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Certain Age Changes in the Structure and Biology of the Chironomid Larvae

(Diptera Chironomidae)

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(From: "Trudy Vsesoyuznogo Gidrobiologicheskogo obshchestva" /Transactions of the All-Union Hydrobiological Society/ volume IX, 1959).

INTRODUCTION

Information on age changes in the biology of the chironomid larvae is beneficial for a sound evaluation of the feeding of many types of freshwater fish. However, the study of the biology of larvae of younger age stages is extremely difficult because of our poor knowledge of their structure. The present paper is devoted to a study of certain general principles of the structure changes and of the biology of the chironomid larvae during their growth. The following species were studied:

Glyptotendipes gracilis K.,
Gl. glaucus Mg.,
Gl. imbecillis Walk.,
Endochironomus albipennis Mg.,
End. impar Walk.,
End. tendens F.,
Stenochironumus gibbus F.,
Pentapedilum uncinatum Goet.,
Chironomus plumosus L.,
Ch. anthracinus Zett.,
Ch. annularius Mg.,
Camptochironumus tentans F.,
Limnochironumus nervosus Staeg.
Microtendipes chloris Mg.,
Stictochironumus histrio F.

Identification was made from a female that had laid eggs from which larvae were grown, or, in the majority of cases, from males subsequently developed from these larvae. Glyptotendipes gracilis was identified according to Kieffer's key (1918); the next seven species were identified from the keys of Edwards (1929) and of Coe (1950). The remaining ones were determined from Geotghebuer's key (1936-1937). From egg masses collected in nature Cricotopus larvae of the Silvestris F. group were grown; they were identified according to Chernovsky's key (1949). The material was collected in the Ucha Reservoir at the base of the Ucha Laboratory of the Moscow Water Supply System. The work was carried out during the period 1953-1955.

I take the opportunity here to thank N. Yu. Sokolova, O. A. Chernova and Ya. A. Bierstein for assistance in my work. I am most thankful for A. A. Shtakelberg's valuable advice who took the trouble to read the manuscript for this paper. My heartfelt thanks go likewise to the Chief of the Ucha Laboratory, A.V. Frantsev, for the working conditions granted to me at the water reservoir.

Age Changes in the Structure of Larvae

Published data on the development of the chironomid larvae are few, and dispersed in individual, often little known works. Even in the compendium of Hennig (1918-1952) and in the monograph of Thienemann (1954) these works are enumerated far from completely. The following published /86 data on this subject are known to us.

Only in five species, namely, Chironomus gregarius K. (Pause, 1918), Ch. cristatus F. (Branch, 1923), Ch. plumosus L. (Yablonskaya, 1946), Ch. dorsalis Mg. (Konstantinov, 1952)[1] and Camptochironomus tentans F. (Sadler, 1935) are all the larval moultings traced and all the larval stages described, but the descriptions and drawings of the oral parts of all the four stages are presented only for Ch. cristatus. Stuart (1941) raised individuals of nine species:

Anatopynia varius F.,
Cricotopus fucicola Edw.,
Cr. silvestris F.,
Cr. silvestris var. ornatus Mg.,
Spaniotoma rubicunda Mg.,
Corynoneura scutellata Winn.,
Chironomus dorsalis Mg.,
Ch. longistylus Goet.,
Polypedilum nubeculosum Mg.

The moultings were established by this author, however, descriptions only of the larvae of the last stage are presented, and newly born larvae of only two species are briefly described (Anatopynia varius and Cricotopus silvestris). Growing of Anatopynia varius larvae was repeated by Morgan (1949). The author has traced the moultings. A more complete description of a newborn larva

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[1] The moultings of Ch. dorsalis were earlier traced by Miall (1900), but he only described two stages: the first and the last.

is presented.

For two species, namely Chironomus decorus Joh. (Ping, 1917) and Anatopynia plumipes Fries. (Zabolotsky, 1937) the larvae were raised and descriptions of larvae of several sizes are given, but the authors did not establish larval moultings in these species, nor did they connect the descriptions of the larvae with the larval stages. Data of a similar kind are also available on the development of the above-mentioned species Ch. plumosus (Potonié, 1931, 1936). Kettisch (1938) raised Cricotopus trifasciatus Panzer. larvae. The author apparently did not observe all the moultings, since he indicates seven (!) larval stages for this species established on the basis of measurements of cephalic capsules. The structure is described exclusively for the last stage. In three species, namely, Zavreliella marmorata v. d. Wulp., Lauterborniella agrayloides K., and Tanytarsus bohemicus K., the larvae were grown by Zavrel (1926). The author established no moultings and described for these species only two larval stages: the first and the last.

For yet a further number of species, larvae of the first stage were hatched from egg-masses and described. The authors did not succeed in growing these larvae to the moulting stage, and the taxonomic classification of these larvae was usually established from a female that had laid eggs in the laboratory. Similar descriptions of larvae of stage I are available for Cricotopus biformis Edw., (Leger et Motas, 1928), Bryophaenocladins virgo Strenzke (Thiememann and Shrenzke, 1940), Psectrocladius obvius Walck. (Dorier, 1933) and for three representatives of the Tanypodinae sub-family (Thienemann and Zavrel, 1916) without an exact indication of their specific affiliation. In the same works the authors usually present descriptions of the larvae of stage IV of the same species. The specific affiliation of the older larvae was established from imagoes cultivated from them.

When comparing the descriptions of larvae of the first and last stages found in the literature, one may see that the authors always record for each species the presence of some differences in the structure, and occasionally also in the behavior, of the larvae of these stages. In some species (for example, Zavreliella marmorata) the larvae of the first and last stages differ to such an extent that they may, according to the present classifications (Chernovsky, 1949; Bertrand, 1954) be erroneously /87 classified as belonging to different genera. The difference in the structure and in the behavior of the larvae of the first and last stages was also often observed by the author of the present paper in the case of the above-mentioned species of larvae, which he had occasion to raise.

On the basis both of published data and of our own material on raising larvae, we came to the conclusion that the morphological and biological changes take place in chironomid larvae during the entire period of the growth of the larvae, during which the latter undergoes three larval moultings. Many common features are observed in the direction of the changes in the structure and biology of chironomid larvae, which permits us to speak about certain regularities in the change of structure and biology in chironomid larvae in general.

In the structure of the larvae changes take place during the growth process that are both connected with the larval moultings, and not directly connected with them. The grouping of the changes in morphological features is given below mainly to facilitate the identification of larvae of various ages. A certain conditionality is natural here.*

*When we speak of changes in the structure of the larvae, we mean, in the majority of cases, only the changes in features that have taxonomic significance.

1. Changes Connected with the Change of Morphological Larval Types

Each moulting brings a number of changes into the structure of the larvae. N. N. Lipina (1928, p.27) recorded that "the sharpest changes take place in the structure of the larva after the first moulting; the subsequent moultings complicate the organization comparatively much less". Here it is necessary to add that certain changes taking place during the first moulting exceed the changes taking place during subsequent moultings not only quantitatively, but also qualitatively they differ from all the other changes that take place during the entire growing period of the larva. The larvae of the first stage, in many cases, differ so considerably from the larvae of the three subsequent stages, that in some species this reminds us of the change in the larval morphological type with age. Here the first morphological larval type coincides in chironomids with the first larval stage, and the second one, with the three subsequent stages.

The structural changes of the larvae during the first moulting is expressed in different species to a different degree. Such changes are most striking when the change in the larval forms is connected with a profound change in the structure of the cuticular parts, in particular with the change in the structure of the oral apparatus, from which identification is often made. The marked extent to which the structure of the oral parts of the larva may change in the first moulting, may be seen from the example of Endochironomus impar. Let us present a brief description of the larvae of the first and of the second stages of this species.

N.B. The morphological terminology is given after A.A. Chernovsky (1949). Revisor's note. The number of this footnote is missing from the body of the text.

