DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE SKRIFTER, BIND VI, NR. 6

CONTRIBUTIONS TO THE METAMORPHOSIS AND BIOLOGY OF THE GENUS ATRICHOPOGON KIEFFER

(DIPTERA, CERATOPOGONIDÆ)

WITH REMARKS ON THE EVOLUTION AND TAXONOMY OF THE GENUS

BY

ANKER NIELSEN

1742

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1951

Det Kongelige Danske Videnskabernes Selskabs publikationer i 8vo:

Oversigt over selskabets virksomhed,
Historisk-filologiske Meddelelser,
Arkæologisk-kunsthistoriske Meddelelser,
Filosofiske Meddelelser,
Matematisk-fysiske Meddelelser,
Biologiske Meddelelser.

Selskabet udgiver desuden efter behov i 4to »Skrifter« med samme underinddeling som i »Meddelelser«.

Selskabets sekretariat og postadresse: Ny vestergade 23, København V.

Selskabets kommissionær: *Ejnar Munksgaard,* Nørregade 6, København K.

DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB
BIOLOGISKE SKRIFTER, BIND VI, NR. 6

CONTRIBUTIONS TO THE METAMORPHOSIS AND BIOLOGY OF THE GENUS ATRICHOPOGON KIEFFER

(DIPTERA, CERATOPOGONIDÆ)

WITH REMARKS ON THE EVOLUTION AND TAXONOMY OF THE GENUS

BY

ANKER NIELSEN

1742

KØBENHAVN
I KOMMISSION HOS EJNAR MUNKSGAARD
1951

CONTENTS

PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI

PREFACE

For several years I have been occupied by studies of the fauna in the great springs of Himmerland, a province in the northern part of Jutland. One of the localities investigated is distinguished by its very rich fauna of *Atrichopogon* larvæ and pupæ. Since the metamorphosis within this genus is not very well known, and since the larvæ living in the locality exhibit a very great diversity of body structure, I have found it worth while making this fauna the subject of special investigations, the result of which is presented on the following pages.

The terminology employed in the description of the cuticular processes and appendages of the developmental instars is the same as in my publications on the metamorphosis of Trichoptera. Especially my paper on the Hydroptilids (13), pp. 3 and 196—97 is referred to.

The laboratory work was carried out at the Freshwater Biological Laboratory of the University of Copenhagen. For financial aid granted by the Carlsberg Foundation I beg to offer my respectful thanks.

INTRODUCTION

In the locality described in the next chapter seven types of *Atrichopogon* larvæ were found. In order to refer them to species a series of rearings were carried out in the years 1947 and 1948. It appeared that two slightly different pupal types were reared from one of the larval types; differences could also be demonstrated in the imagines reared from the two pupal types. Thus eight species of *Atrichopogon* are represented in the locality (cp. however, p. 89). I did not succeed in rearing two of the species, which only occur in very small numbers. In the following chapters these two species are designated as *sp. x* and *sp. y*, respectively.

My endeavours to determine the six other species revealed the fact that it was impossible to find full accordance with any of the specific descriptions available. Indeed, so little has been worked at this genus, that in itself it is not surprising to find six new species in such a special locality. However, the taxonomy of the genus is a very difficult matter. Most of the characters which are employed in separating the species are of a quantitative nature, and though my material is not particularly great, it shows that these characters vary more within the same species than assumed in (most of) the available descriptions. Moreover, the descriptions are probably based upon pinned specimens, on which an exact measuring of some of these characters will be at least very difficult. Hence I was bound to run one of two risks: either to create new synonyms or to refer the larvæ and pupæ to wrong species. I have preferred the former possibility as the lesser of two evils.

Recently Søgaard Andersen has published a paper (19) on the subgenus *Chironomus*, in which he adduces evidence that several species of imagines can be reared from the same larval type, and that the same species of imago can be reared from several larval types. One of the possible explanations (as also has been pointed out verbally by Professor Spärck, Copenhagen) is that those characters which are employed to separate the *Chironomus* species actually are not specific, but characters which vary in the same way within the various species of the subgenus. To me this explanation seems the most probable, since the larval types among other things differ in an ecological respect. Hence, until more reliable imaginal characters have been found, the separation of the *Chironomus* species should rather be based upon the larvæ than upon the imagines.

Though my investigations will seem to show (pp. 88—89; Tables II—V) that those characters which are employed in the taxonomy of the genus *Atrichopogon* differ—at least statistically—in imagines reared from different larval types, the same may to some extent be the case in this genus: the species should so far be defined on the basis of the larvæ (and/or the pupæ) rather than on the imagines. The most important step towards getting the taxonomy of the genus in order will therefore be an exact description of the developmental stages. This will require very great work on the part of entomologists and hydrobiologists.

The metamorphosis of a number of species has been described by Müller (11, pp. 225—28), Speiser (16, pp. 738—40), Goetghebuer (5, pp. 176—80), Bangerter (2, pp. 248—52), Lenz (9, pp. 108—12), Mayer (10, pp. 212—16), and Thomsen (22, pp. 63—65). However, these descriptions are very brief.[1] They may —to a greater or less degree—serve the above-mentioned purpose of distinguishing between the different larval and pupal types, but from a morphological point of view they are of little value. In this respect the developmental instars, and more particularly the larvæ, of the genus must be said to be almost entirely unknown. Saunders (14, pp. 164—211; 15, pp. 252—72) has given excellent descriptions of the metamorphosis of some species of the genera *Forcipomyia*, *Apelma*, and *Thyridomyia*, which also belong to the subfamily Ceratopogoninæ. However, the larvæ and pupæ of these genera are rather different from those of *Atrichopogon*.

The very interesting pharyngeal skeleton of the Ceratopogonine larvæ has been described by Bischoff (3, pp. 14—15), Mayer (10, pp. 212 and 13), and Saunders (14, pp. 174—76 and 185; Plates X and XII). The descriptions of the former two authors are very brief and incomplete and in part quite unintelligible. Saunders' description of the pharyngeal skeleton in *Forcipomyia*, on the other hand, is good, though it needs some supplementary remarks and also some corrections, and the author has not been quite aware of the function of this organ.

As regards the biology of the immature stages we are not much better informed. Winnertz (7, p. 27) has reared *A.* (*Kempia*) *pavidus* Winnertz from larvæ found beneath the bark of trees. I have been unable to find any description of the larvæ and pupæ of this species. Speiser (16, pp. 738—39) found the larvæ of *A. winnertzi* Goetghebuer (6, p. 51) on the moist lower side of a piece of decaying wood lying on the forest-ground. The larva is very different from those described in the present paper and is more like the larvæ of the other genera of the subfamily. The latter is also the case with the larva of *A.* (*Kempia*) *hamifer* Goetghebuer, which according to Bangerter (2, p. 248) leads a terrestrial life, though in moist places in the vicinity of water, but "noch weiter vom Wasser entfernt" than the larva of *A. trifasciatus*. The larvæ of *A. trifasciatus* Kieffer and *mülleri* Kieffer have no small similarity to those of *speculiger* n. sp., *dubius* n. sp., and *cornutus* n. sp., described in the present paper. The former was found by Thienemann (10, p. 214) in brooks by Svarthöll-Kungsör in Central Sweden in "ganz niedriges Wasser im schwachen Fluss, so dass

[1] Unfortunately I have been unable to obtain the paper of Boesel & Snyder (4, pp. 37—46).

die Steine im Bach halb im Trockenen liegen. Larven am Wasserrand auf den Steinen, Puppen ganz auf dem Trockenen der Steine festgeklebt". This locality will seem to have some likeness to that described in the next chapter. BANGERTER (2, p. 250) states a very similar habitat: hygropetrically "auf nassem, faulendem Laub und auf aus dem Wasser ragenden, die Wasser gut aufnehmenden Steinen . . .". MÜLLER (11, p. 224) found the larva of *A. mülleri* in Thüringerwald in "ein sehr kleines Rinnsal, dessen Wasser kaum zwischen den Steinen hervortritt. Dort lebt auf der Unterseite der Steine, vielfach da, wo sie den Boden mit breiter Fläche aufliegen, eine kleine Fliegenlarve . . ." MÜLLER (11, p. 226) holds the erroneous view that the oval, smooth areas on the dorsal side (cp. p. 53) are locomotory organs, "Rückenbeine (Pseudopodien)". The larva of *A. thienemanni* Kieffer will seem to be very closely related to *alveolatus* n. sp. According to THIENEMANN it lives in springs in Holstein "frei auf feuchten Blättern und zwischen feuchten Moos" (21, p. 3). The larva of *A.* (*Kempia*) *fuscus* Winnertz has at least some similarity to that of *polydactylus* n. sp. GOETGHEBUER (5, p. 174) found it on a lump of green algæ which recently had been drawn out of a pond. Finally THOMSEN gives the following information about two North American species: "Larvæ of *A. websteri* Coquillet were found in algæ and on the sides of cement tanks of outdoor *Daphnia*-breeding pools at the Cornell University fish-hatchery . . ." (22, p. 63). ". . . larvæ of *A. perigrinus* Johannsen were found in blanket algæ near the shore of Spencer Lake, New York, as well as in algæ growing near the outlet of a spring in southeastern Missouri" (22, p. 64).

Thus it will be seen that the great majority of the *Atrichopogon* larvæ so far described lead a hygropetric life, though we also know terrestrial species (*pavidus, winnertzi,* and in part *hamifer*) and species which tend towards true aquatic life (*peregrinus* and perhaps *websteri*). In the following chapters it will be shown that within the genus *Atrichopogon* are represented not one, but more evolutionary trends from a terrestrial to an almost purely aquatic mode of life.

GOETGHEBUER (5, p. 175—76) has described the egg-masses of *A.* (*Kempia*) *fuscus* Winnertz. The very elongate, blackish eggs are, 120—150 in number, placed "en forme de rosette" in a gelatinous mass. MUNSTERHJELM (12, pp. 159—60) has observed the oviposition of two ♀♀ of *A. rostratus* Winnertz in aquaria. There is, however, reason to believe that the egg-laying in this case has not been quite normal.

DESCRIPTION OF THE LOCALITY

The beautiful small river Lindenborg Aa runs in a south-northward direction through the forest Rold Skov in an about 65 m deep and rather narrow valley. On the foot of the left (western) side of the valley there is, on latitude 56°48′43—48″ north and longitude 9°47′31—40″ east, a ground (Plate I, fig. 1) which should rather be called an extensive helokrene, if not for the fact that in a thermic respect it is very far from having the character of a spring.

The ground in question, the length of which is 200 m (parallel to the river) and the width 40 m, forms a moist to swampy meadow, overgrown with mosses and low herbs, especially various grasses. In many places, particularly at the edge of the rills mentioned below, there are tiny puddles. Here and there on the lower part of the ground there are small groups of bushes and low trees (*Juniperus, Picea, Alnus, Betula*). The soil must, if anything, be termed a (strongly humified) spring bog peat. The outflowing water runs to the river through a number of small, stony rills (Plate I, fig. 2). Under normal circumstances the water-flow of the rills is very small in proportion to their size; hence the velocity of the current is only small, though the gradient of the bed is very steep. The bottoms of the rills are covered by a very thin layer of water, and all stones over the size of a walnut emerge. Thus the rills must be characterized as a hygropetric locality. Generally the flow of water is very constant, but under special circumstances it is subject to considerable variations. During and after heavy showers of rain the rills become torrents, the water foaming over the totally submerged stones. It is, no doubt, just this fact to which the rills owe their existence; the normal flow of water would by no means be great enough to erode a stony bed.

The meadow slopes towards the ESE at an angle of 8°.7. The average slope of the entire left side of the valley is in that place 6°.4 (= 11.3 $^0/_0$), but in the part immediately above the meadow, the slope, to a vertical extent of 18½ m, is 15°.5 (= 28 $^0/_0$). By an about 170 m broad, rather level area (the bottom of the valley) the ground in question is separated from the right side of the valley, the average slope of which is 6° (= 10½ $^0/_0$). Since, moreover, the right side of the valley is entirely and the left side partly wooded, the locality is especially well protected from winds, and more particularly from the north-westerly wind, which in summer often is very cold. Immediately north of the ground the left side of the valley rises abruptly ten metres to form a sort of terrace, which contributes further to protect the locality from northerly winds. It is more exposed to easterly winds, though a dense growth of alder trees along the river together with the right side of the valley gives some protection. But in summer the easterly winds are nearly without exception warm winds.

Owing to the sheltered and sun-exposed position very peculiar conditions of temperature prevail in the locality. The rills are fed from the subsoil water, which flows out partly through the peaty soil at the edge of the rills, partly in the bottom of the latter. Already during the flow through the peat the water is to some extent influenced by the insolation, and to a still higher degree this is the case in the shallow rills. In Table I the results of a series of temperature measurements are given, and in the comments below is stated the division of the locality which may be made, among other things based upon thermic criteria.

In the table *a* and *b* designate the most typical rills of the locality; *a* is the largest rill, situated just south of a group of trees, and the one in which most of the biological observations have been made, *b* is various other and smaller rills. The table shows that during the whole warm season, even for more than half of the year, the temperature in these rills is considerably higher than the air temperature. In the case of favourable weather (clear sunshine) this is already the case in the beginning of April. The latter observation was made on the 10-4, 1947, after the exceptionally severe winter (the break of the frost occurred on the 22-3), and at the same time as in *a* a temperature of 4° above the air temperature was measured, there lay in places at the edge of the rills remnants of ice (but on a considerably higher level than the water level of that time; cp. below). And even as late as the beginning of November (2-11, 1942) the temperature of the water, in the middle of the day, was a little higher than the air temperature, moreover in unfavourable weather.

From the table it appears (see especially 21-7, 1947) that the absolute maximum temperature as well as the maximum deviation from the air temperature occurs in the early afternoon, at which time the deviation in the case of clear sunshine may be up to +9°. A remarkable exception from this was seen on the 23-7, 1947, with a very high air temperature. It must here be observed that the wind in the afternoon —during increase of temperature—turned towards the northeast, i. e. one of those directions from which the locality is least sheltered.

A comparison between the observations on the various days (thus especially between the 23-7 and the 28-7, 1947) will show that the absolute temperature of the water does not depend so much on the air temperature as on the insolation. However, in summer the latter, even in the case of dull weather (26-7, 1947), is strong enough to raise the temperature of the water somewhat above the air temperature.

Unfortunately I have no observations from very hot and clear days, which sometimes occur in the summer (1-8, 1948: 33°), but on such days the temperature of the water is, no doubt, also higher than the air temperature and may perhaps approach 40°. This will of course act as a limiting factor as to which animals are able to live in the locality.

Table I. The termic con-

In case several temperatures are mentioned, it means that several observations have been made in the rill in question. part. In b, however, the temperatures separated

Date	Hour	Temperature (centigrades)						
		Air	Water					
			a	b	c	d	e	f
6-1 1943	12	$-4^1/_2$	$1^2/_5$	$^2/_3$; $1^2/_3$	. .	$1^2/_5$	$3^2/_3$	$6^1/_3$, $5^2/_3$, $4^3/_4$, $3^1/_2$
10-4 1947	12	7	11	. .	. .	. .	. .	. .
	17	5	$7^1/_2$	. .	. .	. .	. .	. .
24-4 1946	12	$12^2/_3$	$16^1/_3$	. .	. .	. .	. .	. .
	16	. .	$13^2/_3$	. .	. .	. .	. .	. .
28-4 1943	13	14	$13^1/_2$–14	$16^1/_2$; 16; $14^3/_4$	. .	. .	. .	9, $10^1/_3$, 11
	16	13	$15^3/_4$	. .	. .	. .	. .	. .
3-5 1947	14	9	14	. .	. .	. .	. .	. .
	17	7	12	. .	. .	9	. .	. .
19-7 1946	12	22	27	. .	. .	. .	. .	. .
21-7 1947	10	22	23, 24, 25	. .	. .	. .	. .	$10^1/_2$
	13	$22^1/_2$	29	$26^1/_3$	$24^3/_4$	$19^1/_2$, 21, 24, 24	. .	$11^1/_4$
	14	$22^1/_2$	29	. .	. .	. .	. .	. .
	16	21	$26^3/_4$	23	. .	. .	15	. .
	17	. .	$24^4/_5$	. .	. .	. .	. .	. .
23-7 1947	12	24	29	. .	. .	. .	. .	. .
	14	27	$28^2/_3$	. .	. .	. .	. .	. .
	16	$26^1/_2$	27	. .	. .	. .	. .	. .
26-7 1947	14	$21^1/_2$	23	. .	. .	. .	. .	10
28-7 1947	13	$20^3/_4$	$24^1/_2$, $28^1/_3$, $28^1/_2$	$29^3/_4$; 27; 24, 27, 28	$24^1/_3$, 27, $23^3/_4$	$19^1/_2$, $23^1/_2$, $25^1/_4$, $24^3/_4$	$14^3/_4$, $17^1/_2$	$11^1/_2$, 14, $15^1/_5$
	14	$20^1/_2$	$28^2/_3$	. .	. .	. .	. .	. .
5-8 1947	13	22	$27^1/_3$	. .	. .	. .	. .	11
6-8 1942	16	17	. .	18; $17^1/_2$	. .	. .	. .	$9^1/_2$, $12^1/_2$, 13, 14
2-11 1942	14	9	$9^4/_5$	. .	. .	. .	. .	$8^2/_3$, $8^2/_3$, 9

ditions in the locality.

