species from Herzegovina the two examples of which in my possession lack all trace of eyes.

The same series may be made out in *Niphargus*. It is true that species with normal eyes are not known, but *N. elegans*, which is characterized by possessing only the eye-pigment, permits of the assumption that there are species with eyes, and there exists a whole series of completely blind species, as *N. Kochianus*, *Caspary*, *puteanus*, &c. (The work of Viré has not been accessible to me.)

Now it is possible that there are eyeless forms which occur at the same time and in the same place with those possessing reduced and normal eyes. At least "*Gammarus pulex*," from Wädenschwyl in Switzerland, deserves a renewed investigation, as, according to the statement of Asper, it is represented at a depth of 40 m. by individuals with and without eyes. This case of variable development of the visual organs in different individuals of the same species is confirmed among other species of animals by Packard, and Forel particularly notes that in rare and exceptional instances the blind *Asellus Forelii*, Blanc, still bears vestiges of eyes; and in this connexion it may be remembered that years ago I found in a well in Prague both eyed and eyeless forms of the rhabdocoel *Gyrator notops*, Dugès. The eyeless form

has been described by L. v. Graff as a distinct species—*Gyrator coccus*.

The foregoing cases may support the opinion expressed by Packard, and more recently by Chilton, that it is possible that different species, and even individuals from different localities, may exhibit different stages in the reduction of the eyes.

The discovery of *Bathynonyx* offers now excellent evidence as to the probable first stage in the degeneration of the eyes. The ancestors of this genus were certainly closely related to a *Gammarus* with normal eyes, as may be seen from the whole organization and in particular from the capsular segmental cuticular sense-organs. The visual organs also represent the well-known kidney-shaped eyes of a *Gammarus*-like ancestor. The descendants, adapting themselves to live in the dark depths of the lake *, gradually lost the power of seeing with the compound eye, as individual ommatidia remained functionless and consequently the crystalline cones became subject to degeneration. Only the pigment-cells remained and the ommatidia which still retained their functional power appeared then as scattered components of an eye on each side of the head. It is in this stage that *Bathynonyx* now presents itself to us.

But the crystalline cones still present have also undergone degeneration, as is shown by the little homogeneous spheres within the cones. The hypothesis of the progressive reduction of the eyes can, I believe, be supported by the following facts:—

(1) From the variable number of the crystalline cones in one and the same animal on the right and left sides of the head.

(2) From the extremely variable size of the individual crystalline cones, which in one and the same eye present instances of diminution in size so as to finally appear simply as little refractive particles.

(3) From the form of the crystalline cones themselves. The homogeneous spheres within the fine-grained matrix must, I think, be regarded as evidence of degeneration. In this way the crystalline cones lose their dioptric property. The degeneration, however, does not occur in any particular order, but may affect widely separated ommatidia, while the intermediate cones may remain intact.

In consequence of the foregoing, the originally compact

* From the small number of specimens obtained it may be supposed that the species lives perhaps in the mud and only occasionally swims about freely in the water.

eye breaks up into a variable number of scattered elements which occupy a considerable space without any definite arrangement.

From what has been said it appears that we must consider the structure of the eyes in *Bathynonyx* as representing the first stage of degeneration, and therefore this genus as the first which could arise from the *Gammarus*-like ancestor with normal eyes. The ancestry of the blind species of *Gammarus* and of *Bathynonyx* may be represented as follows:—

1. Species of *Gammarus* with eyes.

Gammarus pulex, *fluviatilis*, &c.

2. The forms with reduced eyes mentioned by Schneider and Moniez (*G. pulex* var. *subterraneus*, Schn., *G. fluviatilis* var. *d'Emmerin*, Mon.).

3. *Bathynonyx*, Vejd.
(*B. de Vismesi*, Vejd.).

4. Species of *Gammarus* without eyes (*G. fragilis*, Chilton).

An exactly similar series can be made out in *Crangonyx*, and adopting the same method as above the following result is obtained:—

1. Species of *Crangonyx* with eyes.

Crangonyx gracilis, *recurvus*, &c.

2. *C. compactus* Chilt. (With 2 to 3 crystalline cones.)

3. *C. subterraneus*, Bate. With pigment-veil.

4. Blind species in North America.

5. *Boruta*, Wrzes. (*B. tenebrarum*).