Larval Stage I

In the middle of the submentum (fig. 1,a) there is one triple canine. Its total width slightly exceeds the double width of the first lateral canine. The middle portion of the central canine is longer and slightly wider than the first lateral one; its boundaries are clearly visible to the very rear edge of the submentum, giving it an appearance of a large independent canine which widens towards its base. The lateral portions of the central canine are shorter and almost one and one-half times narrower than the first lateral canine. There are six lateral canines on each side. They all decrease /88 uniformly from the centre of the submentum to its sides. The colour of the canines and of the strip uniting them is light brown. At the centre of each canine is a still lighter strip which continues to the very rear edge of the submentum. This striation gives the submentum an appearance of a comb. The paralabial plates are pale with a convex front edge broken by unevenly rounded denticles. Striation is not visible. The mandible (fig. 1,b) has one interior and four exterior canines. The colour of the canines is light brown. The index of the antennae (fig. 1,c) is 0.3.*) The arista reaches the distal edge of the fourth segment. The segments of the abdomen have each a thin pair of setae which often break in fixed material. The width of the body of a larva exceeds the length of the longest one of these setae approximately by one and a half times. Newborn larvae are colourless, but become pink towards the end of the first stage.

*) The index of the antennae is the ratio between the length of the scape and the length of the flagellum.

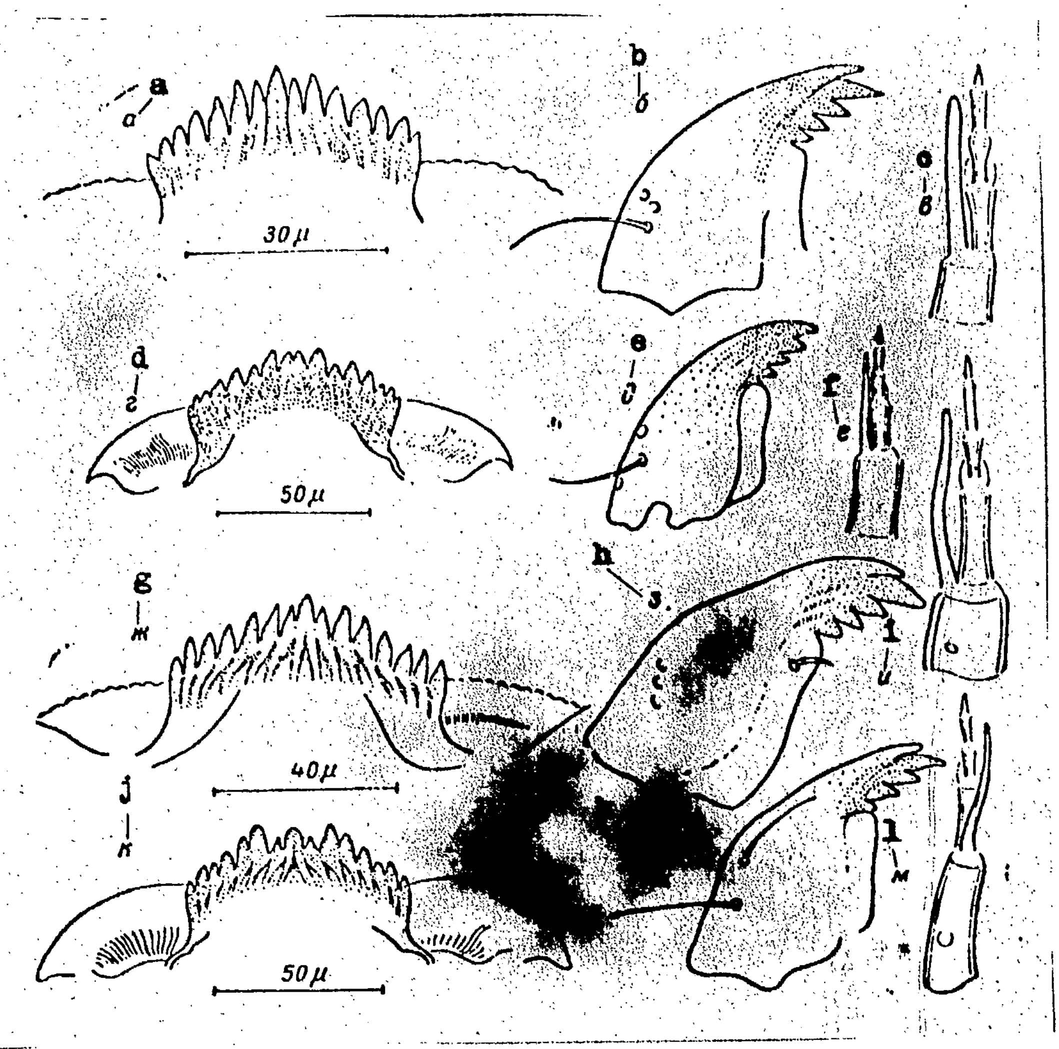

fig. 1. Details of the structure of the oral parts of larvae of Endochironomus impar and Camprochironomus tentans.

a - f End. impar (a - c - larva of the first stage, 15 x 60; d - f - larva of the second stage, 20 x 20); g - l - C. tentans (g - i - larva of the first stage, 10 x 60; k - m - larvae of the second stage, 7 x 60); a, d, g and k - submentum; b, e, h and k - mandible; c, f, i and l - antenna.

Larval stage II.

In the centre of the submentum (fig. 1, d) are two canines. Each of the centre canines is slightly shorter and considerably narrower than the first lateral canine. The bases of the central canines are located considerably more distally than the bases of the second lateral canines. There are seven lateral canines on each side. The first lateral canine are the largest, the second ones are shorter and narrower than the third ones, the fifth are almost equal to the sixth, and the seventh canines are small. The canines of the submentum and the strip uniting them are brown. The light stripes on the submentum are clearly visible. The paralabial plates have a sharp external corner bent beak-like towards the base of the head, and an almost smooth front edge. The radial striation is clearly visible. The mandible (fig. 1, e) has five brown external teeth, four of which are true and one false. The index of the antenna (fig. 1, f) is 0.73. The colour of the larvae is pink.

Thus, after the first moulting in the larvae of End. impar the structure of the oral parts changes considerably: the shape of the submentum changes completely (the tricuspid central tooth turns into a bicuspid one, instead of the six gradually diminishing lateral canines there develop seven canines with a ratio of teeth sizes characteristic of the larvae of the older stages) and the shape of the paralabial plates, the quantity of the mandible canines, etc., changes.

But in certain species of the chironomids the difference in the structure of stage I and stage II larvae is less sharply pronounced. Thus, grown larvae of the subgenera Chironomus s. str. Goet., 1937, and of Camptochironomus K., have a submentum with a tricuspid central canine, six lateral canines on each side, and a mandible with four external canines.

These factors make them resemble the larvae of stage I, which also have the above-mentioned characteristics. The difference in the structure of stage I and II larvae of these subgenera has a more subtle character and is not immediately evident. Let us, as an example, present descriptions of the larvae of stage I and II of one of these species, namely of Camptochironomus tentans.

Larval stage I.

In the centre of the submentum (fig. 1, g) is one triple canine. Its total width exceeds almost three times the width of the first lateral canine. The central portion of the central canine is longer and wider than the first lateral canine, and the lateral portions are slightly shorter and narrower than the first lateral canines. There are six lateral teeth* on each side. They all decrease gradually and slightly from the centre of the submentum towards its sides. The teeth of the submentum and the stripe uniting them are yellow; upon the latter we see clearly darker strips forming a number of sharp angles turned with their apices forward. The paralabial plates have a sharp external corner, which is not bent towards the base of the head. The front edges of the plates have uneven and rather large rounded denticles. The radial striation is visible. The mandible (fig. 1, h) has one yellow internal and four light-brown external teeth. The sword-like seta is well visible. The index of the antenna (fig. 1, i) is 0.36; the arista attains the middle of the fourth segment. The segments of the abdomen have thin setae, which often break off in fixed material. The length of each of the setae is approximately one and a half times less than the width of the larva body. The ventral appendages of the body are absent. The newborn larvae are colourless, but they soon acquire a pink hue.