The first mentioned temperature has been measured in the uppermost part of the rill, the last mentioned in the lowermost by semicolons have been measured in different rills.

g	h	i_1	i_2	i_3	i	Observations
..	..	6, $2^1/_2$	$3^3/_4$	2	1	Light, though cloudy, weather after an—at least partly—clear night. At 8 o'clock the temperature in Rebild, 4 km from the locality, was —6°. See also p. 12.
..	..	..	..	..	..	Bright sunshine. Easterly wind.
..	..	..	..	..	..	
..	..	..	..	..	..	The morning was very windy, the sky half to almost entirely cloudy. At 12 o'clock it is clearing up, but still half-cloudy, and it is still very windy. The wind is southerly and felt rather much in the locality.
..	..	..	..	..	..	
$16^1/_2$	$11^1/_2$	..	..	..	..	Strong wind. Before noon rather cloudy, no sunshine. At 12 o'clock the temperature was only 11°. After noon half-cloudy with some sunshine and some few small showers.
..	..	..	..	..	..	
..	..	..	..	..	..	Bright sunshine. Fresh, easterly breeze.
..	..	..	..	..	..	
..	..	..	..	..	..	The air temperature has perhaps been a little higher earlier in the day. Half-cloudy, gathering thunderstorm.
..	..	..	..	..	..	Light to fresh breeze from the east. The morning half-cloudy. Sometimes it looked like showers. After 10 o'clock several and long bright periods.
..	..	..	..	..	..	
..	..	..	..	..	..	
..	..	..	..	..	..	
..	..	..	..	..	..	
..	..	..	..	..	..	From 9 to 11 o'clock the sky changed from half-cloudy to almost clear, though with a light mist. Light to fresh breeze from the south-east. In early afternoon it was more than half-cloudy. About 14 o'clock the wind turned towards the north-east, and it cleared up a little.
$28^1/_2$	$19^1/_2$	..	..	..	..	
..	..	..	..	..	..	
..	..	..	..	..	..	Cloudy, though with short periods of sunshine. It begins to rain a little.
..	..	..	..	..	..	Clear weather. Westerly wind.
$28^1/_4$	$20^1/_2$	$13^3/_4$	$25^1/_4$	..	$19^1/_2$	
..	..	..	..	..	..	Half-cloudy and slightly misty.
..	..	..	..	..	..	
..	..	..	..	..	..	Humid weather.

If the average deviation from the air temperature in the rills *a* and *b* in the time from 12 to 16 o'clock is computed from the observations at hand (which are not all given in the table), it gives for the season April 10th to November 2nd + 3°.91 ± 0.65, and for the month of July +4°.52 ±1.16. (The computation is carried out in the way that first an average for each day is computed, and from these averages again an average for the whole period). Too much importance should not be attached to these figures; the mean errors are very great, as was also to be expected, considering the—from a statistical point of view—few observations. However, it may be stated that the locality forms a "hydroclimatic enclave", representing a much warmer summer climate than that which now prevails in Denmark.

It will be noted (21-7, 10 o'clock; 28-7, 13 o'clock) that a considerable increase in temperature takes place from the upper to the lower end of the rills, at least in most of the rills.

In winter conditions are quite different. In periods of frost (4-1, 1947; 6-1, 1943) the rills are entirely frozen over. However, in several of the rills the uppermost part, only a few metres long, is ice-free; on 6-1, 1943, a temperature of more than $1^1/_2°$ was measured here. Likewise the ground is free of frost in many places just at the edge of the rills. The water which flows out in these places has to a great extent an outward flow above the ice already formed. Gradually the stones become entirely covered by ice, and the rills will resemble small glaciers. In many places the rills are frozen to the bottom; in other places the water is heard clucking beneath the ice, and in some few places, where this subglacial current is especially strong, there may be small holes in the ice.

The rills are fed by the subsoil water, and the temperature of the rills may also be compared with the temperature of the latter instead of that of the air. In the district the temperature of the subsoil water is $7^1/_2°$. From the above it clearly appears that in winter the rills are considerably colder and on summer days much warmer than the subsoil water. Unfortunately I have no observations from the night, but without drawing excessive conclusions, the following assumptions may possibly be made: Owing to the radiant heat absorbed by the stones and the bottom, as well as to the influence of the air temperature, the rills will also in summer nights be considerably warmer than the subsoil water, their temperature being almost like the air temperature, perhaps a little higher (early night), perhaps a little lower (late night) than the latter. In early spring and late autumn, however, the temperature of the rills at night is lower than that of the subsoil water. (About May 1st and October 14th, resp., the mean temperature of the day (24 hours) passes $7^1/_2°$).

The letters *c*—*f* designate rills which—to an increasing degree—differ from *a* and *b* by being more concentrated and hence not subjected to so great variations of temperature. *c* is a short rill just north of a group of trees and thus somewhat shaded. In summer its temperature is still higher than the air temperature, though not to so high degree as in *a* and *b*. It will be noted (28-7, 1947) that the highest temperature—closely approaching the temperature in *a* and *b*—is found in the middle part of the rill. This is due to the fact that there is rather a considerable outflow of subsoil water in the lower, more excavated and shaded part. *d* is the southernmost rill. In summer the temperature of its uppermost part is lower than that of the air; on its course towards the river its temperature rises considerably, but does not reach so high values as in *a* and *b*. *e* is a very short, deeply excavated rill situated entirely within the group of trees south of the rill *c*. In summer its temperature is almost midway between that of the subsoil water and that of the air, and the rill very much approaches a stenothermous character. Finally *f* is the northernmost and best watered rill. In its whole course it is much shaded by herbaceous marsh-plants. Especially in the uppermost part its temperature does not differ much from that of the subsoil-water, and the rill must be said to have the character of a true spring.

In periods of frost the rills *c* and *d* are very like *a* and *b*, though the ice-free parts are more conspicuous, especially in *d*. The rills *e* and *f*, on the other hand, are entirely ice-free, and appear like oases in the middle of snow and ice.

Along the foot of the slope a ditch has been dug, possibly at the end of the last century (*g*). This ditch is now almost entirely overgrown; in most places there are only some few centimetres of water above the muddy bottom. The greater part of the ditch is covered with grasses, between which there may be mosses. In some places there are growths of partly emerging Characeæ. Since the ditch receives its water from the rills, its temperature is of course influenced by the latter as well as by insolation. The outflow from *f* cuts through the ditch as a particular rill, and hence has no influence on the conditions of temperature, which in summer are entirely identical with those prevailing in *a* and *b*. In periods of frost the ditch is frozen over, and on 10-4, 1947 (after the severe winter) it was still almost entirely ice-bound, only with some minor holes.

In the part of the ditch below the mouth of the rills *c* and *e* the bottom is raised somewhat by washed-out gravel and pebbles. The part below *e* in Table I is considered as the lower part of that rill.

Between the ditch *g* and the river there is a 6—30 metres broad, level ground (*h*). It is covered by alder trees, between which there is a herbaceous vegetation (especially grasses and Cyperaceæ), and between the latter again a growth of mosses. (During the years of war a good many of the alders were felled for fuel, and conditions thus were somewhat altered). The ground is very swampy and in many places there are slowly flowing rills and small puddles with partly emerging moss. It is in the latter that the measurements of temperature (and the collections) have been made. The swamp *h* receives through *g* the outflow from the rills *a*—*e* (*f* cuts through the ground as a small brook), and hence its temperature is influenced by the latter. On the other hand it is rather much shaded, just as there will seem to be some direct outflow of subsoil water. In summer the swamp has always a somewhat lower temperature than the air, though it can by no means be said to have a stenothermous character. The conditions of temperature are almost as in the uppermost part of rill *d*. In periods of frost the swamp is frozen over, and on 10-4, 1947, it was still almost entirely frozen, though with small, open rills carrying water from the slope.

Finally some few measurements are given from a smaller locality somewhat south of that described above. A rill (i) is formed by the union of smaller rills (i_{1-3}). It will be seen that the conditions of temperature are very different in the various small rills, varying from an almost pure spring character to conditions like those in the lower part of rill *c*. On a very limited area there is thus an extraordinarily great thermic variation. Unfortunately the locality is much trampled by cattle, and hence is of no very great value for biological investigations.

In the rills *a* and *b* all the light-exposed surfaces of the stones are covered with several millimetres' thick incrustations of chalk, on the larger stones as high as the current—possibly in part by capillary action—keeps the surface constantly wet. The incrustations are due to the activity of blue-green algæ. Mr. E. Fjerdingstad, Virum, has kindly made the following analysis of this flora.

Cyanophyceæ.

Aphanocapsa rivularis (Carm.) Rabenh.
Calothrix fusca (Kütz.) Born. et Flah.
— *parietana* (Näg.) Thur.
Chlorogloea microcystoides Geitler
Chroococcus turgidus (Kütz.) Näg.
Chroococcopsis gigantea Geitler
Gloeocapsa æruginosa (Carm.) Kütz.
Dichothrix gypsophila (Kütz.) Born. et Flah.
Microcystis parasitica Kütz.
Petalonema crustaceum (Ag.) Kirchn.
Phormidium foveolarum (Mont.) Gom.
— *laminosum* (Ag.) Gom.
Plectonema puteale (Kirchn.) Hansg.
Rivularia Biasolettiana Menegh.
Stigonema mesentericum Geitler
— *informe* Kütz.

Chlorophyceæ s. lat.

Grongosira incrustans Schmidle
Scenedesmus quadricauda Breb. (One specimen)
Spirogyra sp. (One specimen)
Cosmarium sp. (One specimen)
Trachelomonas sp. (One specimen)

Diatomaceæ.

Amphora ovalis Kütz.
Cocconeis (*placentula*?) Ehrbg.
Cymbella microcephala Grun.
Denticula tenuis Kütz.
Epithemia argus Kütz.
— — var. *alpestris* Grun.
— *turgida* (Ehrbg.) Kütz.
Nitzschia angustata (W. Smith) Grun.
Pinnularia gracillima Gregory
Rhopalodia parallela (Grun.) O. Müll.
Moreover some indeterminable fragments of diatoms.

Mr. Fjerdingstad adds the following comments to this list:

"The list of species (except the diatoms) contains the results of more than 30 preparations and thus possibly is practically complete. As regards the diatoms five preparations have been made, and the number of species may perhaps be raised a little by the production of more preparations. . . . The blue-green algæ belong to a great extent to very difficult genera, for which reason a comparison with the exsiccates of the Botanical Museum has been made for a number of species.

The incrustations are chiefly built by the blue-green algæ *Phormidium laminosum* (Ag.) Gom., *P. foveolarum* (Mont.) Gom., and *Dichothrix gypsophila* (Kütz.) Born. et Flah., which on a rough estimate form more than 85 $^0/_0$ of the entire contents of plants. *P. laminosum* and *D. gypsophila* are both discussed by Pia in his paper: "Die Kalkbildung durch Pflanzen" (Beiheft zum Botanischen Zentralblatt, Band 52, 1934, pp. 14—15). The present incrustation is initiated by the *Phormidium* species mentioned above, after which *Dichotrix gypsophila* has appeared, and later on the others—mainly blue-green—algæ, the majority of which are known as chalk-forming species."

The chalk-incrustations are thickest in rill *a*, from which the above-mentioned analysis comes. Especially in rills *c* and *d* they are much thinner and perhaps of a different composition, which, however, has not been investigated. Finally incrustations are entirely lacking in rills *e* and *f*, in which the surfaces of the stones have exactly the same character as in the typical springs of the district.

The incrustations harbour a very interesting animal life. The fauna is dominated by larvæ of the beetle *Eubria palustris* Germar and the Stratiomyid fly *Hermione*. Besides larvæ of *Atrichopogon* play a great rôle.

THE IMAGINES

Only some few features which are employed in the taxonomy will be mentioned here. The most important characters are the shape of and the proportion in length between the joints of the antennæ and the equipment with setæ (macrotrichia) of the wings.

The antennæ are described as consisting of 14 joints. However, the big, almost globular joint which is designated as the first is actually the second joint. This among other things will appear from the fact that it contains the organ of Johnston, which is very well developed, especially in the ♂, in which sex this joint is considerably bigger than in the ♀. The first joint is represented by a narrow, sclerotized ring surrounding the base of the antenna and forming the articulation with the antennifer. Thus the antennæ consist of 15 joints, and in the following sections the antennal joints will be designated accordingly. (By comparison with other descriptions one must therefore be subtracted from the numbers used by me). In the ♀ (fig. 1; Plate II, figs. 1—3) the 3.—10. joints form the funicle of the antenna; the 3. joint is pyriform, the 4.—10. joints are globular or more or less compressed longitudinally. The 11.— 15. joints are elongate, cylindrical, and form a club. The 15. joint terminates with a small, finger-like process. In the ♂ (fig. 2; Plate II, figs. 4 and 5) the club generally consists of only three joints. The 3.—11. joints are somewhat more elongate than the 3.—10. joints in the ♀, and the 12. joint forms a transition to the joints of the club, its distal part being lengthened and cylindrical. In *cornutus* n. sp. the 12. joint is cylindrical in its whole extent, and some of the preceeding joints also approach this shape. In both the ♀ and the ♂ there is a lighter-coloured ring on the basal

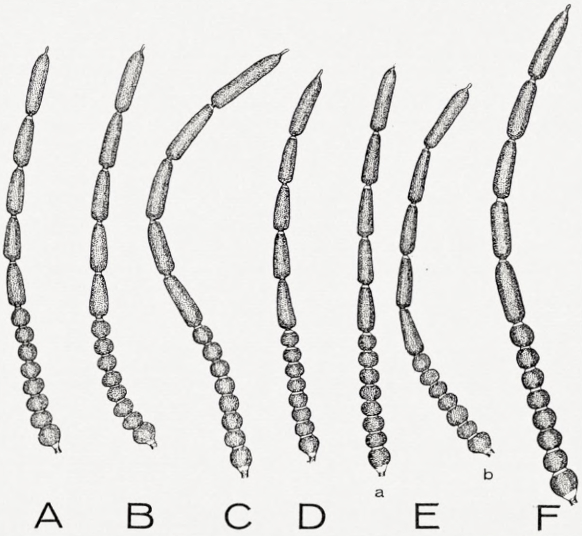


Fig. 1. 3.—15. antennal joints, ♀♀. A: *speculiger*; B: *dubius*; C: *cornutus*; D: *alveolatus*; E: *hexastichus*, a: normal, b: aberrant specimen; F: *polydactylus*. The setæ have been omitted. 75 ×.