For *Niphargus* also a corresponding series of species can, in all probability, be drawn up in spite of the fact that no species bearing eyes are yet known. That such must have existed, however, is proved by the species with rudimentary visual organs.

The series in this case may be shown in the following manner:—

1. *Niphargus* (hypothetical, species with eyes).

2. *N. elegans*, Garb. (With little pigment-flecks.)

3. Eyeless species.

(a) With optic ganglia.
N. Kochianus, Bate.

N. Caspary, Pratz.

(b) Without optic nerves.
N. puteanus, &c.

Literature.

- (1) ASPER, G. "Beiträge zur Kenntniss der Tiefseefauna der Schweizerseen," Zool. Anz. iii. 1880, pp. 130-134, 200-207.
- (2) BATE, C. SPENCE. Nat. Hist. Review, 1859, vi. Proc. Soc. p. 165. Quoted by de Vismes Kane.
- (3) BATE, C. SPENCE, and WESTWOOD, J. O. "A History of the British Sessile-eyed Crustacea," 2 vols. London, 1863-1868.
- (4) BATE, C. SPENCE. 'Catalogue of the Specimens of Amphipodous Crustacea in the Collection of the British Museum.' London, 1862.
- (5) CASPARY, ROB. "*Gammarus puteanus*," Verhandl. nat. Ver. preuss. Rheinl. u. Westphal. Bonn, 1849, pp. 39-48.
- (6) CHILTON, CHAS. "The Subterranean Crustacea of New Zealand: with some general Remarks on the Fauna of Caves and Wells." Trans. Linn. Soc. London. Second Series. Zoology, vol. vi. 1894, pp. 163-284, pls. xvi.-xxiii.
- (7) ——. "The Subterranean Amphipoda of the British Islands," Journ. Linnean Society, Zoology, vol. xxviii. November 1900, pp. 140-160, pls. 16-18.
- (8) DELLA VALLE. "Gammarini del Golfo di Napoli," Fauna und Flora, Monograph xx. 1893.
- (9) FOREL, F. A. "La Faune profonde des Lacs suisses," Mém. de la Soc. Helvétique des Sciences nat. vol. xxix. 1885.
- (10) GARBINI, ADR. "*Gammarus ciechi* in acque superficiali basse," Accad. di Agricoltura Arti e Commercio di Verona, vol. lxx. ser. iii. 8 pp.
- (11) GROCHOWSKI, M. "O rodzaju studniczka (*Niphargus*). Odbitka z czasopisma 'Kosmos.'" S 45 rycinami cynkograficznymi. Lwów, 1904, 75 S.
- (12) HOSIUS, AUG. "Ueber die *Gammarus*-Arten d. Gegend von Bonn," Arch. Nat. 1850, pp. 232-248.
- (13) LEYDIG, F. "Amphipoden und Isopoden, Anat. u. zool. Bemerkungen," Z. f. w. Z. xxx. Suppl. pp. 235-274, Taf. ix.-xii. 1878.
- (14) MONIEZ, R. 'Faune des Eaux souterraines du Département du Nord de la France,' t. i. 1888-89, 68 pp. Lille, 1889.
- (15) PACKARD, A. S. "The Cave Fauna of North America, with Remarks on the Anatomy of the Brain and Origin of the Blind Species," Proc. Acad. Nat. Sci. Phil. vol. iv. pp. 3-156, pls. i.-xxvii.
- (16) PARKER, G. H. "The Compound Eyes in Crustaceans," Bull. Mus. Comp. Zool. Harvard College, vol. xxi. no. 2, 3 pls. Cambridge, 1891.
- (17) PRATZ, ED. "Ueber einige im Grundwasser lebende Thiere," Beitr. z. Kenntn. der unterird. Crustaceen," Dissert. inaug. Petersburg, 1866, 64 pp., 4 Taf.
- (18) ROUGEMONT, PH. DE. 'Étude de la faune des eaux privées de lumière.' 4°, avec 5 planch. Paris, 1876.
- (19) SCHNEIDER, ROB. "Der unterirdische *Gammarus* von Clausthal (*Gammarus pulex* var. *subterraneus*)," Sitzber. königl. preuss. Akad. Wiss. Berlin, 1885.
- (20) STEBBING, T. R. R. 'Report on the Amphipoda collected by H.M.S. 'Challenger' during the Years 1873-1876.' Zool. vol. xxix. London, 1888.
- (21) VEJDOVSKÝ, F. "Ueber einige Süßwasseramphipoden. I. Ueber *Crangonyx*, Sp. Bate," Sitzber. königl. böhm. Gesellsch. Wiss. Prag, 1896, x.