* Revisor's note. From here, please read "canine" for "tooth".

Larval stage II.

In the centre of the submentum (fig. 1, j) is one triple tooth. Its width is almost three times as great as the width of the first lateral tooth. Its central portion is wider, but considerably shorter than the first lateral teeth, while the lateral portions are shorter and almost three times narrower than the central portion. There are six lateral teeth /90
on each side. They decrease from the centre of the submentum towards its sides; the fourth lateral tooth is equal to or even somewhat smaller than the fifth one. The colour of the teeth and of the strip uniting them is light brown; darker strips are clearly visible upon the latter; these strips are similar to those of the larvae of stage I. The paralabial plates have sharp external corners bent towards the base of the head, and smooth front edges. The radial striation is clearly visible. The mandible (fig. 1, k) has one light internal and four brown external teeth.*) The index of the antenna (fig. 1,l) is 1.0. The eighth abdominal segment has ventral processes. They are straight and somewhat longer than the pushers. The seventh segment of the abdomen has no lateral processes; they appear only in larvae of stage III. The colour of the body of the larva is pink.

The idea of the high morphological uniqueness of the chironomid larvae of stage I was not sufficiently stressed by the researchers who carried out the cultivation of the larvae. This is explained by a number of reasons.

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*The fourth tooth lightens and decreases with age. In larvae of stage IV it merges with the base of the mandible.

Thus, for example, the structure of the larvae of all the four stages was described only for the representatives of the subgenera Chironomus s. str. and Camptochironomus, i.e., exactly of those subgenera in the representatives of which, as just mentioned, the larva is subjected in its first moulting to the least sharp changes. It is natural that in such cases the researchers basically only paid attention to the absence or the poor development in newborn larvae of certain features inherent in adult larvae: hemoglobin and ventral processes of the body; they sometimes considered as absent those parts of the body which were poorly visible because of their transparency or because of their small size, as for example, the paralabial plates. Stuart (1941), who cultivated larvae which are subjected during the first moulting to very considerable changes, did not pay any attention to the structure of the oral parts of the newborn larvae. A.A. Zabolotsky (1937), who successfully cultivated Anatopynia plumipes larvae, did not establish any larval moultings, etc.

However, the idea of the replacement in chironomid larvae, during the process of growth, of two larval forms was expressed. This idea belonged to the authors, who, although they did not carry out any cultivation of larvae, nevertheless studied the structure of the oral parts of the newborn larvae, which differed very considerably morphologically from adult larvae (Thienemann and Zavrel, 1916; Dorier, 1933).

Of greatest interest to us is the statement of Dorier (1933), who knew the first and last stages of the Psectrocladius obvius larvae. Dorier believes that during the process of growth the P. obvius larva changes to such a degree that one may speak about the presence of two larval morphological types in this species: the first type, which lasts from the moment of hatching to the moment of a certain still not established moulting, and the second one, which ends with pupation. The author recommends that the larva of the first morphological type be called: "larvula"*, keeping the term "larva"** only for the larvae of the second morphological type.

Lacking material on the development of the larvae, the above-mentioned authors could not answer the question: how and when the "definitive form" originates from the "embryonal form" (the terminology of Thienemann and Zavrel 1916). Dorier expresses the assumption that the crucial moulting is the first moulting. Thienemann (1954), without presenting new data on the development of the larvae, expressed now the opinion that "larvula", in the /91 understanding of Dorier, is a larva prior to the first moulting.

Our data permit us to extend the opinion expressed by Dorier about the change in the larvae of P. obvius during the growth process of two larval morphological types, to many species of the chironomids. They support the assumption of this author concerning the crucial character of the first moulting. The data on the development of St. gibbus indicate that a change in the morphological type may also begin even prior to the first moulting (see p. 104).

2. Changes gradually accumulating during the process of the formation of an adult larva.

During the growth period of a larva an additional number of changes in its structure usually takes place; these changes are not connected with the change in the morphological larval types. Such changes were disregarded by the authors, who justly noted the transforming significance of the first moulting, but who incorrectly considered it as the only and final stage in the formation of the larva (Miall and Hammond, 1900; Dorier, 1933; Kettisch, 1938).

*Revisor's note. Appeared in text as "larvule".

**Revisor's note. Appeared in text as "larve".

Gradual changes that take place during the moultings.

A number of morphological transformations connected with the moultings take place in the larvae gradually with each of the three moultings. With each of the moultings the relative length of the ventral body appendages increases. Apparently the increase, with age, of the index of the antenna is characteristic of all chironomids (Chernovsky, 1949; Konstantinov, 1952). In all the larvae whose development we have observed, the basal segment of the antenna in larvae of stage I is considerably shortened. During the first moulting the index of the antenna increases the most, but still does not attain its final size characteristic of an older larva: it increases somewhat with each subsequent moulting. Neither are the oral parts of the larvae fully formed after the first moulting: with each subsequent moulting the sharpness and the relative length of their teeth decrease, the sclerotization of certain portions intensifies or, conversely, decreases sometimes the number of certain small parts increases (denticles and incisions), sometimes the lateral notches are smoothed gradually out on the central tooth, pairs of some lateral teeth come closer etc. A good example of such changes is the formation of the submentum in the Chironomus cristatus larva (Branch, 1923).

Gradual changes unconnected with moultings. A number of gradual changes in the larvae are not connected directly with the moultings. Thus, during the course of the entire growth period the quantity of haemoglobin increases in the larvae. Its presence becomes noticeable at different times in different species: in larvae of Chironomus anthracinus, Camptochironomus tentans and of Endochironomus impar the pink color becomes visible, according to our observations already at stage I, in End. tendens at stage II, in Glyptotendipes glaucus and Gl. gracilis at stage III, while in End. albipennis, most often, only at larval stage IV. A certain elongation of the ventral appendages of the body during the period between moultings, occurring evidently, from the smoothing-out of the folds of the larval integuments, may also serve as an example of such changes.

We consider it most beneficial for the correct interpretation of larval development to distinguish clearly the morphological changes connected with the change of morphological larval types from the changes that gradually take place in the process of larval growth. By distinguishing the changes /92 in these two groups it is easier to foresee the path to be taken by the change in the structure of various larvae. Thus, for example, taking into consideration the changes in these two groups, one has to doubt the correctness of the hypothesis expressed by Zavrel (1926), that the Zavrelliella marmorata larva moults twice before attaining its final form. Chironomid larvae usually do not attain their final form during the second moulting, because the subsequent period of growth, in particular the third moulting, adds to their structure still a number of changes. One might assume that Zavrel meant by the "final form" merely the second morphological larval type according to our understanding; however, even the latter in the chironomid larvae is not attained after the second larval moulting, but already after the first one.

3. Temporary changes.

Besides the changes of the first and second groups, the accumulation of which characterizes the formation of an adult larva, within the framework of each stage we observe also a number of temporary changes reversible within the framework of the larval phase. Some of them are connected with the wear of the cultiɑular cover of the larva at each stage. Towards the end of the existence of a stage, the teeth in the oral portions are somewhat worn off, they become more blunt and lower, sometimes they merge with each other or are even broken off. Thus in larvae with a bicuspid central tooth of the submentum, this tooth, when worn off, loses its central incision and becomes in its exterior appearance similar to a simple tooth. Also the physiological condition of the larva probably changes within the boundaries of one stage: thus, we have noted that a freshly moulted larva has a lower concentration of haemoglobin in the haemolymph than a larva of the preceding stage that is close to moulting. The freshly moulted larva, in the same way as a larva freshly hatched from an egg, has different proportions between the size of the head and of the body than the larvae close to moulting; the chitinous portions in such a larva are still only faintly coloured.

4. Changes connected with the insect's transition from one phase of metamorphosis to another

In chironomid larvae, in the same way as in certain other insects with complete transformation, we observe changes connected with transition of the insect from one metamorphic phase to another. These are the features that remain a certain time in the larva after the hatching from the egg (for example, the presence of embryonal yolk in the intestine) and the characteristics of a nymph occurring in larvae towards the end of stage IV (for example, on the back of larvae of Gl. glaucus "rocket-like traces" begin clearly to shine through, and the thoracic segments swell and whiten).