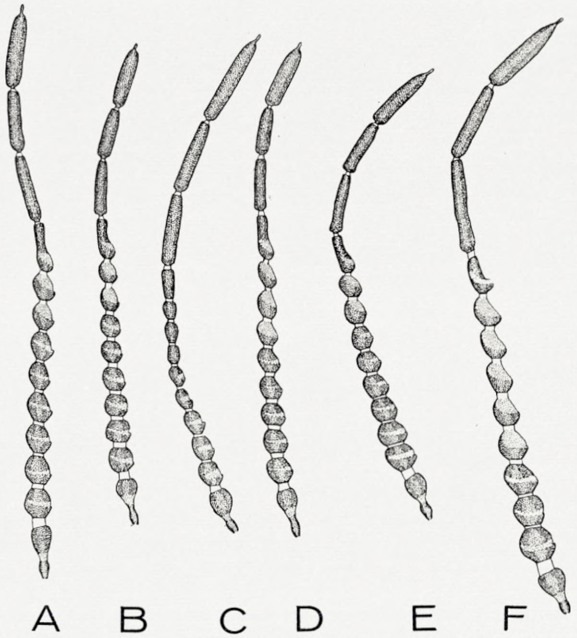


Fig. 2. 3.—15. antennal joints, ♂♂. Lettering as in fig. 1. The setæ have been omitted. 75 ×.

part of the 3. joint, which perhaps indicates that this joint is of a complex nature, so that the antennæ originally consisted of 16 joints. Especially the antennæ of the ♂ are suggestive in this respect, the 3. joint having a slight bulging proximally to this ring. All the antennal joints are covered with setæ. In the ♀ a circle of strong setæ, two to three times as long as the joint in question, around each of the joints 3—10, will especially be noted. On the 4.—12. joints in the ♂ the number of these setæ is very much increased, and only two of the setæ are developed as in the ♀. The rest, which are placed on the proximal margin of a membraneous area, are very long and very close-set. Together these long setæ on the 4.—12. joints form a "beard", which nearly reaches the apex of the antenna. In *cornutus* n. sp., however, the "beard" is more feebly developed and stretches only from the 4. to the 10. joint.

The proportion in length between the funicle and the club, especially in the ♀, is of great importance in taxonomy, and also the mutual lengths of the joints of the club have been employed. I have measured these proportions (Tables II and III; figs. 3—5) on antennæ mounted as slide preparations in Canada balsam. Between the individual joints there are short intersegmental membranes. In the proportion between funicle and club these membranes are included; in the proportions between the joints of the club only the sclerotized parts have been considered. I have found

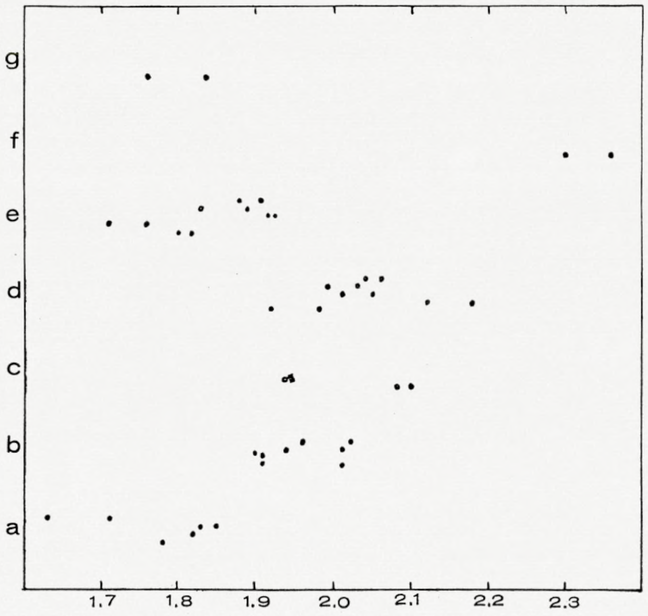


Fig. 3. Antennæ, ♀♀. Graphic representation of the proportion in length between the 11.—15. and the 3.—10. joints. a: *speculiger*; b: *dubius*; c: *cornutus*; d: *alveolatus*; ef: *hexastichus*, normal and aberrant specimen, resp.; g: *polydactylus*.

Table II. Antennæ. ♀♀.

The figures given in brackets are average values.

Species	Length of joints 11–15 in proportion to joints 3–10	Length in proportion to the 11th joint of			
		joint 12	joint 13	joint 14	joint 15
speculiger.......	1.63–1.85	1.00–1.07 (1.04)	1.06–1.18 (1.10)	1.08–1.18 (1.12)	1.43–1.93 (1.68)
dubius..........	1.91–2.02	0.98–1.12 (1.04)	1.08–1.21 (1.14)	1.08–1.29 (1.18)	1.45–1.71 (1.61)
cornutus........	1.99–2.10	0.95–1.08 (1.02)	1.07–1.16 (1.12)	1.18–1.28 (1.23)	1.66–2.00 (1.83)
alveolatus.......	1.92–2.18	0.90–1.12 (1.02)	0.90–1.08 (1.01)	0.90–1.16 (1.04)	1.43–1.73 (1.52)
hexastichus, normal	1.71–1.92	0.97–1.10 (1.03)	1.05–1.19 (1.10)	1.05–1.23 (1.12)	1.50–1.71 (1.60)
hexastichus, aberrant.........	2.30–2.36	1.06–1.11 (1.09)	1.03–1.08 (1.06)	1.11–1.16 (1.14)	1.62–1.66 (1.64)
polydactylus.....	1.76–1.84	0.92	0.94	0.92–0.98 (0.95)	1.33

Table III. Antennæ. ♂♂.

The figures given in brackets are average values.

Species	Length of joints 12–15 in proportion to joints 3–11	Length of joints 13–15 in proportion to joints 3–12	Length in proportion to the 12th joint of		
			joint 13	joint 14	joint 15
speculiger.......	0.87–0.89	0.60–0.61	1.40	1.21	1.67–1.68 (1.68)
dubius..........	0.85–0.98	0.59–0.65	1.35–1.57 (1.46)	1.10–1.38 (1.23)	1.53–1.82 (1.64)
cornutus........	1.07–1.17	0.85–0.91	2.40–2.67 (2.54)	2.42–2.48 (2.45)	3.25–3.40 (3.33)
alveolatus.......	0.80–0.84	0.52–0.58	1.08–1.34 (1.23)	1.02–1.19 (1.09)	1.39–1.75 (1.57)
hexastichus	0.84–0.94	0.58–0.67	1.44–1.67 (1.52)	1.15–1.40 (1.28)	1.47–2.04 (1.76)
polydactylus	0.94–0.95	0.71	2.19–2.25 (2.22)	1.81	2.31

these proportions considerably more varying within the same species than assumed in (most of) the specific descriptions available. Generally I have measured both antennæ of each specimen. In figs. 3—5 two dots placed on the same horizontal line denote the two antennæ of one specimen, and it will be seen that the proportion is not only different in different specimens, but that there may also be rather a great difference between the two sides of the same animal.

In addition to the antennæ the number and placement of the macrotrichia of the wing (Tables IV and V; Plate II, figs. 6—13) are the most important characters used in taxonomy. The terminology employed in the description of the wing will appear from fig. 6A. The "intermediate fork" is here considered the posterior main branch of the radius, which has lost its connection with sector radii (rs). The distal part of rs forms an anastomosis with r_1 (the radial cross-vein: r.c.). The cell between r_1 and rs is R_1. R_2 denotes the cell between c and $r_{2,3}$. The latter term is not quite correct, but since it is generally employed in descriptions of Ceratopogonids, it has been retained here. The vein r_3 is only faintly—often very faintly—indicated. The vein m is trifurcate; I consider the intermediate branch, which does not reach the margin of the wing, as m_2 and accordingly the posterior branch as m_{3+4}. Between m and cu there is a slightly indicated vein (s.v.), which does not reach the base of the wing; it is probably a secondary vein. The two anal veins are feebly developed.

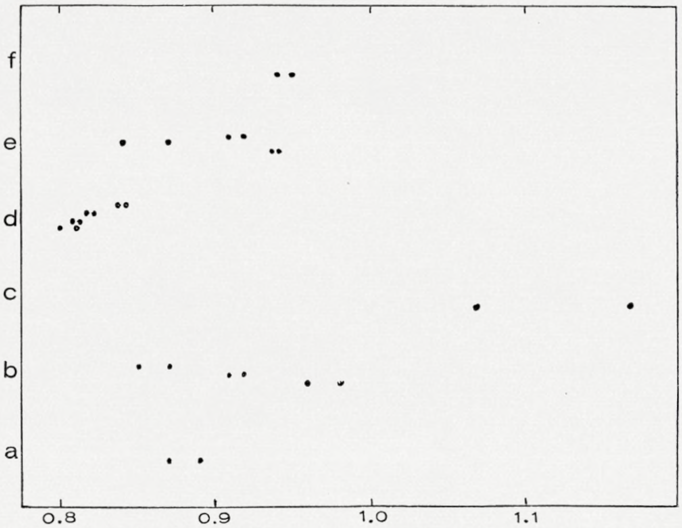


Fig. 4. Antennæ ♂♂. Graphic representation of the proportion in length between the 12.—15. and the 3.—11. joints. a: *speculiger*; b: *dubius*; c: *cornutus*; d: *alveolatus*; e: *hexastichus*; f: *polydactylus*.

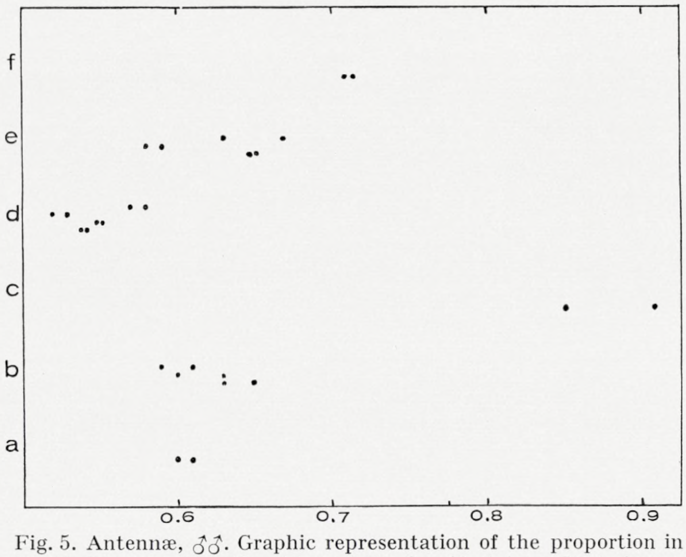


Fig. 5. Antennæ, ♂♂. Graphic representation of the proportion in length between the 13.—15. and the 3.—12. joints. Lettering as in fig. 4.

In all species and in both sexes the margin of the wing is covered with macrotrichia, which are much stronger on the costa than on the rest of the margin. The anterior half of the margin is rather densely covered with macrotrichia; on the posterior half they are placed in a single row, in which a longer and a shorter seta are regularly alternating. Besides, the following macrotrichia are of constant occurrence: One dorsally and quite proximally on r (fig. 6 B). One (rarely two) proximally on the ventral side of rs. One dorsally and distally on $r_{2,3}$, flanked by the two campaniform sensilla described below (fig. 6 C). This seta is the most distal—and in the ♂ generally the only one—of the macrotrichia on $r_{2,3}$. Further there is a number of light-coloured, semiglobular, campaniform sensilla: Proximally on sc one dorsal and two ventrals (fig. 6 B); the latter, which are placed a little more distally than the former, are comparatively small. One almost in the middle of the dorsal side of r_1, and one a little proximally to the middle of the ventral side of rs (fig. 6 C). Two distally on the dorsal side of $r_{2,3}$ (fig. 6 C). Finally there are about ten campaniform sensilla on the sclerites of the wing base. The other macrotrichia of the veins, if present, are placed ventrally on sc (only in *polydactylus* ♀), dorsally on r (in one *dubius* ♀ also one ventrally), dorsally and sometimes also ventrally on r_1, dorsally on rs, dorsally and ventrally on $r_{2,3}$, ventrally on $r_{4,5}$, r_4, and r_5, dorsally on m_1, m_2, cu, cu_1, cu_2, and a_2. Finally there may be a single dorsal or ventral seta on the radial cross-vein

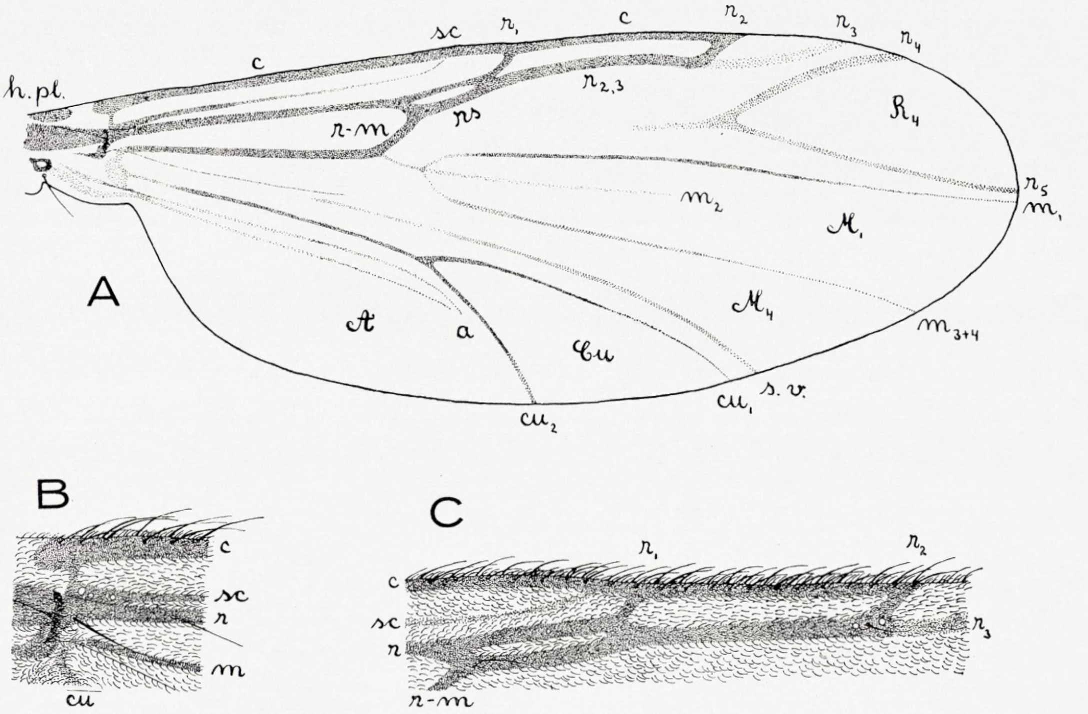


Fig. 6. A: *cornutus* ♀; veins of the wing; *h.pl.* humeral plate. B: *alveolatus* ♀; base of the veins c, sc, r, m, and cu. C: *alveolatus* ♂; the cells R_1 and R_2. A: 60 ×; B and C: 160 ×.

and (*polydactylus* ♀) one dorsal seta on r–m. In R_4, M_1, and M_4, the macrotrichia are placed both dorsally and ventrally, in Cu and A only dorsally. Generally the wings of the ♂ are much more sparsely furnished with macrotrichia than those of the ♀. The wings of the ♂ are also much narrower than those of the ♀.

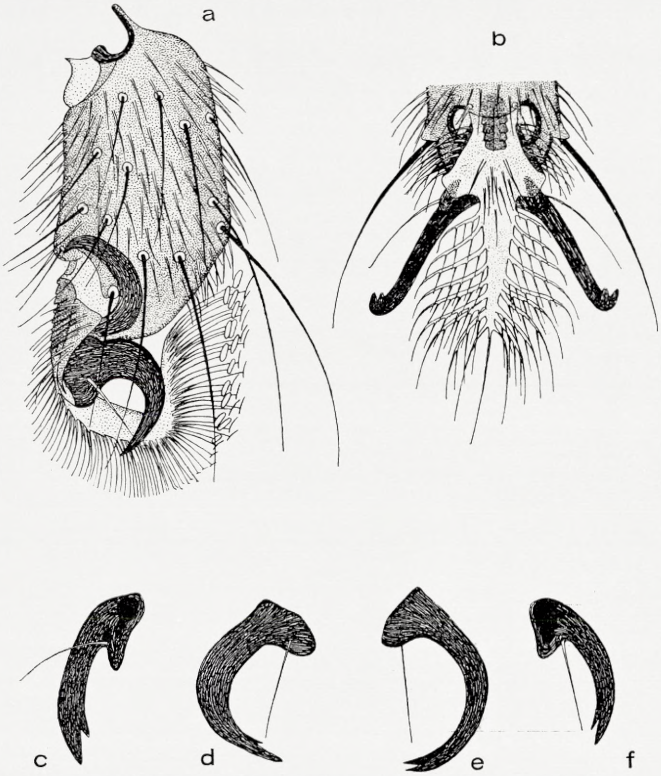


Fig. 7. *a*: right hind leg of *alveolatus* ♀: fifth tarsal joint and pretarsus in posterior view. *b*: right middle leg of *polydactylus* ♂: pretarsus and distal end of fifth tarsal joint in ventral view. *c—f*: claws of *polydactylus* ♀ (*c*: left middle leg, anterior claw; *d*: left hind leg, posterior claw), *polydactylus* ♂ (*e*: right middle leg, posterior claw), and *speculiger* ♀ (*f*: right middle leg, anterior claw). *c* and *f* are seen partly from the internal side, partly from the basal end, *d* and *e* from the external side. 615 ×.