- (22) VEJDOVSKÝ, F. "Ueber einige Süßwasseramphipoden. II. Zur Frage der Augenrudimente von *Niphargus*," *ibid.* 1900.
- (23) VISMES KANE, W. F. DE. "*Niphargus Kochianus*, Bate, in an Irish Lake, and *N. subterraneus*, Leach, in Kent," *Ann. & Mag. Nat. Hist.* ser. 7, vol. xiv. 1904, pp. 274-283, pl. viii.
- (24) WRZEŚNIEWSKI, AUGUST. "O trzech kielżách podziemnych. De tribus Crustaceis Amphipod. subterraneis," *Pam. fyziogr.* viii. 1888.
- (25) ——. "Ueber drei unterird. Gammariden," *Z. f. w. Z. B.* 50, pp. 600-725, 1890, Taf. xxviii.-xxxii.

EXPLANATION OF THE PLATES.

General significance of the letters.

<i>c.</i> Cuticle.	<i>n.</i> Secondary branch of the first antennæ.
<i>db.</i> Ordinary setæ.	<i>p.</i> Pigment-cells.
<i>hk.</i> Hyaline spheres in the crystalline cones.	<i>r.</i> Retinula-cells.
<i>hp.</i> Hypodermis.	<i>sp.</i> Sensory brushes.
<i>kr.</i> Crystalline cones.	<i>spo, spo'.</i> Segmental cuticular sense-organs.

PLATE XI.

- Fig.* 1. *Bathynonyx de Vismesi* under low magnification. The appendages of the left side only are shown.
- Fig.* 2. Portion of the third joint of the upper (first) antennæ, with the accessory branch (*n*).
- Fig.* 3. Terminal portion of the antenna, with two hyaline clubs [so-called olfactory clubs] and a sensory brush.
- Fig.* 4. Mandible, left side, from below.
- Fig.* 5. Maxilla of first pair; the inner lobe is not visible in this position.
- Fig.* 6. *a*, inner, *b*, outer teeth of the middle lobe of maxilla of first pair.
- Fig.* 7. Maxilla of the second pair.
- Fig.* 8. Maxillipede of the left side.
- Figs.* 9-11. Gnathopods of the first (*a*) and second (*b*) pairs of three individuals under nearly equal magnification, in order to show the moderate variability of their form.
- Fig.* 12. Uropod of the third pair.
- Fig.* 13. Telson from above, in order to show the position of the sensory brushes.
- Fig.* 14. Outer (*c*) and fibrous (*c'*) cuticle, in which the urn of a sensory brush is embedded. *ne*, nerve-ending.
- Fig.* 15. Double hooks of the first and second pleopods.

PLATE XII.

- Fig.* 16. Distribution of the crystalline cones in the pigment and on its periphery under low magnification. *Bathynonyx*.
- Fig.* 17. Head from the left side, with basal joints of the first and second antennæ, the diffuse eye, and the segmental cuticular sense-organs. Highly magnified.
- Fig.* 18. Head of the same animal seen from the right side, in order to show the variable number of crystalline cones.

Fig. 19. Section through the diffuse eye of a specimen preserved in formol. The cuticle (*c*) is widely separated from the hypodermis (*hp*). *rt*, retinula.

Figs. 20–30. Segmental sensory capsules of different representatives of the genera *Gammarus*, *Niphargus*, and *Crangonyx*.

Fig. 20. *Gammarus* sp., from Herzegovina (22 μ long).

Fig. 21 *a, b*. *Gammarus* from Lautenthal (16 μ).

Fig. 22. *Niphargus elegans* from Modena.

Figs. 23, 24. *Niphargus puteanus* from Prague (12 μ).

Fig. 25. *Crangonyx compactus*.

Fig. 26. *Niphargus tatrensis* (Switzerland).

Fig. 27. *Niphargus* from Lille.

Fig. 28. *Niphargus Caspary* from Munich.

Fig. 29. *Niphargus Kochianus* from Lough Mask; *b*, in optical section.