Thus during the process of its growth the larva is subjected to morphological changes of the following order: 1) changes connected with the change in the morphological larval type, and restricted basically to the period of the first moulting; 2) changes connected with the gradual formation of the adult larva, and those that take place during the entire growth period of the larva; 3) cyclic changes that occur within the framework of each stage; 4) changes connected with the transition of the insect from one metamorphosis to another.

At the present time, when data on the structure of growing chironomid larvae are still extremely scarce, such information on the direction of the changes in the morphological features of the larvae is acquiring a certain practical importance. Such information may help when identifying larvae of /93
stages II and III from existing identification tables, and prevent gross errors when identifying larvae of stage I. It indicates that the following should be considered during identification.

1. One cannot identify chironomid larvae of stage I from the existing identification tables constructed on the basis of morphological features of adult larvae, because at the first moulting a number of profound rearrangements take place in the structure of the larva. In particular, it would have been erroneous to classify as Chironomus s. str. Goet. and Camptochironomus K. all the larvae of stage I that have a submentum with six lateral teeth on each side, a tricuspid central tooth and a mandible with four exterior teeth, since according to our observations such features occur in newborn larvae of very many species. Because of the peculiarity of the structure of the chironomid larvae of stage I it is necessary to set up identification tables for these larvae. At the present time, it is possible

to identify a larva only after growing it to stage II. At the end of the chapter is presented a brief identification table of newborn larvae which is merely a first attempt to compile tables of such kind.

2. It is possible to identify larvae of age stages II and III from identification tables compiled on the basis of morphological features of adult larvae. It should, however, be taken into consideration that certain organs change in the larvae during the course of the entire period of growth. The trend of the changes to which the larvae of stages II - IV are subjected during the process of growth is as follows: 1) the relation between the dimensions of certain parts changes (the index of the antenna increases, the relative size of the head capsule decreases); 2) the ratio between the width and the length of certain organs changes; usually a tendency to their elongation is observed (an increase in the height of pencil receptacles, in the length of ventral processes, and in the length of the maxillary palpi); 3) the number of small body appendages increases (teeth of pseudoradula, notches on paralabial plates) and the disarticulation of certain body sections intensifies; 4) the sclerotization of the integuments and the concentration of the hemoglobin in the hemolymph are intensified, and because of this the colouring of the larvae becomes more intensive, etc.

3. One should not be guided during the identifications by features developing in the larvae only temporarily. Thus, for example, recently moulted larvae of stages III and IV may not be red, as according to the identification tables, but light green; in larvae close to pupation or

to moulting the double central tooth of the submentum if often worn off and resembles a simple tooth; in larvae that have moulted long ago and particularly in those that have hibernated, many teeth in the oral parts may be broken off; a recently moulted larva of stage IV may be half the size of an adult larva of the same species.

Identification Table for Newborn Chironomid larvae.

1 (2) Upon the hypopharynx is a glossa with four teeth on the distal end. The abdominal segments I - VII have upon each side three long setae................................ Tanypodinae (*Procladius* sp., *Ablabesmyia* sp., *Anatopynia plumipes* Fries., *An. varius* F.*).

2 (1) The glossa with four teeth is absent. The number of setae on the abdominal segments is different....................................

3 (8) The eyes of one side of the head are situated one above the other. At a magnification of 15 x 40, and at a certain diaphragmation, we see the front edge of the paralabial plates. The antenna consists of five segments. The distal edge of the second segment of the antenna has two opposing lauterborn organs. The abdominal segments I - VII have on each side two long setae, the front one of which may be shorter; on segment VII there may be only one seta on each side.. Chironominae (some). /94

4 (7) The central tooth of the submentum is either simple or tricuspid...

* The development of these four species was not studied by us; published data were used (Thienemann and Zavrel (1916); Zabolotsky, 1937; Morgan, 1949).

5 (6) The central tooth of the submentum is simple, approximately twice as wide as the first lateral one, with gentle steps on the sides. The submentum has three lateral teeth on each side. The arch of the submentum is concave. The mandible has four true black teeth. The rear pushers are cylindrical and longer than the segment carrying them. On the abdominal segments I - VI on each side there are two very long setae (twice as long as the width of the body segment); on segment VII there is one seta on each side..Stenochironomus gibbus F.

6 (5) The central tooth of the submentum is tricuspid. Its central portion is longer than the lateral portions and the first lateral teeth. There are six lateral teeth on each side. The teeth decrease uniformly from the center of the submentum to its sides. The submentum arch is convex. The mandible has four true exterior teeth. The lateral setae of the abdominal segments, are either approximately equal to each other (for example, in Endochironomus impar), or the front seta of each segment is shorter (for example, in Limnochironomus nervosus)........................

.... Chironomus plumosus L., Ch. anthracinus Zett., Ch. annularius Mg., Camptochironomus tentans F., Glyptotendipes glaucus Mg., Gl. gracilis K., Gl. imbecillis Walk., Endochironomus albipennis Mg., End. tendens F., End. impar Walk., L. nervosus Staeg., Polipedilum nubeculosum Mg., and many others)*.

7 (4) At the center of the submentum are two narrow teeth. There are seven lateral teeth on each side. The first lateral teeth are not wider than the central ones, but are rather shorter. The second lateral teeth are considerably wider and longer than the first ones. The subsequent five lateral

* These larvae differ in their finer morphological features, which are not considered here because of the temporary character of the tables.

teeth decrease [in size] gradually in the direction towards the sides of the submentum, the seventh teeth being very small. The abdominal segments I- VII have on the anal-lateral corners one long thick seta each, and in the middle of the lateral edges, one short thin seta each.....................................
....................<u>Microtendipes</u> <u>chloris</u> Mg.

8 (3) The eyes of one side of the head are one behind another and are markedly connivent; the front ocellus is several times smaller than the rear one. The paralabial plates are absent. The abdominal segments I - VI have on the anal-lateral corners one very long seta each (one and a half times longer than the width of the segment), and in the middle of each of the lateral edges of the segments there is one very short seta. The second lateral teeth of the submentum are not merged with the first ones. The mandible has no notches along the outer edge. The antennae are less than half as long as the mandibles...

..........Orthocladiinae (<u>Cricotopus</u> from the group <u>silvestris</u> F.)

Age Changes in the Biology of Larvae.

1. Peculiarities in the Biology of Newborn Larvae.

The literature contains data on frequent observation of a peculiar behavior in newborn chironomid larvae: they show a clear positive phototaxis, which is not characteristic of adult larvae of the given type, as well as an ability to remain for a considerable period of time swimming in open water. This is recorded for newborn larvae of <u>Chironomus</u> <u>gregarius</u> (Pause, 1918), Ch. cristatus (Branch, 1923), Camptochironomus tentans (Sadler, 1935), Cricotopus fucicola Edw., (Stuart, 1941), Ch. dorsalis (Konstantinov, 1951a, b, 1952, 1953), Glyptotendipes pallens and Gl. paripes (Mordukhay-Boltovskoy and Shilova, 1955) and for representatives of a number of other genera without any indication of species affiliation (Alexseyev, 1955). We have observed this phenomenon in all the chironomid species whose larvae the author had a chance to cultivate. According to information kindly supplied by L.G. Baz' and Yu. P. Silina, this phenomenon is observed also in larvae of Microtendipes pedellus Degeer, Limnochironomus lobiger K. and L. pulsus Walk.