Also the proportion in length between R_2 and R_1 plays a rôle in taxonomy. In this respect the same holds good as said about the antennæ: the proportion varies much more within the same species than assumed in (most of) the descriptions available. Thus I found in the two wings of an *alveolatus* ♀ the proportions to be 2.1 and 2.8, respectively.

The measurings and countings are carried out on wings mounted as slide preparations in glycerine. If the constantly occurring macrotrichia mentioned above are the only ones on the vein in question (or on the side in question of this vein), they are not given in Tables IV and V. The length of the wing is measured from the proximal end of the humeral plate to the apex of the wing.

Proximally on the external side the tarsal claws (fig. 7 c–f) carry a slender, hair-like spinule, which is almost as long as the claw itself. Except in *alveolatus* ♀ (fig. 7 a; and one aberrant *hexastichus* ♀) the claw has a bifid apex. Generally the internal tooth is smaller than the external one, but in the ♂♂ of *alveolatus* and *polydactylus* (fig. 7 e) the two teeth are of equal size. The empodium is a narrow and rather thick, membraneous plate, longer than the claws. In most species its lower side is shaggy with simple, hair-like spinules; in *alveolatus* ♀ (fig. 7 a; and one aberrant *hexastichus* ♀) the spinules on the distal part of the empodium are developed as small, long-stalked sucking discs. In *polydactylus* (fig. 7 b) the empodium is narrower than in the other species and carries two rows of vigorous spinules, which—except the most distal ones—are pectinate on the lower side.

Table IV. Proportions and

		speculiger	dubius	cornutus
Proportions	$\frac{\text{width}}{\text{length}}$	0.352–0.378	0.36–0.38	0.375
	$\frac{r}{\text{length}}$	0.31–0.32	0.31–0.37	0.296–0.306
	$\frac{r}{R_1 + R_2}$	0.91–0.98	0.88–1.07	0.82–0.88
	$\frac{R_2}{R_1}$	2.4–3.2	2.6–3.0	3.2–3.6
Macrotrichia, veins	sc	. .	. .	. .
	r	10–17	15–19	17–18
	r^1	2–8 dorsally 0–3 ventrally	7–9 dorsally 1–4 ventrally	5–7 dorsally
	rs	2–5	2–6	5–6
	$r_{2,3}$	10–14 dorsally 5–9 ventrally	11–15 dorsally 5–10 ventrally	15–18 dorsally
	r. c.	0(–1) dorsally 0(–1) ventrally	0(–1) ventrally	. .
	r–m	. .	. .	1 dorsally
	$r_{4,5}$	0–2 distally	1 to some few distally	distally
	r_4	$^1/_1$	$^1/_1$	$^1/_1$
	r_5	$^1/_1$	$^1/_1$	$^1/_1$
	m_1	almost $^1/_1$	almost $^1/_1$	almost $^1/_1$
	m_{3+4}	almost $^1/_1$	scarcely so far proximally as on m_1	almost $^1/_1$
	cu	2–6 in the distal $^1/_3$	distal $^1/_2$–$^3/_4$	distal $^3/_4$–$^1/_1$
	cu_1	$^1/_1$ or almost $^1/_1$	$^1/_1$	$^1/_1$
	cu_2	$^1/_1$	$^1/_1$	$^1/_1$
	a	8–17, more often 8–9	13–21	22–24
Macrotrichia, cells	R_4	almost $^1/_1$	$^1/_1$ or almost $^1/_1$	$^1/_1$
	M_1	distal $^1/_2$–$^2/_3$	distal $^1/_2$–$^3/_4$	almost $^1/_1$
	M_4	more often scarcely so far proximally as in M_1	just or scarcely so far proximally as in M_1	just as far proximally as in M_1
	Cu	2–6(11) distally	9–15 in the middle of the distal $^1/_2$	14–15 distally in the middle
	A	4–12(23)	(12)22–25	37–39

macrotrichia of wings. ♀♀.

alveolatus	hexastichus normal	hexastichus aberrant	polydactylus
0.355–0.400	0.35–0.38	0.37	0.378
0.31–0.36	0.30–0.35	0.32	0.296–0.300
0.86–1.06	0.94–1.05	0.96	0.80–0.83
2.0–2.8	2.3–3.0	2.5	3.62–4.06
. .	. .	. .	3 in the middle
9–16	10–15	12	17–18
5–7 dorsally 0(–1) ventrally	5–7 dorsally 0(–2) ventrally	6 dorsally	8 dorsally 3–4 ventrally
2–5	1–4	2	3–5
11–15 dorsally 0(–1) ventrally	9–13 dorsally 3–5 ventrally	19 dorsally	24–26 dorsally 15–16 ventrally
. .	0(–1) dorsally 0(–1) ventrally	. .	1 dorsally 1 ventrally
. .	. .	. .	1 dorsally
. .	0–1 distally	. .	distally
some few distally	distal $^1/_2$ to (more often) $^1/_1$ or almost $^1/_1$	some few distally	the vein is very indistinct
distal $^1/_2$–$^2/_3$, rather sparse	distal $^1/_3$–$^1/_1$	< distal $^1/_2$	$^1/_1$
distal $^1/_2$–$^3/_4$	almost $^1/_1$	distal $^1/_2$	almost $^1/_1$
distal $^1/_2$–$^3/_4$	scarcely so far proximally as on m_1	distal $^1/_2$	almost $^1/_1$
. .	0–2 distally	. .	almost $^1/_1$
distal $^1/_2$–$^3/_4$	almost $^1/_1$	5 in the distal $^1/_2$	$^1/_1$
generally $^1/_1$, but sometimes only 1 or some few in the middle	proximal $^2/_3$–$^1/_1$	2 in the distal $^1/_2$	$^1/_1$
0–3 distally	1–5 as far as the distal $^1/_2$	2 distally	24–27
distal $^1/_2$(–$^2/_3$)	(distal $^1/_2$–)almost $^1/_1$	distal $^1/_2$	$^1/_1$ or almost $^1/_1$
distally	distal $^1/_3$–> $^1/_2$	distally	almost $^1/_1$
0–3 distally	almost as far proximally as in M_1	. .	almost as far proximally as in M_1
. .	0–8 distally	. .	26–28 in the distal $^1/_2$ or a little farther proximally
. .	0–7	. .	29–34

Table V. Proportions and macrotrichia of wings. ♂♂.

		speculiger	dubius	cornutus	alveolatus	hexastichus	polydactylus
Proportions	$\frac{\text{width}}{\text{length}}$	0.265	(0.25) 0.28–0.30	0.32	0.29–0.31	0.27–0.29	0.265
	$\frac{r}{\text{length}}$	0.38	0.34–0.37	0.32	0.35–0.39	0.33–0.36	0.37
	$\frac{r}{R_1 + R_2}$	1.65	1.41–1.55	1.03	1.43–1.55	1.55–1.67	1.62
	$\frac{R_2}{R_1}$	2.3	2.1–2.4	3.1	1.55–1.95	2.1–2.3	4.1
Macrotrichia, veins	r	4 on the proximal $^1/_3$	. .	14	. .	. .	6 on the proximal $^3/_4$
	r_1	. .	. .	2 dorsally	. .	. .	. .
	rs	. .	. .	2 on the distal $^1/_2$	. .	. .	. .
	$r_{2,3}$	. .	. .	18 dorsally	1–2 dorsally and distally	1–2 dorsally and distally	2 dorsally and distally
	r_4	. .	. .	3 on the proximal $^1/_2$	. .	. .	. .
	r_5	. .	. .	a little less than distal $^1/_2$	. .	. .	. .
	m_1	. .	. .	almost $^1/_1$	0–1 a little distally to the middle	. .	. .
	m_2	. .	. .	almost $^1/_1$	. .	. .	. .
	cu	. .	. .	2 distally	. .	. .	. .
	cu_1	. .	. .	$^1/_1$	. .	. .	. .
	cu_2	. .	. .	4 on the proximal $^2/_3$	. .	. .	. .
	a	. .	. .	$^1/_1$ (11 setæ)	. .	. .	. .
Macrotrichia, cells	R_4	. .	. .	almost $^1/_1$	. .	. .	1 dorsally in the middle
	M_1	. .	. .	distally in the anterior $^1/_5$; the field continues in a single row of setæ, which reaches the middle of the cell	. .	. .	2 dorsally and rather distally
	M_4	. .	. .	10 in the distal $^1/_3$	. .	. .	1 rather distally
	Cu	. .	. .	2	. .	. .	. .
	A	. .	. .	7	. .	. .	. .

In contrast to many (not to say most) other insects the genital appendages (the "hypopygium") are of very little value in taxonomy, being extremely uniform in most species. The harpagones are generally simple, claw-like. In a small group of species (of those treated in the present paper only *cornutus*; fig. 8) its shape is, however, a little more complicated.

For the sake of clearness I have found it most convenient to give the taxonomic characters of the antennæ and the wings in tabular form (Tables II—V). In the descriptions below the number of species on which the measurements and countings are based is stated. This does not necessarily mean that more specimens of the species in question have not been reared. The holotypes are in the Zoological Museum, Copenhagen, preserved partly in alcohol, partly as slide preparations.

A. speculiger n. sp. (figs. 1 A, 2 A, and 7 f; plate II, fig. 6). Thorax dark brown, shining; the "shoulders" and the scutellum a little lighter. Halteres white. The abdomen and the legs are much lighter than the thorax.

Scutellum with two pairs of longer bristles. The internal tooth of the apex of the claw is about half as big as the external one. Empodium with simple spinules.

Length of the wing: ♀: 1.34—1.59 mm; ♂: 1.65 mm.

Holotype: ♀ (rearing no. XXIX; antennæ and right wing mounted as slide preparations). Allotype: ♂ (rearing no. IX; head, right wing and hind tarsus, as well as the abdomen mounted as slide preparations). Paratypes: 3 ♀♀. Measurements and countings based upon 4 ♀♀ and 1 ♂.

The specific name is suggestive of the unpaired, oval, smooth and thin-walled areas ("mirrors") on the dorsal side of the segments in the larva.

A. dubius n. sp. (figs. 1 B and 2 B; plate II, fig. 7). Colour as in *speculiger*.

The scutellum with 1—3 pairs of longer bristles. In two specimens there was one more on one side of the thorax than on the other. Pretarsus as in *speculiger*.

Length of the wing: ♀: 1.55—1.85 mm; ♂: 1.52—1.53 mm.

Holotype: ♀ (rearing no. XXI; head, right wing, left hind tarsus, and abdomen mounted as slide preparations). Allotype: ♂ (rearing no. XXXII; head, wings, and abdomen mounted as slide preparations). Paratypes: 3 ♀♀, 2 ♂♂. Measurements and countings based upon 4 ♀♀ and 3 ♂♂.

The specific name is chosen because it may be questioned if the specimens recorded under this name actually are specifically different from *speculiger* (cp. pp. 88—89).

A. cornutus n. sp. (figs. 1 C, 2 C, 6 A and 8; Plate II, figs. 1, 5, 8, and 9). Thorax dark brown with yellow "shoulders" and scutellum as well as a pair of anteriorly narrower, posteriorly a little broader, yellow, longitudinal stripes. Abdomen lighter than the thorax. Legs yellow except the distal part of the external side of the femora. Halteres white.

The scutellum with 2—3 pairs of longer bristles. The internal tooth of the apex of the claw is $^1/_2$—$^2/_3$ as big as the external one (♀) or a little smaller than the latter (♂). Empodium with simple spinules.

In the ♂ the "beard" of the antenna is much more feebly developed than in the other species (Plate II, fig. 5) and restricted to the 4.—10. joints. The 9.—11. joints have a much simpler structure than in the other species, and the 12. joint is developed entirely as the joints of the club, except that it is much shorter. The abdominal segment IX (fig. 8A) is very broad. The harpagones have three teeth distally (fig. 8BC); the dorsal one is very blunt, the ventral one is the biggest and slightly bifid.

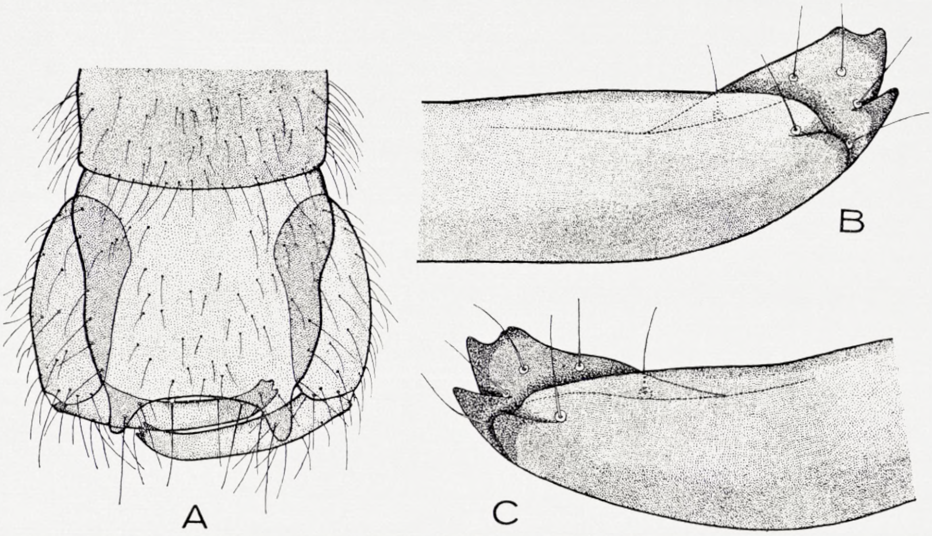


Fig. 8. *A. cornutus* ♂. "Hypopygium" in dorsal view (A). Apex of left (B) and right (C) harpagone in dorsal view. A: 80 ×; B and C: 500 ×.

Length of the wing: ♀: 2.01—2.08 mm; ♂: 1.88 mm.

Holotype: ♀ (rearing no. XIa). Allotype: ♂ (rearing no. XIV; head, right wing and hind tarsus, as well as the apex of the abdomen mounted as slide preparations). Paratypes: 2 ♀♀. Measurements and countings based upon 2 ♀♀ and 1 ♂.

The specific name is suggestive of the horns on the lateral side of meso- and metathorax in the pupa.

A. alveolatus n. sp. (figs. 1D, 2D, and 7a; Plate II, figs. 4 and 10). Thorax dark brown, shining; abdomen and especially the legs lighter. Halteres white.

Scutellum with one pair of longer bristles placed medially. In the ♀ the apex of the claw is simple, in the ♂ it its bifid and the two teeth of almost equal size. In the ♂ all the spinules of the empodium are simple, in the ♀ those on the distal part of the empodium are developed as small, sucking discs with a long stalk inserted a little eccentrically.

Length of the wing: ♀: 1.42—1.62 mm; ♂: 1.34—1.49 mm.

Holotype: ♀ (rearing no. XXXIX). Allotype: ♂ (rearing no. XXXVIII). Paratypes: 5 ♀♀, 4 ♂♂. Measurements and countings based upon 5 ♀♀ and 4 ♂♂.

The specific name is suggestive of the alveoloate, respiratory processes of the larva.