Fig. 30. *Crangonyx subterraneus* from Podbaba, near Prague.

[The foregoing paper by Prof. Vejdovský, of Prague, has been translated by my friend Mr. D. J. Scourfield, and would have appeared in print last year, but that it seemed desirable if possible to supplement the information by the result of further researches. Unfortunately three days' dredging undertaken last summer, and again this year, failed in securing any additional specimens of *Bathynonyx de Vismesi*, although 251 examples of *Niphargus Kochianus*, Bate, were taken in Lough Mask. The bright orange colour which characterizes them all, as well as *Bathynonyx*, from the lake, finds a parallel in the observation of M. Chevreux referring to *Niphargus Plateaui*, var. *robustus*, captured in an open basin formed by the source of the Robine at the foot of the mountains of Gardiole, the adult specimens of which he described to be of a salmon-red, paler in the younger individuals. The probability that these animals might have been originally introduced from the underground streams that percolate the limestone strata about Lough Mask suggested an investigation of these latter. Accordingly, Lord Ardilaun's permission having been given, a research was conducted into the subterranean waters in his extensive grounds near Cong. This resulted in the discovery of thirteen *N. Kochianus* in one cave and a single specimen in another. All fourteen were of the usual translucent hue which I am accustomed to see in examples of *Niphargus* taken from wells, but, with the exception of their colour, were in every respect identical with those of the lake. Hence it is now scarcely open to doubt that the blind species of *Niphargus* recorded as occurring in Lough Mask, the Lake of Geneva, the Lake of Zirknitz in Carniola, and some Swiss lakes, have been derived from their congeners inhabiting subterranean waters, and that the orange or salmon-red colour of those in Lough Mask and those cited

by M. Chevreux is an attribute of the changed environment. I do not know whether a similar colour characterizes those of other open waters. As to the origin of *Bathynonyx*, however, we have so far no indication of its derivation from subterranean ancestors; and it appears probable, according to Prof. Vejdovský, whose judgment is based upon its general characteristics and the details of its organization, that its progenitors lived in the open waters of Lough Mask and that its present characters are the result of its existence in the lowest depths. My latest researches have also strengthened the probability of his suggestion that a habit of burrowing in mud may have enabled *Bathynonyx* to escape capture by the dredge, which skims the surface of the lake-floor. Nevertheless a considerable amount of mud was subjected to examination on each occasion, which produced nothing but some *N. Kochianus*.

The latter portion of Prof. Vejdovský's paper on the synonymy of

Gammarus Caspary, Pratz,
Gammarus Kochianus, de Rougemont,
Niphargus Kochianus, Vejdovský,
Niphargus Caspary, Wrześniowski,
Niphargus Kochianus, Chilton,

has been omitted.—WM. F. DE VISMES KANE.]

XXXVIII.—*Observations on the Trematode Parasites of British Birds.* By WILLIAM NICOLL, M.A., B.Sc., Gatty Marine Laboratory, St. Andrews.

TOWARDS the end of last spring I had an opportunity of examining several of the commoner species of shore-birds. These were, unfortunately, in most cases not in the best condition for helminthological investigation, as I seldom received them till at least a day after they were killed, when the parasites were almost always dead. The immediate application of weak formalin, however, preserved their anatomical details rather well, although it rendered them unfit for histological work. For this reason important features in some cases are only superficially described, a matter which I hope to improve shortly with the help of better material. These observations are thus to be regarded, to a certain extent at least, as merely preliminary.

Vejdovský, František. 1907. "XXXVII.—On some freshwater Amphipods: The reduction of the eye in a new Gammarid from Ireland." *The Annals and magazine of natural history; zoology, botany, and geology* 20, 227–245.

<https://doi.org/10.1080/00222930709487331>.

View This Item Online: <https://www.biodiversitylibrary.org/item/85040>

DOI: <https://doi.org/10.1080/00222930709487331>

Permalink: <https://www.biodiversitylibrary.org/partpdf/64144>

Holding Institution

Smithsonian Libraries

Sponsored by

Smithsonian

Copyright & Reuse

Copyright Status: Public domain. The BHL considers that this work is no longer under copyright protection.

This document was created from content at the **Biodiversity Heritage Library**, the world's largest open access digital library for biodiversity literature and archives. Visit BHL at <https://www.biodiversitylibrary.org>.