Under laboratory conditions one always notices a characteristic behavior of the newborn larvae, which consists in the fact that many larvae that just have left the egg-mass do not remain in cases on the bottom, as is done by more mature larvae of pelophiles, fouling organisms or miners, neither do they wander about the bottom as do some predatory larvae, but gather at the wall of a vessel that is turned towards the light and beat against it, as if trying to come closer to the source of the light. The statement of Potonié (1936) (which at first glance appears to contradict our observations) that the freshly hatched larvae of Chironomus plumosus have supposedly a well-pronounced negative phototaxis, is probably based upon a misunderstanding: Potonié proceeded from the fact that newborn larvae contained in a Petri dish concentrate themselves near the wall of a vessel turned towards the light, at a point where a slight shadow from the glass wall falls upon the bottom of the dish. But he did not take into consideration that the larvae gather at this shadowed section because their movement is directed towards the source of the light, i.e., to the wall turned towards the light.

Under natural conditions the larvae of stage I show, just as in the laboratory, a peculiar behavior: for Chironomus cristatus (Branch, 1923), Camptochironomus tentans (Sadler, 1935), Cricotopus jucicola (Stuart, 1941), and for the representatives of a number of other genera (Alekseyev, 1955), we have data that the newborn larvae swim away to the illuminated portions of the water body, where they remain for a time at the surface of the water, accumulating here in considerable numbers. The presence of a temporarily planktonic form of life is recorded also for the Glyptotendipes larvae (Mordukhay-Boltovskoy and Shilova, 1955).

The peculiar behavior of newborn larvae has caused certain researchers to speak about the dispersing role of the larval juveniles. Here some authors (Forel, 1884: Mordukhay-Boltovskoy and Shilova, 1955) do not consider the newborn larvae able to regulate the stocking areas of the water basin, while others (Alekseyev, 1955) do not deny this ability in the newborn larvae.

To elucidate the biological importance of the peculiar behavior of these larvae we have endeavoured to determine the causes of their swimming upwards, the time they stay in the suspended state and the causes for their sinking. We succeeded to elucidate the following.

1. One cannot assume that the swimming upwards of the larvae takes place mechanically because of their small specific gravity. The larvae can swim upwards in quiet water only by means of active S-shaped movements of their bodies. When this motion is discontinued, the larva turns with its head downwards and begin to plunge at a rate of 0.4 - 0.7 mm. per second. However, the buoyancy of the bodies of newborn larvae is very high: even insignificant upgoing convectional streams formed by water evaporation in the vessel are able to stop the plunging of immobile larvae or even to pull them upwards.

2. One of the factors forcing the larva to swim up is the presence in them of positive phototaxis. Larvae of stage I, which have not yet built cases, move always very fast towards a bright source of light. Because of this, the active movement of the larva that leaves an illuminated egg-mass becomes immediately a directed movement. Having attained the surface of the water in a water body illuminated from above, or the glass wall in a vessel illuminated from the side, the larva beats against this boundary. Periods of active movement alternate with periods of rest. /96
Having ceased movement for a while, the larva may reach the substratum and built there its case. A larva that did not build its case will move (creep, swim), and its movement will again be directed by the source of the light, i.e., the larva may again swim up into the water mass. The larvae swim up particularly actively during the morning hours. Evidently, it is bright sunlight that is the cause of mass swimming up and the accumulation in the plankton of larval juveniles in small water basins that are well

penetrated by the sun (Branch, 1923; Sadler, 1935; Alekseyev, 1935). However, the light is not the only cause for swimming up. It has been established that the larvae may swim up also in darkness. Thus, newborn Endochironomus impar. larvae, having left the deep cylindrical egg-mass lying on the bottom, rose to a height of 45 cm even when the vessel had remained in complete darkness after the egg-mass was placed into it. Neither does the time of the transition of the larvae to a settled life on the substratum coincide with the moment of change in the larvae of the phototaxis sign. Although the phototaxis remains, as a rule, positive even in young larvae of stage II, the larvae are capable of building cases, according to our observations, already on the first day after emergence from the egg-mass.

3. It was noted that the length of the vagrant, in particular of the planktonic, period of life depends, in the newborn chironomid larvae, in the majority of cases only on the presence or absence in the substrate of suitable conditions under which the larvae may conduct a settled way of life. Thus, larvae of Chironomus anthracinus recently emerged from an egg mass and placed in cylinders on the bottom of which was a thin layer of plant detritus, began immediately to build their cases. After one hour, 30% of the larvae had already finished cases. The larvae in these cylinders did not even swim up. In the cylinders, however, which did not have on the bottom material for the construction of casings and for feeding, the larvae swam up and were beating at the illuminated wall of the vessel for many days, sometimes more than two weeks. The same phenomenon could be observed also in the Petri dishes: when a thin layer of detritus was present on the bottom, the larvae built cases on the day of their emergence from the egg mass, and only

rare individuals were swimming at the illuminated wall of the vessel; in the dishes, however, filled with pure tap water, larvae that had emerged from an egg-mass were pounding at the illuminated edge of the dish for several days until they starved to death.

One of the causes preventing the larva from settling and forcing it to come to the surface is overpopulation, which is occasionally observed in vessels where the larvae are kept. It should be noted that the larvae living in cases have no possibilities to build their cases too close to each other. The minimum distance between the cases is the body length of the largest of the neighbouring larvae. This is explained by the fact that the newborn larvae feed by intensively scraping up the substratum around their houses (chambers). Feeding in this manner, each larva hinders another one from rebuilding its house within the boundaries of its activity sphere. Therefore only a limited number of houses can have space on the bottom of the vessel. After the bottom of the vessel and the lower parts of the walls, which are slightly covered with detritus, are covered with cases, there is no place for the new larvae, hatched from the egg-masses later, to settle, and they swim up towards the source of the light and accumulate at the illuminated wall of a Petri dish or rise upwards in tall cylinders. Under conditions of such overpopulation the larvae often disturb each other trying to get inside each other's
cases. The larvae that have been disturbed often leave their houses and /97
join the larvae which are swimming in the water mass or which are accumulated at the illuminated wall of the vessel.

In such vessels the planktonic period of life of the larvae may be considerably prolonged. Thus, the larvae of *Chironomus plumosus* which had emerged from an egg-mass lying at the bottom of a cylinder (the bottom of the vessel was covered by a thin layer of vegetation detritus) behaved in the following manner. A portion of the larvae, during the very first days after their emergence from the egg-mass, covered the entire bottom of the cylinder with cases at uniform distances from each other. The remaining larvae, devoid already of the possibility to build cases on the bottom, rose upwards and for a period of 17 days were beating against the cylinder wall turned towards the light. At times they came up to an altitude of 30 - 40 cm, then plunged or temporarily settled on the bottom, in order to again swim upwards shortly after and join the larva group beating against the wall of the cylinder. Under the conditions of this experiment the swimming larvae, evidently, were feeding both at the bottom of the vessel during their short plunges there, and also in the suspended condition during their planktonic life.

The ability, while swimming, of newborn chironomid larvae to swallow food particles suspended in the water was noted by A.S. Konstantinov (1952 and 1953), who discovered that the swimming larvae of *Chironomus dorsalis* swallow particles of India ink suspended in the water. F.D. Mordukhay-Boltovskoy and A.I. Shilova (1955) also found particles of detritus in the intestines of newborn swimming *Glyptotendipes* larvae. However, in both cases the possibility was not excluded that the larvae were feeding at the bottom, during their brief plunges, or collecting ink and detritus particles from the walls of the vessel. The experiment below, it seems, proves the ability of newborn larvae to feed in suspended state.

In order not to give the newborn larvae an opportunity to feed during the experiment on the bottom, we placed them in a Torricelli tube filled with a suspension of India ink. The major part of the larvae during the experiment (it continued 30 minutes) moved from the tube into the dish. These larvae were considered as having left the experiment, since they had been in the vessel on the bottom of which ink particles might have been present. But concerning the larvae which after the end of the test were discovered in the tube, one might say with certainty that for them the possibility to feed on the bottom was excluded: the larvae that moved from the narrow (diameter 1 cm) tube into the wide dish, actually could not return into the tube during the experiment. In order that the larva should not settle upon the wall of the tube and scrape off ink particles settled here, the tube during the entire experiment was continuously and sharply rotated between the fingers (clockwise and then immediately counterclockwise). The larvae from the tube that were inspected after the termination of the test had nevertheless ink particles in their intestines. For the experiment were used newborn larvae of *Glyptotendipes glaucus* and of *Gl. gracilis*. The test was repeated several times and gave consistent results.