A. hexastichus n. sp. (figs. 1 Ea and 2 E; Plate II, figs. 2 and 11). Thorax brown, shining; the "shoulders" a little lighter. The colour of the scutellum varies from yellow to only a little lighter than the rest of the thorax, perhaps depending on age. Halteres white. Abdomen and legs yellow; the knees are, however, very dark.

The scutellum with 2—3 pairs of longer bristles. The internal tooth of the apex of the claw smaller than the external one. Empodium with simple spinules.

Length of the wing: ♀: 1.44—1.62 mm; ♂: 1.39—1.48 mm.

Holotype: ♀ (rearing no. XLb). Allotype: ♂ (rearing no. LIIc). Paratypes: 6 ♀♀, 3 ♂♂. Measurements and countings based upon 6 ♀♀ and 3 ♂♂.

The specific name is suggestive of the six rows of gills on the abdomen of the larva.

In all 17 specimens of this species were reared. Among these one ♀, reared from the aberrant pupa mentioned on p. 74, was aberrant. In this ♀ the number of joints in the antenna is reduced by one, so that the funicle consists of seven joints only (fig. 1 Eb; Plate II, fig. 3), which of course exerts a strong influence upon the proportion between the lengths of club and funicle (Table II). The 5. joint is comparatively big and carries an additional (distal), though very incomplete circle of big setæ. Thus the reduction in number has, no doubt, arisen through coalescence of the 5. and 6. joints. It is still more surprising that the pretarsus shows two characters which otherwise distinguish the *alveolatus* ♀: the claws have a simple apex, and the spinules on the distal part of the empodium are developed as small, long-stalked sucking discs. From Table IV it appears that the equipment of the wing with macrotrichia is comparatively sparse, in which respect the ♀ in question also approaches *alveolatus*.

A. polydactylus n. sp. (figs. 1 F, 2 F, and 7 b–e; Plate II, figs. 12 and 13). Thorax brown, shining, with small, darkish marks, among which a narrow, transverse band on the lateral side just behind the "shoulder" especially will be noted. Scutellum somewhat lighter. Halteres white. Legs yellow. Abdomen pale with a blackish marking on the dorsal side, consisting of broad, segmentally arranged, transverse bands, which in the middle are nearly quite broken by pale spots.

As in *A. rostratus* Winnertz the proboscis is extraordinarily long. Scutellum with two pairs of longer bristles. In the ♀ the claws are much stronger than in the ♂, and the internal tooth of the apex is smaller than the external one; in the ♂ the two teeth are of equal size. The empodium is narrow, with two longitudinal rows of strong, though slender spinules; the three distal ones (one unpaired, terminal) are simple, the others are pectinate on the lower side.

Length of the wing: ♀: 1.97 mm; ♂: 1.96 mm.

Holotype: ♀ (rearing no. LV). Allotype: ♂ (rearing no. LIV; head, right wing, middle and hind tarsi, as well as the abdomen mounted as slide preparations). Paratype: 1 ♀. Measurements and countings based upon 1 ♀ and 1 ♂.

The specific name is suggestive of the finger-like gills in the pupa.

All the species described above belong to the subgenus *Atrichopogon* Kieffer.

THE LARVÆ

The *Atrichopogon* larvæ are small animals, the size of the species described below being 1.9—4.3 mm. The body is broadest in the middle and most attenuated towards the posterior end. In most species it is rather flattened, chiefly owing to the fact that the lateral sides of the segments protrude into processes. In *sp. y* and *hexastichus,* however, these processes are filiform, and the shape of the body itself approximately cylindrical, though—as in the other species—the segments are separated by rather deep constrictions.

The very movable *head* (fig. 9) must be said to be of the orthognathous (= hypognathous) type with downward directed peristome. Certain features in its structure, especially the large, entirely sclerotized posterior side of the head capsule, however, indicate that the orthognathy is secondary, i. e. that *Atrichopogon* must be derived from ancestors with prognathous larvæ. In the following sections the terms dorsal, ventral, anterior, and posterior will be applied as if the head was typically orthognathous.

The head capsule is oviform and much attenuated towards the peristome. On each side three stemmata are found, placed on an almost semiglobular or (*cornutus* and *alveolatus*) more prominent dome (*the larval eye*) anteriorly and quite dorsally on the lateral side. The greater, distal part of the dome is hyaloid and on the top carries three facets, corresponding to three dark eye-spots, one of which is generally smaller than the two others and sometimes lacking. Somewhat behind the larval eye is a flatter, also hyaloid dome. Towards the end of the larval period some of the ommatids of the imaginal eye will be seen inside the latter dome. These ommatids are already at that time pigmented and thus possibly functional. In the following sections the dome will be termed *the imaginal eye.*

The most prominent appendage of the head is the big, spurlike *antenna* (fig.10). On closer examination it proves to be composed of two coalescent sensilla, of which the smaller median one is issued proximally on the bigger lateral one. In almost their entire length the lumina of the two sensilla are separated by a distally thinner septum. In the thin-walled apex the septum is lacking, and here a minute, internal, cuticular tube, probably the insertion of the sensory fibrils, is seen. The antenna is, no doubt, an organ of smell. It rises from a circular, membraneous area, which is generally situated on the top of a big, upward directed process, the antennal socle, laterodorsally on the anterior side of the head. In *sp. y* and *hexastichus* the membraneous area is almost semiglobularly vaulted, but the socle is lacking, and the antenna is not placed nearly so dorsally as in the other species.

The structure of the antenna deviates rather much from the description which Saunders (14, pp. 171—72) gives of the antenna in *Forcipomyia*. The same author

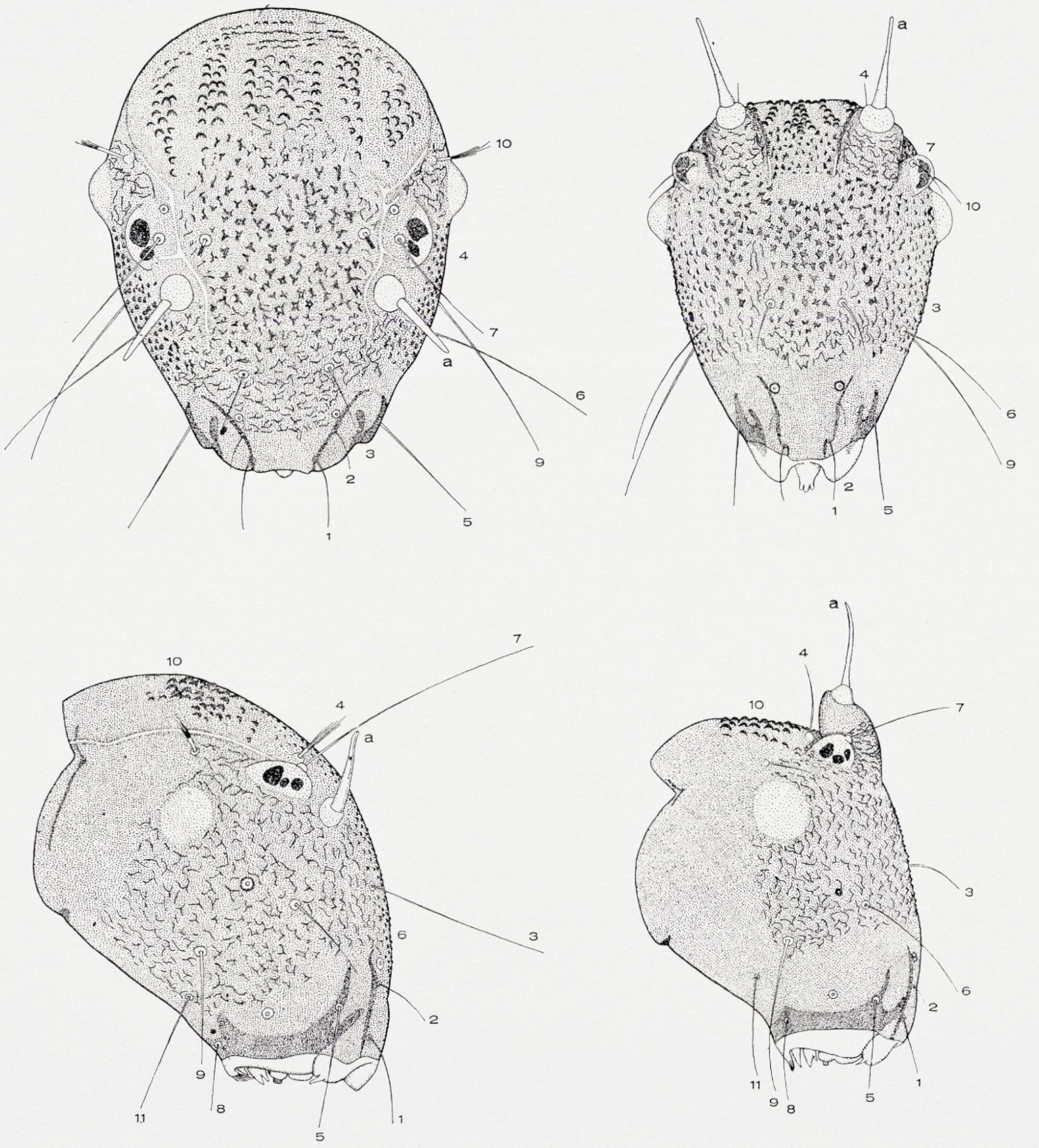


Fig. 9. Heads of larvæ of *hexastichus* (left) and *alveolatus* (right) in anterior (above) and lateral view (below). *a*: antenna; *1—11*: setæ. 130 ×.

describes other forms of antennæ again in *Thyridomyia* and *Apelma* (15, pp. 225 and 229). Thus it seems that the structure of the antennæ varies rather much within the subfamily.

Laterally on the dorsal side of the head a light, arched (laterally convex) line of weakness is found, which goes from the posterior margin of the head to a point medial to the antennal socle, and which most probably corresponds with the frontal suture. Thus frons comprises the greater part of the dorsal side of the head, and —as in many other Nematocerous larvæ—it borders on the foramen occipitis with a broad margin, the coronal suture being entirely lacking. In *sp. y* and *hexastichus* the frontal suture stretches, according to the more ventral position of the antenna, considerably farther ventrally than in the other species. Other sutures are not found, and the distal part of frons as well as clypeus (cp. p. 42) are not separated from the epicranium.

Ventrally on the anterior side of the head two pairs of darker lines are seen, which divide that part of the anterior side into three fields, an unpaired median one and a pair of smaller lateral ones. Each field is somewhat vaulted transversally. The two lines on each side converge a little dorsally. From the median one arises the *articulatory apodeme of the premandible,* from the lateral one the posterior leg of the apodeme which connects the articulatory plate of the mandible with the head capsule (for further details see below). The anterior leg of that apodeme arises from a shorter, black line, situated between the two dark lines and ventrally coalescent with the lateral one (fig. 11). The ventral end of the last-mentioned line marks the end of a broad, blackish stripe, which on the lateral and posterior sides stretches along the ventral margin of the head capsule, and which corresponds to a faint internal thickening. Latero-anally it has a small, triangular enlargement, which indicates the origin of the tentorium.

Fig. 10. Right antenna of *alveolatus* larva in anterior view. 500 ×.

The *tentorium* (fig. 14 A) consists of the posterior arm only, which as a sclerotized rod stretches laterally to the mouth cavity, approximately to middle of the head. It is somewhat sagittally compressed, especially in the distal part, which is divided into two branches; the anterior of these is a continuation of the shaft. At an acute angle with this branch originates from it a slender, downward directed, chitinous rod, whose apex is curved forward, and which seems to be connected with muscles moving the maxilla (see p. 39). This rod is described by Saunders, who erroneously assumes that it is "imbedded in the sides of the labrum to support it laterally". On the connections between the tentorium and the pharyngeal skeleton see below.

Saunders (14, pp. 174—75) describes the tentorium in *Forcipomyia,* though in details of a little different shape. He writes that "it is possible that this system of rods is derived from the tentorium, but at present there is no evidence to support such a view". I do not see any reason to doubt that it really is the tentorium. Saunders (14, p. 178), however, holds the erroneous view that these structures are situated in the wall of the mouth cavity.

The head capsule carries 12 pairs of setæ, which for the sake of clearness I shall designate with numbers. Setæ 1—4 are placed in a longitudinal row on the frontoclypeal region (which probably also comprises the labral sclerite; see p. 33). Seta 1 and 2 stand on the dark line from which the articulatory apodeme of the premandible arises, seta 3 approximately in the middle of the anterior side of the head, and seta 4 anteriorly on the dorsal side, behind the antenna. In *sp. y* and *hexastichus* seta 4, owing to the more ventral position of the antenna, stands on the anterior side of the head. Setæ 5 and 8 stand ventrally on the lateral side of the head, the former at the origin of the apodeme which connects the articulatory plate of the mandible with the head capsule, the latter at the origin of the tentorium. The last-mentioned number represents two setæ, of which, however, the lateral one is very minute and not quite easy to detect (fig. 11). Setæ 6 and 9 are placed somewhat dorsally to setæ 5 and 8, respectively. Seta 7 stands proximally on (in *alveolatus* almost in the middle of) the anterior side of the larval eye, seta 10 a little dorsally to the imaginal eye, and finally seta 11 rather ventrally and laterally on the posterior side of the head. Setæ 6 and 9 are the longest, seta 10 the thickest of the setæ of the head. Further there are four pairs of sensorial pits, one behind seta 2 (medially to the median of the two dark lines), one between the larval eye and the frontal suture, one between setæ 5 and 8, and one dorsoanally to seta 6.

It is possible to homologize the setæ and the pits with those described by Saunders (14, fig. 4, p. 171) in *Forcipomyia*. Since, however, there is no full agreement, I have preferred to designate the setæ with numbers instead of using the letters employed by Saunders. Below is given a comparison between *Atrichopogon* and *Forcipomyia* according to Saunders: seta 1: x; seta 2: lacking in *Forcipomyia*?; seta 3: t; seta 4: p; seta 5: w; seta 6: u; seta 7: q; seta 8: o; seta 9: v; seta 10: s; seta 11: y; the pit behind seta 2: z; the pit at the larval eye: r; the two lateral pits: lacking in *Forcipomyia*?

The anterior and the lateral sides of the head are covered with low, somewhat irregular nodules, which often pass into a partly reticulate sculpture of fine ridges. The dorsal side may have the same sculpture as the anterior and lateral sides (*polydactylus*), but generally it is provided with five longitudinal fields (an unpaired median one and two pairs of lateral ones) of big and tall, regularly rounded nodules. In *sp. y* there are only four fields, and the nodules are pointed.

The *apparatus of ingestion*. The mouth (fig. 11) has the shape of an approximately oval, longitudinal cleft, surrounded by a thick, membraneous, *peristomal fold* It leads into a cavity which, in a dorsal direction, stretches to the middle of the head (fig. 15). In the following sections this cavity will be designated as the mouth cavity, though various facts (the lack of circular musculature, the position of the labrum and the mandibles, and of the orifice of the salivary duct) show that it is a secondary structure, arisen by invagination, and that accordingly the functional mouth is not the morphological mouth.

The *peristomal fold* is differentiated into several parts. In front of the mouth it forms an unpaired, somewhat pointed process. It is the distal end of the *labrum* (figs. 11 V and 12 D) which as a high, membraneous fold projects from the anterior wall of the mouth cavity, which is nearly filled by it. In a proximal (dorsal) direction the fold becomes considerably lower, due to the fact that the antero-posterior width of the mouth cavity rapidly decreases. In lateral view the outline of the labrum falls into two parts: a distal, straight part, which forms an obtuse angle with the anterior side of the head capsule, and which by a rounded-rectangular corner is separated from the much greater, faintly convex, proximal part.

On the lateral side of the labrum lies a rod-shaped sclerite, which certainly represents the *premandible*. Its proximal end forms an articulation with a plate-shaped apodeme, which is issued from the median of the dark lines described above (p. 31). In anterior view the apodeme is approximately triangular, a little varying in shape in the different species (fig. 12 B C), in ventral view (fig. 12 A) it is quite narrow, proximally directed posteriorly and medially, but curved in such a way that the distal end points straight medially. The articulation between the apodeme and the premandible is effectuated in the following way: The latter is proximally bent at a right angle, so that the tongue-shaped, proximal end, which lies at the bottom of the furrow between the labrum and the lateral wall of the mouth cavity, points in a dorsal direction. At the point of curvature an apodeme is issued, which forms an internal continuation of the main part of the premandible. The proximal end of the premandible thus forms a fork, which ventrally and posteriorly embraces the distal end of the articulatory apodeme.