Speaking about the feeding of the newborn larvae, it is interesting to note that a certain quantity of embryonal yolk is found in their intestines. This fact was recorded by Miall and Hammond (1900) for the newborn larvae of *Ch. dorsalis*. It is possible that the yolk supports initially the existence of the larva, which, after emergence from the egg-mass, encounters conditions in which there is an acute shortage of food.

Thus the observations carried out to elucidate the biological significance of the swimming upwards of newborn larvae, have shown that the latter's stay in the plankton during a certain more or less prolonged period of time is not, evidently, necessary: under suitable conditions the larvae may settle immediately after emergence from the egg-mass. The capacity for a planktonic mode of life which the newborn larvae have (buoyancy and ability to feed in a suspended state), and the positive phototaxis characteristic of them, in accordance with which the light has a certain activating effect upon the larvae (it forces the homeless creeping larvae to tear themselves away from the substrate and to swim) - all these are adaptive features that facilitate for the larva the finding of suitable habitats and that aid it to avoid overpopulation. The young larva may settle many times upon the substrate and each time leave it again, if the conditions that it finds there are not suitable to it* The larvae which swim up may be taken and carried away by the waves and currents rapidly from places where the living conditions for the larvae were found to be unsatisfactory. In small quiet water basins, of similar importance, evidently, is the horizontal shifting of the larvae swimming after the movement of the sun. Naturally, not for all newborn larvae do these wanderings end favorably, and many larvae perish.

* Our data concerning the presence in the newborn chironomid larvae of selectivity in respect to the substrate agree well with published data concerning the presence of similar selectivity in pelagic larvae of many marine benthonic invertebrates (Savilov, 1949; Wilson, 1954 and others).

2. Changes in the Biology of Growing Larvae.

The biology of the chironomid larvae after their settlement upon the substrate continues to have certain changes during the growth process of the larva. In larvae a change of the phototaxis sign takes place. In Chironomus gregarius the sign of phototaxis changes to negative during the period between the beginning and the middle of the second larval stage (Pause, 1918). In Ch. cristatus (Branch, 1923) and in Camptochironomus tentans (Sadler, 1935) negative phototaxis was noted by the authors at the stage III. The change of the phototaxis sign in larvae of Chironomus dorsalis (Konstantinov, 1952) takes place after the first moulting. According to the observations of N.K. Alekseyev, 1955) the larvae of various ecological groups may lose the sharply pronounced positive phototaxis of stage II. According to our observations, the sign of phototaxis changes in a number of larvae during stage II. The sign of phototaxis has an effect on the selection by the larvae of the construction place of the case in the laboratory vessel.

There are only few published data on the age changes in the biology of settled growing chironomid larvae. According to the data of Alekseyev (1955) the miners and certain pelophiles live during the initial period in cases attached to the surface of the underwater portions of plants. According to our observations, the larvae capable of filtration feeding during the initial time feed (more often than grown larvae) by means of collecting detritus around their cases.

In larvae of certain species a regular gradual change in habitat takes place with age, a phenomenon that may be called age migrations. This phenomenon is well described by Branch (1923) for Ch. cristatus larvae: on the third and on the fourth days of their life the larvae of stage I build cases on floating portions of plants and upon projections of stones near the shore. While in stage II they occur considerably deeper than the stones and the vegetation, and during stages III and IV they plunge to the bottom where they lead the life of typical pelophiles. A similar phenomenon is recorded by N.K. /99
Alekseyev (1955) for the pelophile larvae of Chironomus f.l. plumosus and by A.F. Gun'ko (1955) for certain rheophiles. According to the data of L.G. Baz' (present compendium), in larvae of Microtendipes gr. chloris one observes also that, with age, migration from water level to the depth of the canal takes place. According to our observations, the phenomenon of the age migration is observed in the Ucha Reservoir in larvae of Chironomus annularius. Egg-masses of this species, attaching themselves to the surface of submerged objects, at times accumulate in considerable quantities at the littoral.* Here also stay the newborn larvae hatched from the egg-masses. However, adult larvae of this species live on the silty bottom of the sublittoral or of the profundal and do not occur on the littoral.

* Under natural conditions the females of the majority of chironomids drop egg-masses in water without attaching them to the substrate. Egg-masses of many species are capable of staying for a certain period of time on the water surface. The attachment of the egg-masses to the substratum takes place when the sticky portion of the slime of the egg-mass comes in contact with the surface of a submerged or a semi-submerged object.

However, apparently, it is not characteristic of all the growing larvae of the profundal to undertake considerable age-migrations from the water surface to the depth. Thus, during the period of the mass oviposition by another "deep-water" species, Chironomus anthracinus, its egg layings were not observed near the water surface. Adult larvae of this species are restricted more rigidly than larvae of the preceding species to greater depths of the profundal (Sokolova, present compendium). Its females throw the egg-masses far from the shore above those depth from where they emerged themselves. The egg-masses soon go down and plunge to the bottom approximately at those points where adult larvae of the same species are living. Similar oviposition, far from the shore, was observed earlier by other authors (Wesenberg-Lund, 1909, 1913; Zschokke, 1911; Thienemann, 1922 and others). There is no doubt that the fate of the larvae that have emerged from egg-masses occuring at considerable depth differs from the fate of larvae that have emerged from littoral attached egg-masses; it is, however, doubtful that larvae that have emerged from "deepwater" egg-masses would rise from a depth of many metres to the surface of the water, leaving places which were apparently specially chosen for them by the females (Kalugina, 1957).

Laboratory tests have shown that newborn larvae of Ch. anthracinus are capable of swimming in water similarly to the larvae of the littoral species. In a cylinder 0.5 m in height, illuminated from above by a bright lamp, they may rise to the very surface of the water, but in cylinders that are dark from the sides and poorly illuminated from above they do not rise higher than 12 - 15 cm.

In surface catches by means of a plankton net over considerable depths during the periods of oviposition of *Ch. anthracinus*, no newborn larvae of this species were detected in the plankton. However, in bottom catches by means of a Greze trawl (correct spelling unknown to the translator) we were finding larvae at these depths. The flight of *Glyptotendipes glaucus* took place simultaneously with *Ch. anthracinus*, the former being a denizen of the littoral. Its egg-masses are thrown by the females near the water level and are attached in mass quantities to submerged objects at the littoral. Newborn larvae of this species, without occurring in the same catches with the Greze trawl, were repeatedly caught in the above mentioned surface catches. Apparently, the newborn larvae of *Ch. anthracinus* that have emerged from egg-masses lying in the depth do not leave these depths, if they find there conditions suitable to them. It is possible that in poorly illuminated depths the larvae rise above the bottom to a small altitude, as they did in the laboratory vessels. Here they may be carried away by the bottom currents /100
to a certain distance from the egg-mass. No such considerable and regular age migrations of growing larvae, as one observes, for example, in *Chironomus cristatus* (Branch, 1923) apparently occur in species similar to *Ch. anthracinus*.

Growing and grown larvae of species in which until now one had not observed any great age-migrations, also have the ability to change places of habitation, looking for more favourable conditions. Thus, the predatory vagrant larvae of tanypods constantly move in search of food, and the semi-settled larvae of orthocladiae often wander. Even settled chironomid larvae living in cases may change their place of habitation. How often the settled larvae of the older stages may wander can be seen in the example of Endochironomus albipennis, the larvae of which live in cases on the surface of objects immersed in the shallows. The older larvae of this species so often leave their dwellings and are carried so far away by the waves, that their cases rapidly appear on any laboratory instruments hung on buoys far from the coast. Therefore in the Borutsky traps placed above considerable depths, often soon after the setting up of the instruments, to the astonishment of the researchers, begin to emerge green gnats of End. albipennis, the larvae of which, as we know, are restricted to small depths. The larvae of this species wander so often over a water body possibly because they have the ability to leave their cases at the least alarm: for example, during careful measurement of water in the dishes with the culture of End. albipennis larvae, the majority of them usually jump out of their cases and begin to swim in the water. During identical procedures the larvae of other miner species or of species living in cases demonstrate considerably less anxiety. Nevertheless these larvae also often occur in plankton. We have information that larvae of certain species leave their cases by night and swim about in the water. Such observations are made by Pause (1918) on Chironomus gregarius and by Sadler (1935) for stage III of the larvae Camptochironomus tentans. We had an opportunity to observe this phenomenon in adult larvae of Glyptotendipes gracilis, Gl. Glaucus and Endochironomus impar.