In their relations to the premandibles the articulatory apodemes have so great a resemblance to the tormæ of Chironomid larvæ that it is natural to assume a homology. This seems to show that the most ventral (and median) part of the anterior side of the head capsule represents the labral sclerite, which has entirely merged into the first mentioned one. In the Chironomid larvæ the tormæ are—as in other insects—external structures, in *Atrichopogon* they seem to be internal, which must be considered a secondary feature.

The tormæ of the *Atrichopogon* larvæ suggest those (apparently external) structures which Anthon (1, pp. 17—18) has described in various Nematocerous larvæ under the name of *Clypeussklerite*. Anthon's *Epistomalrand* (1, p. 15) is, no doubt, homologous with the ridge from which the tormæ arise in *Atrichopogon*.

On each side of the distal part of the labrum two single-jointed, cylindrical sensilla and a minute, club-shaped seta are found. The sensilla and the setæ of the two sides are arranged in two posteriorly converging rows, the setæ most anally. By a pair of longitudinal furrows the apex of the labrum is divided into three lobes of which the greater, median one projects most. At the bottom of each furrow three sense-organs are found: anteriorly a minute, thin seta and just behind it a sensorial pit, posteriorly a lanceolate (in the middle compressed) seta. Ventrally on the proximal part of the labrum two pairs of setæ and one pair of sensorial pits "ride" on the edge; on each side they are placed in a longitudinal row with the pit in the middle. The distal seta is smaller than the apical, lanceolate one, the proximal one is long and vigorous. Further there is a rather big, sensorial pit on the lateral side of the labrum. (I.a. the rich provision with sensilla, setæ, and pits shows that the organ is the labrum and not the epipharynx). The setæ as well as the pit arise at the bottom of deep, narrow invaginations. Hence their bases in lateral view are removed rather far from the edge of the labrum; in posterior view the two alveoles in each pair nearly touch.

On the edge of the proximal part of the labrum, between the distal seta and the pit, a rather strong and basally much sagittally compressed spine is found. In lateral view it is much attenuated towards the penicillate apex, in ventral view it is nearly equally thick in its whole length. Basally the two spines nearly touch. Proximally to the spines the edge of the labrum is covered with hair-like spinules.

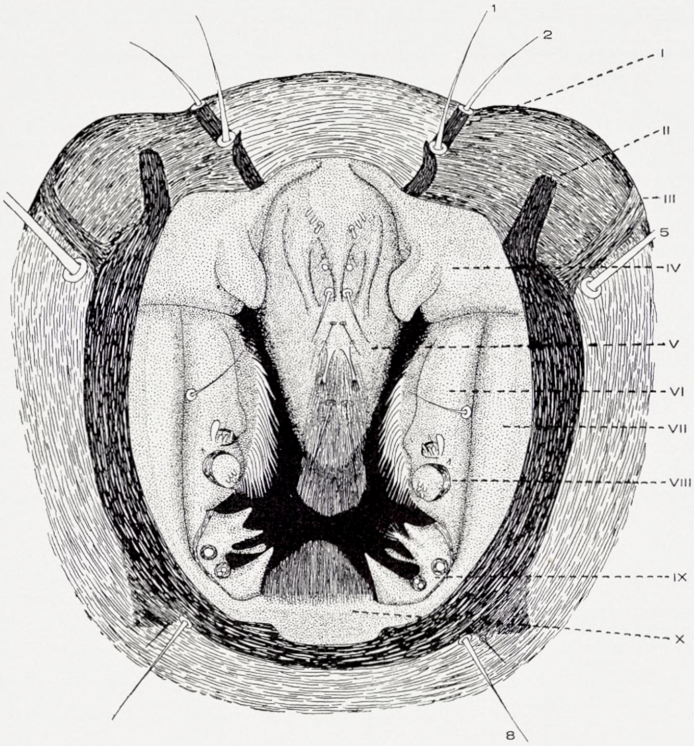


Fig. 11. *speculiger* or *dubius* larva. Peristomal field of the head in ventral view. *I*: origin of the articulatory apodeme of the premandible. *II*: origin of the anterior leg of the apodeme which connects the articulatory plate of the mandible with the head capsule; *III*: origin of the posterior leg of the same apodeme; *IV*: articulatory membrane of the mandible; *V*: labrum; *VI*: anterior maxillary lobe; *VII*: lateral part of the peristomal fold; *VIII*: maxillary palp; *IX*: posterior maxillary lobe; *X*: posterior part of the peristomal fold; *1*, *2*, *5*, and *8*: setæ of the head capsule. 500 ×.

The labrum is moved by three pairs of muscles (fig. 15, p. 45). A rather strong muscle (m. 1), inserted into the apex of the premandibular apodeme, issues from the area between the two antennæ. A more slender muscle (m. 2) issues from the anterior wall of the head capsule, dorsally to seta 3, and is inserted in the middle of the labrum near the edge. Where the two muscles cross, muscle 2 is lateral to m. 1. The third pair of muscles (m. 3) arise close together more ventrally on the anterior wall of the head capsule and are inserted proximally in the labrum near the edge. Muscles 1 and 2 correspond, no doubt, to the usual fronto-labral muscles, m. 3 probably to the compressor muscle of the labrum in other insects.

Proximally (i. e. dorsally) to the labrum and separated from this by a narrow, transversal cleft a smaller lobe projects from the anterior wall of the mouth cavity. This lobe, the *epipharynx* (fig. 15 VII, VIII) is somewhat broader than the labrum and only separated from the lateral walls of the mouth cavity by narrow clefts; in transverse section it is approximately rectangular, the width of the organ constituting the long sides. On the posterior side of the epipharynx there are two deep, semicircular (dorsally concave), transverse clefts. The fold which is demarcated by these clefts—in the following sections called the epipharyngeal comb—is incompletely paired through a small, median incision. Its free edge is densely covered with hair-like spinules, which point somewhat proximally. The epipharyngeal comb thus issues from a pouch-shaped, transverse furrow. The ventral side of the pouch is fused together with the ventral side of the comb, and in this part of the integument there is a sclerite—or rather an apodeme—composed of an unpaired middle part and two pairs of branches, a longer and weaker anterior one and a shorter and stouter posterior one. The former would seem to be connected with the anterior branch of the tentorium, a point which, however, I have been unable to decide with absolute certainty. In *Forcipomyia* Saunders (14, p. 175) describes this sclerite as "a bridge between the two lateral rod systems".

In the epipharynx two pairs of slender muscles are inserted (fig. 15, m. 4). They arise behind each other laterally on the frontoclypeal region and converge towards the median line of the epipharynx. One is inserted into the middle part of the sclerite described above, the other into the posterior side of the epipharynx distally to the comb.

Laterally to the distal end of the labrum the peristomal fold forms a rounded lobe (fig. 11, IV), which is nothing but the *articulatory membrane of the mandible*. Each lobe issues a thin, rather sharp fold in front of the labrum; the two lobes, however, do not reach each other. Distally on the median side of the lobe there is a slender, conical process of a slightly different shape in the various species.

Distally the articulatory membrane of the mandible is separated from the rest of the lateral part of the epistomal fold by a transverse cleft. Proximally the course of the cleft is soon altered, so that it becomes nearly sagittal, and the articulatory membrane—which proximally is connected with the mandible—projects as a rounded lobe into the mouth cavity laterally to the labrum. In the part of the lateral wall of the mouth cavity which adjoins the articulatory membrane and the proximal part of the mandible there is an obliquely cordate sclerite, the *articulatory plate of the mandible* (fig. 12 E) with a broadly rounded ventral apex and a bilobed dorsal edge. This plate is connected with the wall of the head capsule by a vigorous apodeme (fig. 13 A), which in ventral view has the shape of a short, distally obliquely cut-off column. It is excavated from the dorsal side, so that two lamellæ arise. The anterior lamella, which forms an internal continuation of the plate itself, is connected with the head capsule at the black line described above (p. 31), the posterior one at the lateral of the dark lines.

The *mandibles* (fig. 13) issue from the anterior wall of the mouth cavity behind their articulatory membranes and laterally to the labrum. Their bases are thus completely concealed within the mouth cavity, and in the resting position nothing is seen of the mandibles outside the mouth. They move in an approximately sagittal plane (with the "back" ventrally) and have entirely lost the normal articulation with the head capsule; the only articulation is formed by the plate described above.

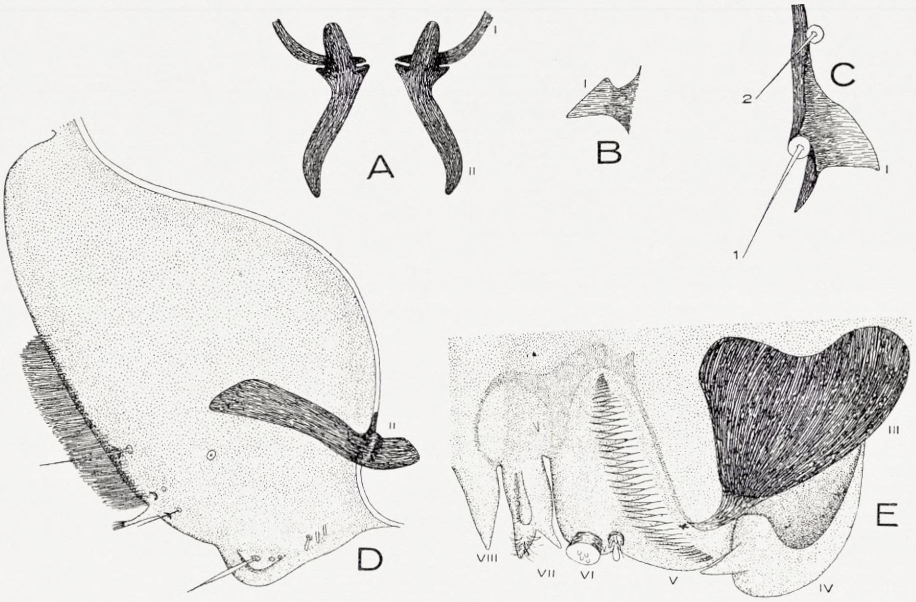


Fig. 12. A: *alveolatus* larva; the premandibles and their articulatory apodemes in ventral view. B: *hexastichus* larva; articulatory apodeme of the left premandible in anterior view. C: *alveolatus* larva; articulatory apodeme of the right premandible in anterior view. D: *alveolatus* larva; labrum in lateral view. E: *alveolatus* larva; left side of the peristomal field seen from the inner side (median view); the tendinous plate is seen shining through. *I*: articulatory plate of the premandible; *II*: premandible; *III*: articulatory plate of the mandible; *IV*: articulatory membrane of the mandible; *V*: anterior maxillary lobe; *VI*: maxillary palp; *VII*: anterior process of the posterior maxillary lobe; *VIII*: posterior process of the same lobe. A, C, D, and E: 500 ×; B: 315 ×.

The mandible is rather clearly divided into two parts, a thicker, subcylindrical, proximal part and a slightly longer and considerably thinner, distal one. In ventral view the median sides of the two parts are nearly flush, and in lateral view the same is the case as regards the ventral sides (the "back"). In transverse section the distal part has a strongly convex ventral side and—especially distally—a somewhat concave dorsal side. The faintly upturned and a little broader distal end is divided into three low, rounded teeth, the lateral one of which is considerably smaller than the two others; the median one projects farthest distally.

The laterodorsal half of the mandible is much longer than the medioventral half, the proximal margin thus forming a broadly rounded, laterodorsal point. With the exception of the medioventral fourth the proximal margin of the mandible has a vigorous, internal thickening. Dorsally the line of attachment between the mouth cavity and the mandible does not coincide with the proximal margin of the latter, but forms a distally directed bend, so that the dorsal side of the proximal part of the mandible constitutes an internal, apodemal structure (Cp. below, the insertion of m. 6).

Distally on the proximal part of the mandible there are three big, sensorial pits, a median one and two lateroventral ones.

The mandible is moved by two fan-shaped (sagittally compressed) muscles (fig. 15, p. 45), each issuing with two parts from the dorsal side of the head capsule. One (m. 5) is inserted laterally into the proximal margin of the mandible. It will be noted that in a characteristic way it "rolls" over the laterodorsal point (fig. 13 C). Its anterior part (m. 5 a) issues between the larval eye and the imaginal eye, its posterior part (m. 5 b) dorsoanally to the imaginal eye. The other, far stronger muscle (m. 6) is inserted distally into the dorsal side of the proximal part of the mandible. Its anterior part (m. 6 a) issues dorsally to the imaginal eye (the posterior part of 6 a just dorsally to 5 b), its posterior part (m. 6 b) from the posterior part of the dorsal (proximal) margin of the head capsule. The muscles 5 and 6 represent, no doubt, the abductor and the adductor mandibulæ, respectively.

Maxillary lobes (figs. 11, VI, IX and 12 E). Two membraneous lobes issue medially on that part of the epistomal fold which occurs behind the articulatory membrane of the mandible. The anterior lobe has the shape of a low dome. It carries in the middle of the lateral side (or perhaps rather laterally on the ventral side) a small, thin seta and anally the maxillary palp. The latter is quite short, about as broad as it is long and consists of a single joint, which on its dome-shaped, membraneous, distal end is furnished with four small, single-jointed sensilla. In a low transverse furrow in front of the palp there is a smaller, basally faintly scleroticized elevation, which carries four sensilla: a big club-shaped, single-jointed one, and medially to this three smaller sensilla, one of which is two-jointed with a fine, hair-like distal joint. Finally there is just laterally and anteriorly to the palp a minute, single-jointed, conical sensillum.

The posterior, much smaller lobe is divided into two conical processes, the anterior one of which again is bifurcate; the median side of the posterior branch is covered with hair-like spinules. On the median side of the anterior process there is a short and thin membraneous lamella; proximally to the posterior process a thick membraneous fold, the anal fold, runs on the posterior part of the lateral wall of the mouth cavity as far as the epipharyngeal region. The height of the anal folds soon increases, so that on a level with the distal margin of the head capsule they nearly touch; from here their height decreases gradually. The posterior lobe carries three sensorial pits, one rather proximally on the lateral side and two close together in the furrow between the two processes; apparently there may also be three pits in the latter place. Finally there is a single-jointed, conical sensillum proximally on the median side.

It seems beyond any doubt that the two lobes together represent the maxilla. They suggest very much the structures which ANTHON (1, pp. 38—43) has described in certain Nematocerous larvæ as palpifer and lacinia. Especially as regards the anterior lobe the designation may be appropriate, but, no doubt, also other parts of the maxilla are concerned with the formation of the lobes. The three (four) pits on the posterior lobe remind of ANTHON's *Cardo-Sklerit*. The small, sensory papilla in front of the palp may represent the galea.

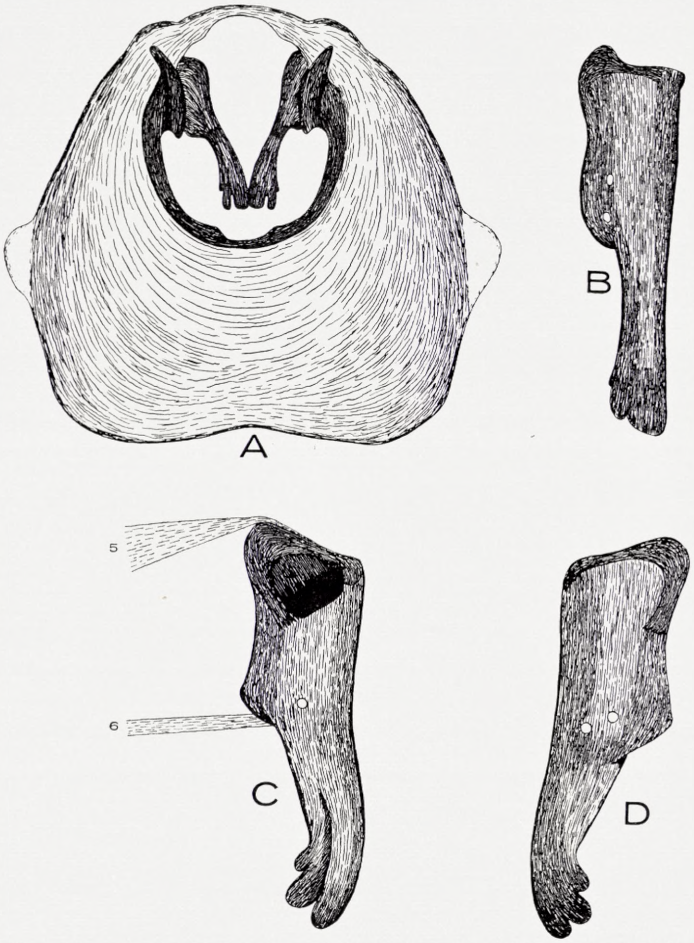


Fig. 13. *alveolatus* larva. A: head capsule with the mandibles in situ in ventral view. B: right mandible in ventral view. C: left mandible in median view. D: same in lateral view. *5* and *6*: muscles of the mandible. A: 205 ×; B—D: 500 ×.