The larvae of these species are capable even of leaving the vessel by night in which they are kept, by crawling over the wall. All these wanderings are evidently connected with the search for better conditions. Thus, it has also been noted that at the slightest stagnation of the water the larvae usually leave their houses together and wander about the vessel. Also evidently the seasonal migrations of many chironomid larvae are connected with similar wanderings in search of more favourable conditions. However, not all the grown larvae succeed in actively leaving the places in which unfavourable conditions have occurred, and some of them perish. Thus, for example, during the winter in water reservoirs the miners of piles and stumps freeze to death when the piles and stumps stick out from under the ice and snow, when the water level drops.

3. Concerning Biology of the Nymph.

The behavior of the larvae of stage IV changes sharply prior to pupation. The larvae living in cases rebuild their houses. Thus, for example, the plant-tissue-mining larvae of Glyptotendipes imbecillis gnaw at one end of the mine a U-shaped fissure in the epidermis; this forms a valve through which the chrysalis may leave the mine. The larvae of Gl. gracilis make the epidermis thin at a small section at the end of the mine, and the chrysalis leaves it tearing through the center of /101 the thin layer.

The chironomid nymph does not eat. If artificially deprived of its house, the nymph usually cannot, anymore, build a new shelter and often perishes in such cases during the pupation.

According to the observations of A. A. Zabolotsky (1939) in the larvae prior to pupation, the negative sign of the phototaxis changes to a positive one.

Connection between the morphological and the biological age changes in larvae.

Zavrel (1926) explains the considerable morphological uniqueness of the newborn chironomid larvae by their primitivity and by their greater closeness to the ancestral larval form. It is difficult to judge the accuracy of the statement expressed by Zavrel on the basis of the limited material in our possession. The following fact, however, is evident. The elder larvae of the chironomids of various species (or various groups of species) have usually well-pronounced morphological distinctions used by specialists as taxonomic features. It is possible that the origin of a number of such features is connected with the narrow adaptability of the larvae of different species to different complexes, specific for each species, of environments. But, as a rule, in the structure of newborn larvae these morphological peculiarities are still not fully manifested. Consequently, the newborn larvae of different taxonomic and ecological groups manifest a considerably higher morphological similarity to each other than larvae of the same species when grown up. Thus, in species with extremely narrowly specialized larvae, the newborn larvae do not yet have any features of such a narrow specialization. A more extensive adaptability is beneficial to the newborn larvae, because after the emergence from the egg-mass they do not always succeed immediately in getting into conditions suitable for the development of the larvae of the species in question. Occasionally they have to live through a prolonged period of migrations and to exist for some time in the most disparate biotopes, sometimes completely unsuitable for larvae of the given species.

Let us follow through, using the example of Stenochironomus gibbus, the connection between the morphological and the biological age changes in a larva.

The larvae of Stenochironomus gibbus are narrowly specialized miners. In the Ucha Reservoir they occur almost exclusively inside rotten wood decaying in the water. The body of the grown larva Stenochironomus gibbus, resembling in its shape the body of a wood mining larva of the metallic wood borer [Buprestidae] is not adapted to moving outside of the substratum which it mines. It is not capable either of the wavy S-shaped swimming motions characteristic of chironomid larvae, or of the looping, measuring-worm movement equally characteristic of the same (terminology of Zenkevich, 1944). A larva artificially taken out from wood contorts helplessly on the bottom of the water vessel, until it attaches itself to a piece of wood, brought to it, which it begins to enter. In connection with the fact that such larvae cannot independently move about in the water medium outside of wood, it remains a mystery as to how the larvae of Stenochironomus gibbus after emergence from the egg-mass succeed in finding in a reservoir such a narrow specific biotope, as for example, an individually standing submerged tree stump. The study of the development of the larvae aids in answering this question. It turned out, that the newborn larva

St. gibbus is completely different in its external appearance and behavior from a grown larva of the same species. Let us compare the /102 larvae of stages I and II of St. gibbus.*

Where the grown larvae of St. gibbus have a body with an extended muscular thorax and a thin long flabby abdomen (Fig. 2, i), the newborn larvae have a body of the characteristic "chironomid" shape (Fig. 2, g) and swim well by means of S-shaped body motions. In larvae of stages II - IV the pushers are not adapted for crawling along the surface of the substrate: the front pushers look like a low ridge with short hooks, and the rear ones (Fig. 2, k) are very short and directed towards the rear. In newborn larvae, however, the front and the rear pushers are well developed and excellently adapted for crawling (Fig. 2, j). The oral portions of the newborn larvae (Fig. 2, a, b) are heavily /103 sclerotized, as in larvae of the subsequent stages (Fig. 2, d and e). But in their structure they are somewhat less narrowly specialized. Thus, a mandible of a moulted larva (Fig. 2, e) has a rectangular base. Its medial side is very wide and together with five teeth (from the side one sees only three of them) forms a wide concave "scoop", which is adapted only for the gnawing and swallowing of wood. The mandible of the larva of stage I (Fig. 2 b) has a triangular base. Its medial side is narrower, its teeth are arranged one above another. Such form of the mandible is more universal, and is characteristic of many omnivorous larvae. All this makes the newborn larvae adapted to search for suitable biotopes: they move easily within a free water medium and may exist at first in more diverse conditions than grown larvae. The distribution of the larvae of St. gibbus by stages is evidently carried out basically by this mobile life form, i.e. by the newborn larva.

*The description of the metamorphosis and of the larval stages of Stenochironomus gibbus is presented in a separate paper (Kalugina, 1958).

/102
(continued)