Proximally to the maxillary lobes there is a rather complicated, tendinous plate along the lateral wall of the mouth cavity. Its central part is roughly Y-shaped. The ventral end of its shaft is connected with a small, semilunular sclerite, which is situated on the lateral side of the posterior lobe. The anterior branch of the Y is by a narrow "bridge" connected with a triangular sclerite, which forms a lighter coloured, ventroanal continuation of the articulatory plate of the mandible. In ventral view this sclerite is curved into a quarter of a circle, so that its distal end (fig. 12 E×) points straight medially. This shape of course corresponds to the rounded corner on the lateral side of the proximal part of the mandible. Another bridge connects the posterior branch of the Y with a minute sclerite, situated in the furrow between the two processes of the posterior lobe and carrying two of the sensorial pits described above. In ventral view the tendinous plate is strongly curved with a median concavity, so that it is "concentric" with the outline of the mouth cavity. In its dorsal edge probably some small muscles are inserted, which issue from the tentorium. In *Forcipomyia* SAUNDERS (14, p. 174) describes the tendinous plate as "a curving internal support" issuing from the side wall of the head.

On the lateral wall of the mouth cavity, along and just behind the "bridge" which connects the Y with the articulatory apodeme of the mandible, a row of vigorous spinules is seen. In ventral view the spinules are elongate-triangular with a faintly convex median side and a faintly concave lateral side and tapering to a slender point. Seen from the edge they have rather slender bases and are evenly attenuated towards the apex. Thus we are concerned with close-set, plate-like structures. In the natural position of the mouthparts these spinules adjoin those on the edge of the labrum.

The posterior part of the epistomal fold (fig. 11 X) is considerably thinner than the lateral part. The edge is here covered with close-set, long, slender spinules. Their shape is somewhat different in the various species. In *hexastichus* they are brownish, hair-like, directed anteriorly and ventrally, in *alveolatus* they are colourless, thicker, pointed like a sewing needle, and directed straight ventrally.

In the posterior wall of the mouth cavity, on a level with the ventral margin of the head capsule, there is a rather feebly sclerotized and faintly convex plate, which is connected with the tentorium by small apodemes.

The mandibles are scraping organs, but have no power of mastication. This process is taken over entirely by an elaborate, very dark coloured *pharyngeal skeleton*, which is found in the middle of the head (figs. 14 and 15).

The transverse section of the mouth cavity is here shaped like a U with forward directed concavity. In the posterior wall of the mouth cavity the bottom and part of the branches of the U are formed by a very strong, unpaired sclerite, the *posterior plate*. Quite ventrally the external (posterior) side of this plate is plane, dorsally it becomes transversally convex, though this feature in lateral view is obscured by a vigorous, dorsally higher ridge which projects from the lateral part of the posterior side of the plate; the ridge does not, however, reach the dorsal margin of the plate. Near the dorsal edge the thickness of the plate decreases considerably and abruptly. The excavation thus formed is densely covered with hair-like, but rather strong spinules.

In the anterior wall of the mouth cavity the bottom of the U is formed by a very strong, unpaired sclerite, the *anterior plate*, which is about one and a half time as long as the posterior plate. On the distal (ventral) half of the inside run two low, rounded, transverse ridges, the ventral one of which is again divided into three low teeth, an unpaired median one and a pair of lateral ones. The dorsal ridge is longer than the ventral one and curved in such a way that its ends come to be lateral to the three teeth mentioned above. Hence the internal outline of the anterior plate is quintuple in a ventral view. The external (anterior) side of the plate is scooped out like a spoon. Ventrally the edge of this area is rather steep, so that a thick ridge is formed, connecting the two ventral corners of the plate. Dorsally it merges evenly into the thinner, dorsal edge of the plate, which projects freely into the lumen of the postpharynx and is divided into about 20 spines. A little dorsally to the middle the plate carries a vigorous, unpaired, columnar apodeme, which forms an articulation with the *wings of the pharyngeal skeleton.* Each wing is composed of a sclerite which in the anterior wall of the mouth cavity forms the branch of the U and anteriorly is prolonged into an apodeme of about the same length as the sclerite itself. The sclerite and the apodeme together form an approximately triangular plate, though with much rounded corners; especially the distal (anterior) corner is much rounded. Ventrally the proximal edge of the wing is contiguous with the lateral edge of the anterior plate, thus forming the ventrolateral point of articulation. (I have not been able to decide with certainty whether the two sclerites here are connected by thickened, but elastic endocuticle). Otherwise the proximal edge is separated from the anterior plate by a narrow, membraneous area. The wing is consolidated by two plate-shaped,

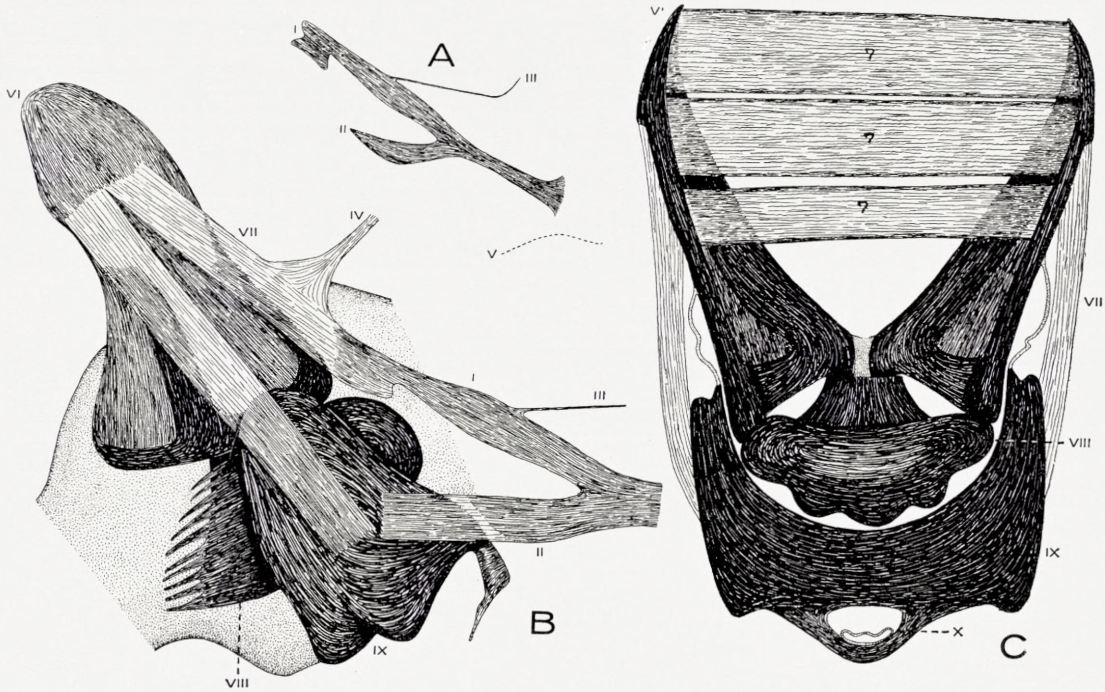


Fig. 14. *alveolatus* larva. A (ventral direction towards the right): tentorium in lateral view. B (do.): pharyngeal skeleton in lateral view. C: same in ventral view. *I*: anterior branch of tentorium; *II*: posterior branch of same; *III*: subordinate branch of anterior branch, from which probably muscles originate which are inserted into the maxillary lobes; *IV*: cord connecting the band between the wing of the pharyngeal skeleton and the tentorium with anterior side of the head capsule; *V*: outline of the posterior side of the head capsule; *VI*: distal end of the wings of the pharyngeal skeleton; *VII*: bands connecting the wing with the tentorium and with the posterior plate; *VIII*: anterior plate; *IX*: posterior plate; *X*: salivary duct; *7*: the adductory muscles of the wings. Membranes dotted. A: 315 ×; B and C: 500 ×.

triangular apodemes, which rise at right angles to its median side and to each other, one lengthwise on the wing and approximately in the middle of this, the other at the proximal margin of the wing. The common, median point of the two apodemes rests on the columnar apodeme of the anterior plate, thus forming the mediodorsal point of articulation. Here the two wings and the anterior plate are connected by elastic endocuticle. The free edges of the two triangular apodemes are thickened, thus forming strong ridges, which connect the two points of articulation mutually and with the distal end of the wing. The ventrolateral point of articulation is also connected with the distal end of the wing by a somewhat weaker ridge.

Two strong, endocuticular bands connect the distal end of the wing with the anterior branch of the tentorium and with the posterior plate, respectively. Such a band also connects the posterior plate with the posterior branch of the tentorium.

From the band which connects the wing with the tentorium issues a thinner, cord-like band, which is inserted into the anterior wall of the head capsule just above the dorsal end of the median of the dark lines described on p. 31. It will probably not be unjustifiable to consider this band as the anterior arm of the tentorium.

The above description deviates on some points from that which Saunders (14, pp. 174—76) gives of the pharyngeal skeleton in *Forcipomyia*. Though there may be generic differences, I am inclined to believe that his descriptions of the epipharyngeal comb and the dorsal edge of the anterior plate are due to misinterpretations. According to Saunders the sculpture of the anterior plate in *Forcipomyia* shows specific differences. Owing to the opaqueness of the structures in question I have been unable to decide if the same is the case in *Atrichopogon*, but even so, it will not—for the same reason—be of use in taxonomy.

The *salivary duct* passes through a transverse, elliptic "window" in a hoop, which rises ventrally from the external side of the posterior plate. The dorsal edge of the hoop in the middle protrudes into a lamella only half as broad, which, again, in the middle has a considerably narrower, tongue-shaped prolongation; in all the length of the lamella is about half that of the posterior plate. Passing the hoop the salivary duct is much flattened, with a convex posterior side and a doubly concave anterior side; more ventrally the anterior side is a simple concave. The salivary orifice is a transverse cleft in the posterior wall of the mouth cavity in the epipharyngeal region a little in front of the pharyngeal skeleton.

The muscles of the pharyngeal skeleton (fig. 15). Three very strong muscles (m. 7) connect the distal halves of the wings of the pharyngeal skeleton (fig. 14C). A fan-shaped (sagittally compressed) muscle (m. 8) originates on the anterior wall of the head capsule just behind (and a little laterally to) seta 3, and is inserted into the transverse apodeme of the wing. (The origins of muscles 4 and 8 occur in a longitudinal row). A very strong bundle of muscles (m. 9) originates on nearly the whole dorsal part of frons and is inserted into the dorsoanal corner of the wing. A small muscle (m. 10) originates from the dorsal part of frons laterally to m. 9 and is inserted into the distal end of the wing. Finally a fan-shaped (sagittally compressed) muscle (m. 11) originates on the posterior wall of the head capsule and is inserted lateroventrally into the posterior plate.

The anterior arm of the tentorium issues from the lateral end of the clypeal suture, when this suture is present. It is therefore reasonable to assume that also in *Atrichopogon* the anterior tentorial invagination indicates the dorsolateral corner of the clypeus. Muscles 1 and 2 are, no doubt, frontolabral muscles. If, however, we consider m. 3 as an internal labral muscle and m. 4 as clypeopharyngeal muscles —and there seems to be some reason to do so—it means that the clypeo-labral and fronto-clypeal sutures—if they were present—would have a much curved (dorsally convex) course.

Proximally (dorsally) to the pharyngeal skeleton the cylindrical postpharynx begins. Distally the anterior wall of this organ forms a smooth pouch, which projects over the spines of the anterior plate. In the corresponding part of the posterior wall there are three narrow longitudinal furrows, an unpaired and two paired ones. Farther proximally the wall of the postpharynx is thrown into irregular folds. The circulatory musculature begins immediately proximally to the dorsal edge of the posterior plate. At first the muscles have the shape of semicircles, there being no musculature in the wall of the pouch described above. Into the posterior wall of the pharynx small dilator muscles are inserted.

Homologies of the pharyngeal skeleton. Without knowledge of any intermediate stage of phyletic development it is impossible to say anything definite about this question, except that it must be considered fairly certain that muscles 4, 8, 9, 10, and 11 belong to the dilator muscles of the pharynx.

In Chironomid larvæ there are two epipharyngeal combs. The distal one consists of (or is covered with) rather fine, hair-like spinules. The proximal one consists of rather vigorous teeth, which (at least very often) issue from a more or less distinctly tripartite plate and are directed proximally. In my opinion there cannot be much doubt that the epipharyngeal comb in *Atrichopogon* is homologous with the distal of the epipharyngeal combs in Chironomid larvæ, and it also seems rather reasonable to me to assume that the anterior plate and perhaps also the wings are homologa of the tripartite plate in Chironomid larvæ. Another explanation, however, may also be given of the origin of the wings, namely that they are the suspensoria of the mouth angle, and that the band connecting them with the tentorium represents the retractor muscle of the mouth angle (cp. below), though this muscle typically takes its origin from the frons. In most insects the salivary orifice is situated between the labrum and the hypopharynx. This seems to indicate that the posterior plate is, at least partially, derived from the hypopharynx. Hence the band which connects the posterior plate with the tentorium represents the retractor muscle of the hypopharynx. (Perhaps it is not superfluous to mention in this connection that the labium is entirely lacking in *Atrichopogon* as in nearly all other Dipterous larvæ). Probably muscles 7 belong to the circulatory musculature of the pharynx, and perhaps they represent the anterior part of the semicircular muscles in the posterior wall of the pharynx described above.

Also the band connecting the wing with the posterior plate may be derived from the circulatory musculature through a vigorous development of the tendinous part at the expense of the muscular part.

The feeding mechanism (fig. 15). Introductorily it should be observed that *protraction* means a movement in a ventral (distal) direction, *retraction* in a dorsal direction, *levation* is a movement forwards, *depression* backwards.

In the living larva the head capsule is transparent enough to allow the following observations: The larva scrapes the substratum, the two mandibles working alternately at rather a fast pace, though not faster than that their movements can easily be followed. (The mandibles have a faint resemblance to the forelegs of a digging dog). Occasionally slower and more energetic scratchings of the mandibles are also seen, if necessary assisted by small jerks of the head. The mandibles swing in planes which are not quite parallel with the sagittal plane, but dorsally as well as posteriorly converge somewhat towards this plane. The result is that the two mandibles scrape on the same point of the substratum. At the same time the pharyngeal skeleton is working. The anterior plate + the wings move like a swing round an axis which goes through points near the distal ends of the wings. Thus the anterior plate is protracted and retracted in relation to the posterior plate. The retraction takes place at rather a slow rate, and during this movement the wings are somewhat adduced. The protraction on the other hand is a quick movement, reminding of a relaxed spring, and simultaneously a rolling of the posterior plate round its transverse axis is seen (depression of the anterior margin). If these observations are compared with the morphological description given above, the function of the mouth parts may be deduced.

Owing to the peculiar insertion (rolling over the laterodorsal point; fig. 13C), the contraction of m. 5 will cause a protraction of the mandible. The retractor mandibulæ is m. 6. The movements of the mandible are controlled by its articulatory plate. This very loose articulation allows a great freedom of movements. One has an impression that the mandible cannot only be protracted, but that it can also be protruded a little through the mouth opening. The latter movement may be brought about by m. 1; during contraction of this muscle the premandible is protracted and, owing to its close connection with the labrum, also the base of the mandible. The antagonist of m. 1 is m. 2, which, together with m. 3, can also function as levator labri.