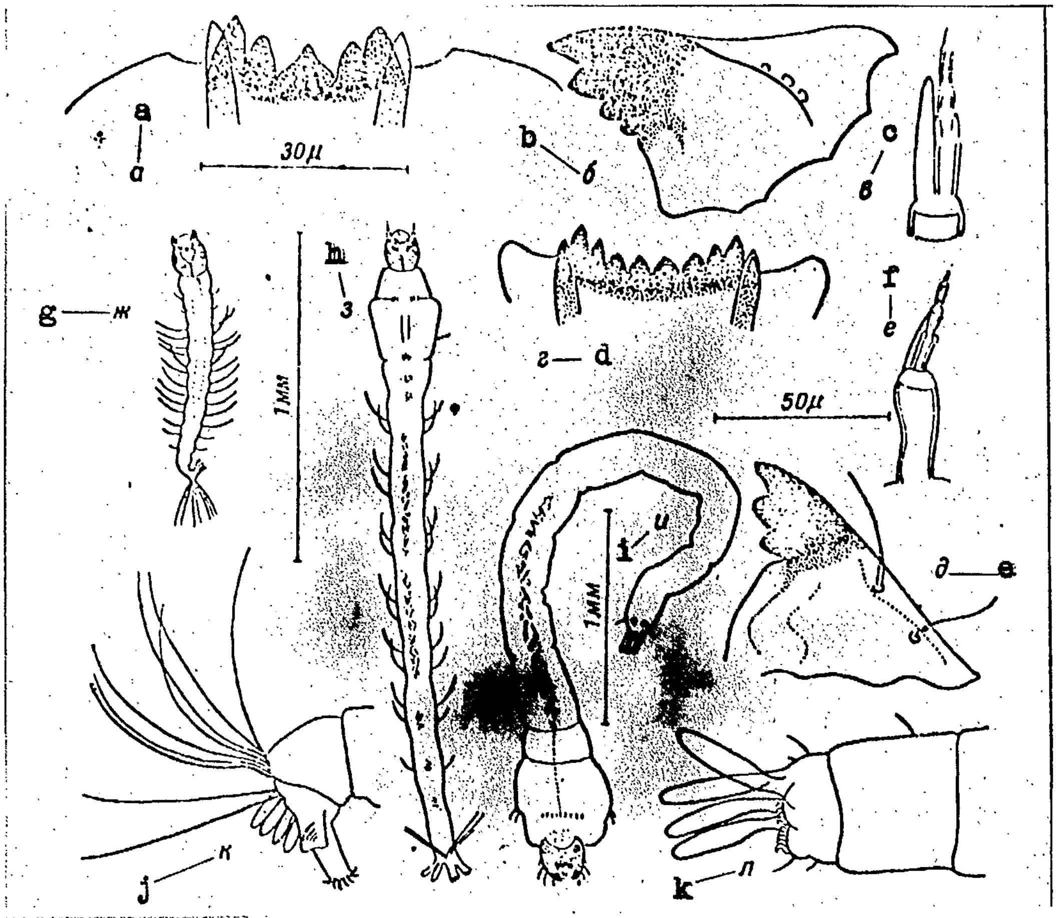

Fig.2 The structure details and general aspect of larvae of Stenochironomus gibbus.

a - f structure of the mouth portions and of the antennae (a - c - larva of stage one, 10x60; d - f - larva of stage II, 10x20); a and d - submentum; b and e - mandible; c and f - antenna; g - i - general aspect of the larvae (the bodies of the larva are somewhat flattened out by the cover glass); g - newborn larva (h - larva of stage 1 from wood; i - larva of stage II); j - the end of the body of a larva of stage I; k - the end of the body of a larva of stage II.

The above-mentioned morphological features bring the newborn larvae of St. gibbus closer in appearance to the grown mobile larvae of such species, as, for example, Endochironomus albipennis, than to their own grown larvae. It is possible that here is expressed the origin of St. gibbus from a form with a free-living mobile larva. However, a number of morphological features distinguishing the newborn larvae from not fully grown larvae, originate in them [the former] evidently, secondarily, in connection with their ability to lead a planktonic form of life. Thus, the newborn larva of St. gibbus has, besides the features of the mobile organism, also additional features of a planktonic organism: long setae protruding to the sides upon the abdominal segments. Most probably this is a secondary feature assisting the larva to stay in suspended condition during its wanderings.

In all the chironomid species whose development we had the opportunity to observe, the newborn larvae have a greater mobility than the grown larvae: they crawl better and swim considerably better. This may be explained by the special part the newborn larvae play in ontogenesis, which requires greater mobility. The female selects, only approximately, during oviposition, the biotopes of the future larvae. The larva that has emerged from the egg-mass has for the first time in its life to seek for itself a suitable microbiotope for its development, a fact which may be connected with considerable migrations. Furthermore, the larva that has emerged from the egg-mass is compelled in certain cases to avoid actively the crowding that may develop near the maternal egg-mass. In this connection it is interesting to note that in newborn larvae of St. gibbus the features of the mobile and the features of the planktonic organism are considerably more strongly pronounced than in young larvae of other species that have not lost their mobility even in the older larval stages. It appears here that the reverse relation is expressed between the ability of larvae of the first stage to migrate in a water body, and the mobility of larvae of older stages. Thus, not a single one of the newborn larvae known to us has such long setae upon the abdominal segments nor is capable of such fast movement in the water, as a young larva of St. gibbus of stage I: by means of sharp and frequent S-shaped movements of the body it moves very quickly through the water, being able to cross in 15 - 18 seconds such a vessel as a Petri dish. It is interesting to compare the movement rate in the water of larvae of stage I of different species (see table).

Table

Speed of Movement of Day-old Larvae

Name of organism	Length of body, in microns	Speed of Movement	
		Absolute in microns/ sec.	Relative
Chironomus plumosus................	910	2180	2.4
Glyptotendipes glaucus..............	800	1440	1.9
" gracilis.............	720	1750	2.4
" imbecillis...........	650	1688	2.6
Stenochironomus gibbus	710	4047	5.7
Endochironomus impar................	650	1379	2.1
" albipennis	650	1567	2.4

As we see from the table, the relative speed of movement of newborn larvae of St. gibbus is more than twice that of any other newborn larva among the species studied. This may be explained by the fact that because of the loss of the abilities of grown mining larvae of this species to move in a water body, the task of finding a suitable substrate is placed upon the newborn larvae to a greater degree than in other species, the larvae of which retain the ability to migrate at all the other stages: the place chosen by the newborn larva is already permanent for the grown larvae of St. gibbus. Furthermore, the narrowness of the biotope in whose conditions the larvae develop is apparently also important: search for tree stumps (and stumps with roots) dispersed in a water body involves very considerable migrations. Out of the six remaining species, the ones least adapted to life outside of the mined substrate are the grown larvae of Glyptotendipes imbecillis, which occur inside the fresh stems of arrowhead and rice. As we see from the table, the newborn larvae of this species also exceed somewhat the remaining ones in relative movement rate. It is possible that such a considerable rate of movement and the unusual length of the setae on the body segments in newborn larvae of St. gibbus will find, in future investigations, a different explanation. Thus, for example, one may assume that they are connected with the increase in the weight of the cuticula of the head in larvae of this species (during swimming they compensate the increased specific gravity of the larva).

The larval dimorphism recorded by us in St. gibbus which manifests itself in the change by the larva of its life forms during its development, does not constitute an exceptional phenomenon in the world of insects.

It should be noted that in our case the change in the life form of the larva takes place already prior to the first moulting. Having found a suitable substrate, the larva of Stenochironomus gibbus of stage I penetrates into wood, and soon thereafter changes the shape of its body. The thorax of the larva widens, while the abdomen elongates almost by three times. The larva acquires in this manner a "woodborer-like" shape of the body in the mature larva. A late larva of stage I of St. gibbus taken out of wood behaves the same as larvae of older stages of the same species: it wriggles helplessly on the bottom of the vessel, almost without propelling itself anywhere, and without showing any positive phototaxis. But right to the first moulting, it retains in the structure of its cuticular portions features of a mobile planktonic organism: long, retractable /105 pushers, setae upon the abdominal segments and long pencils. All these features are lost after the first moulting, when the larva obtains, in all respects, the features of narrow specialization. Thus, here the change of the life form somewhat forestalls, as it were, the complete change of the structure. Replacement of the cuticula is possible only after moulting, and in order to moult, the larva must grow, feeding intensively upon its specific food: wood, i.e., it must already prior to moulting switch over from its free form of life to mining.

Thus, in St. gibbus, because of the narrow, one-sided specialization of the larvae, it is easy to observe the connection between certain of their morphological and biological age changes.

CONCLUSION

From the moment a larva has left its egg to the moment of pupation a number of changes take place in its structure. The larvae of the first stage differ so much morphologically from the larvae of the three subsequent stages that for their identification is required a compilation of an independent set of identification tables. Changes that take place in the structure of the larvae after the first moulting have the character of small, gradual quantitative changes, a fact that permits the identification of larvae of stages II - IV according to the same identification table compiled with consideration of age changes of the larvae belonging to these stages. The chironomid larvae of stage I, because of a number of their morphological and physiological peculiarities, are well adapted to search for conditions suitable for them and occasionally also for larvae of all subsequent stages. During their wanderings, the biological cause of which is the search for better conditions, the larvae may disperse far in a water body, a fact contributing to the settlement of the individuals. The age changes in the biology of growing larvae have still been studied only to a limited extent. In the majority of species the larvae are not devoid of the ability to change the places of their habitation during all the stages of growth. In some species one observes a regular change, with age, of the habitation places, a phenomenon that may be called age migration of the chironomid larvae. A connection between certain morphological and biological age changes in the larvae is distinctly manifested in *Stenochironomus gibbus*.

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