The mandibles scratch off food-particles and transport them, probably assisted by the labrum, to the proximal part of the mouth cavity. From here they are transported to the entrance to the pharyngeal skeleton by the epipharynx and especially by the spinules on the comb of the latter; in the resting position the points of the spinules lie close to the curved cleft between the anterior and posterior plates. The muscles m. 4 function as levatores epipharyngis, but I have been unable to detect any muscle which might act as depressor epipharyngis. This movement is probably caused by the elasticity of the organ; if the epipharyngeal sclerite really is connected with the tentorium, this feature will contribute much to the elasticity.

The muscles which connect the tentorium with the tendinous plate proximally to the maxillary lobes allow some movement of the latter, a movement which of course will be of importance to the eating. The fact that the width of the mouth opening is rather different in the various preparations indicates that it really is so. The bridge which connects the tendinous plate with the articulatory plate of the mandible allows only a limited retraction of the former, and thus probably serves to transform the retractory movement of the muscles into an adductory movement of the maxillary lobes.

The plate-like spinules on the lateral wall of the mouth cavity may perhaps, together with the edge of the labrum and the anal folds, serve to filter superfluous water from the food-particles in a way analogous to the baleen apparatus of the whales. The small size of the objects (the width of the head being only about $\frac{1}{3}$ mm) and the fact that only a limited magnification can be employed in connection with the living larva have made direct observations on this point impossible.

Muscle 8 has a double function: it partly acts, together with m. 11, as a dilator of the pharyngeal skeleton. Since the bands which connect the posterior plate with the wings prevent a levation of the distal ends of the latter, a levation of the anterior plate will cause an abduction of the wings. It partly acts as a protractor of the anterior plate, in which movement it is assisted by the small m. 10. In the first place this muscle prevents a protraction of the distal end of the wing, secondly it takes an active part in the movement, its point of insertion being somewhat distal to the axis of rotation, determined by the insertion of the band which connects the wing with the posterior plate. The retraction of m. 11 also causes a depression of the ventral margin of the posterior plate (its point of insertion being ventral to the insertion of the band which connects the plate with the wing), a movement which probably is of importance to the transport of the food-particles into the lumen of the pharyngeal skeleton. The retraction of the anterior plate is carried out by m. 9. The band which connects the wing with the tentorium prevents a retraction of the distal end of the former, the swinging movement thus being accomplished. At the same time the muscles m. 7 adduce the wings of the pharyngeal skeleton. Since, as mentioned above, the bands which connect the posterior plate with the wings prevent a levation of the distal ends of the latter, the adduction will result in a depression of the anterior plate, transmitted from the wings through the two points of articulation. It is thus during the retraction that the chewing process proper (and the transport of the food into the pharyngeal skeleton) is carried out. Hence it is easy to understand that the retractor muscles are much stronger than the protractor muscles, and that the retraction takes place at a much slower rate than the protraction. The violent, dorsally directed pull to which the posterior plate is subjected through the chewing process is balanced by the bands which connect the plate with the tentorium. It will be seen that the connections with the tentorium are of the greatest importance to the function of the pharyngeal skeleton.

The spinules on the dorsal margin of the posterior plate, together with the spines

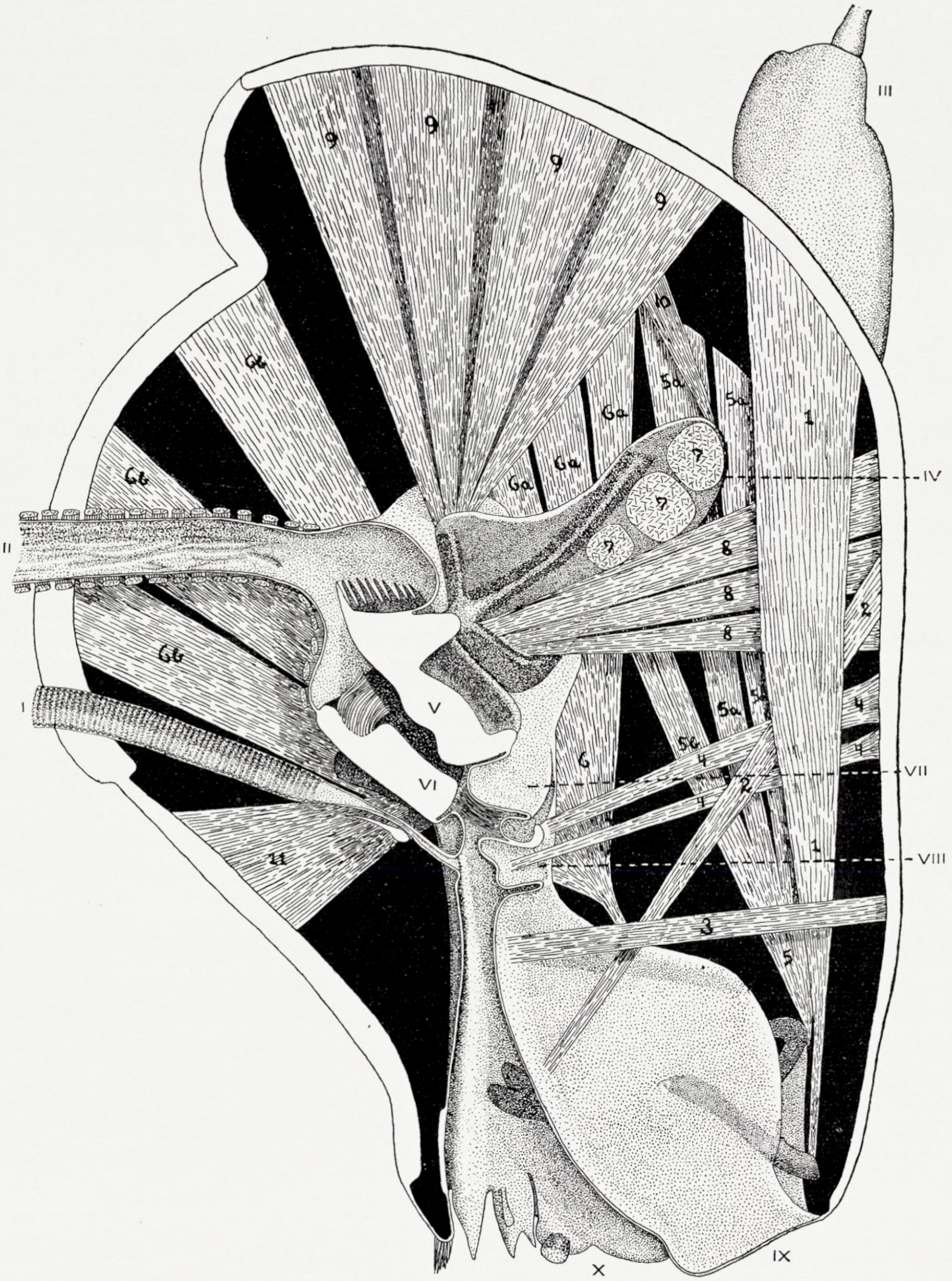


Fig. 15. *alveolatus* larva. Left half of the head seen from the inner side; shows the apparatus of ingestion and its musculature. *I*: salivary duct; *II*: oesophagus; *III*: antennal socle; *IV*: distal end of left wing of pharyngeal skeleton; *V*: anterior plate of pharyngeal skeleton; *VI*: posterior plate of same; *VII*: dorsal (proximal) part of epipharynx; *VIII*: ventral part of same; *IX*: labrum; *X*: maxillary lobes; *1—11*: muscles (see pp. 34, 35, 37, and 41—42). 400 ×.

on the dorsal edge of the anterior plate, form a very effective filter apparatus, which only allows very finely divided particles to enter the pharynx. The spinules are so close-set that practically they will only allow passage of fluid matter. Hence it is probably during the extreme protraction of the anterior plate that the comminuted food-particles are sucked into the pharynx between the spines on the dorsal edge of the plate. This sucking may of course also contribute to the transport of the unchewed particles into into the lumen of the pharyngeal skeleton.

The *body segments* (fig. 18, p. 52; fig. 20, p. 55; fig. 22, p. 58; fig. 23, p. 60; fig. 24, p. 63). The abdominal segments I—VIII are of a nearly uniform shape; meta- and especially mesothorax deviate somewhat, prothorax and especially abdominal segment IX very much from this shape.

The *abdomen* is a good deal flattened, chiefly owing to the fact that the lateral side of each segment protrudes into a big *lateral process*. Without these processes, i. e. in the intersegmental regions, the abdomen approaches the cylindrical shape. The lateral process carries three *lateral setæ*, an apical one and two subapical ones; the latter two are generally placed dorsally and ventrally, respectively. On segment VIII the dorsal of the subapical setæ is lacking.

More proximally on the dorsal side a *laterodorsal seta* is found, generally placed on a *laterodorsal process*. This process may be minute (*cornutus*), but it may also be so big that the distal end of the lateral process becomes bifurcate (*alveolatus*, *polydactylus*, *sp. y*, and *hexastichus*). In the three last-mentioned species the dorsal branch is developed as a filiform, silvery, tracheal gill, and in *hexastichus* the same is the case with the ventral branch. In *sp. y* and *hexastichus* the lateral process itself is, at the same time, reduced in size, so that the body approaches the cylindrical shape.

Approximately in the middle of the dorsal side of the lateral process there is a small, thin, *intermediate dorsal seta* which is lacking on segment VIII. Finally there is a *mediodorsal seta* proximally to the lateral process, generally placed on a higher or lower, *mediodorsal process*, and most often developed as a spur or a spur-like bristle.

Anally, at the base of the lateral process, there is a *dorsoanal process*. Generally it is short, finger-like, and covered with vigorous spinules. It may be lacking on segment VIII, and in *polydactylus* and *sp. y* it is lacking on all the segments. In *hexastichus* it is developed as a filiform, tracheal gill, like the two branches of the lateral process in this species.

The abdominal segments are each furnished with two pairs of *sensorial pits*. One is situated laterally or lateroanally to the mediodorsal seta, the other medially or orally on the base of the dorsoanal process, if this process is present.

On *metathorax* the lateral process is developed nearly or completely as on the abdominal segments, on the *mesothorax* it is always much reduced and may be entirely lacking. On both these segments, however, a well developed laterodorsal process, generally (except in *speculiger* and *dubius*) of the same shape as on the abdominal segments. On meso- and metathorax there are only two lateral setæ, the dorsal or (polydactylus) ventral of the subapical ones being lacking; in *sp. y* there would seem to be only one lateral seta (the apical one) on these two segments. The mediodorsal seta is developed as on the abdominal segments, and if these segments are furnished with mediodorsal processes, such ones are also found here. The intermediate, dorsal seta is on mesothorax considerably stronger than on the following segments (except in *polydactylus*) and resembles the mediodorsal seta, i. e. it is generally developed as a spur or a spur-like bristle. On meta- and especially on mesothorax the dorso-anal process is much smaller than on the abdominal segments; on the latter thoracic segment it may be entirely lacking (*speculiger, dubius, cornutus*). If this process is lacking on the abdominal segments (*polydactylus, sp. y*), it is also lacking on meso- and metathorax, and the same may be the case, even if it is well developed on the abdominal segments (*hexastichus*). Meso- and metathorax have two sensorial pits like the abdominal segments.

On *prothorax* a lateral process is always entirely lacking (except perhaps in *cornutus*; p. 54), and the three lateral setæ are placed at rather great mutual distances above each other. Lateroorally on the dorsal side there is a seta-bearing laterodorsal process of a rather varying shape. It may be developed as on the following segments, though never as a filiform, tracheal gill; in *polydactylus* and *sp. y* it is much reduced. In *speculiger* and *dubius* the laterodorsal process is finger-like, directed lateroanally, and covered with strong nodules, and it has the same shape on meso- and metathorax in these two species. With the exception of *polydactylus* the prothorax is always furnished with a dorsoanal process, also in those cases where it is lacking on the following segments. It is directed laterally, thicker or thinner, finger-like, and covered by vigorous spinules. In addition to the laterodorsal seta the prodorsum carries only one seta, which is placed near the anterior margin. Since the mediodorsal and the intermediate dorsal setæ on the mesothorax are alike, it is not easy to decide which of these two setæ the seta on the prodorsum represents, but as the oral one of the sensorial pits described below lies laterally to the seta, it is reasonable to assume that it is the mediodorsal seta. It is never placed on a process. Like the following segments the prothorax is furnished with two pairs of sensorial pits. One lies at or on the base of the laterodorsal process, the other on the dorsoanal process.

Saunders (14, pp. 177 and 196) has described the chætotaxy in some *Forcipomyia* larvæ. Possibly his seta a corresponds to the mediodorsal seta in *Atrichopogon*, setæ b and d to the laterodorsal and the intermediate dorsal seta, respectively, and setæ c, e, and f to the three lateral setæ in *Atrichopogon*.

The prothorax moreover differs from the following segments in carrying the *anterior proleg* (fig. 16A–C), which consists of rather a thick-walled, basal part, which orally and laterally is covered with spinules or nodules, and a thin-walled distal part or planta, which is smooth with the exception of some few, very inconspicuous, transverse rows of extremely fine and slender spinules. The planta is bilobed. Each lobe—left and right—carries two transverse rows of "claws", i. e. very strong, backward curved spines. Especially the brown spines in the posterior row, six in number, are very vigorous, whereas the four, light spines in the anterior row, which alternate regularly with the five lateral spines in the posterior row, are more slender. Basally all spines, however, are thickened and much sagittally compressed.

The anterior proleg is moved by the following muscles (fig. 16C): Lateroventrally on the intersegmental region between the pro- and the mesothorax, two muscles originate, of which the lateral one (m. 1) is inserted into a furrow orally at the base of the proleg, the median one (m. 2) into the planta right in front of the claws. Farther medially on the intersegmental region three muscles originate, of which the two lateral ones (m. 3) are inserted into a furrow anally at the base of the proleg, whereas the median one (m. 4) is inserted anally into the furrow between the basal part and the planta. Laterodorsally in the prothorax three muscles originate in a longitudinal row between the laterodorsal and dorsoanal processes. The anterior one (m. 5) is inserted immediately laterally to m. 1, the intermediate one (m. 6) near m. 2, and the posterior one (m. 7) laterally to m. 4. It is quite clear that these muscles are derived from the ventral and the dorso-ventral musculature of the segment and have nothing to do with the imaginal leg-musculature, just as the position of the peripodial cavities will show that the proleg is a structure quite independent of the later, imaginal forelegs.

The anterior proleg plays an important rôle in the movements of the larva. The principal movement of the proleg is a swing forwards and backwards. The forward movement is probably carried out by the muscles m. 1 and m. 5, the opposite movement by m. 3. During the forward movement the claws are raised from the substratum in a manner like those of a cat, probably by the muscles m. 2 and m. 6. During the opposite movement the claws are fastened into the substratum. This probably to a great extent takes place through blood pressure, but m. 4 and m. 7 may also be contributive, just as these muscles probably assist m. 3 in the backward bending of the proleg; (it is natural that this movement, which is the properly active movement in locomotion, will require a greater muscular strength than the forward bending). The planta can be invaginated into the basal part of the proleg, and this again into the prothorax. The former movement may be accomplished by simultaneous contraction of the muscles m. 2, m. 4, m. 6, and m. 7, the latter by simultaneous contraction of the muscles m. 1, m. 3, and m. 5. The evagination must take place through blood pressure.

The ventral side of the segments carries four *ventral setæ*. One is placed orally and rather medially, on the prothorax lateroorally on the distal margin of the basal part of the proleg. Two of the others are on the thoracic segments developed as "twin setæ", i. e. they are very slender and so close-set that their alveoles nearly touch; on the prothorax they stand just lateroanally to the proleg. On the abdominal segments these two setæ are normally developed and placed at a greater mutual distance behind each other approximately in the middle of the half in question of the segment (fig. 23B, p. 60). The fourth seta stands lateroanally on the venter; in *poly-*

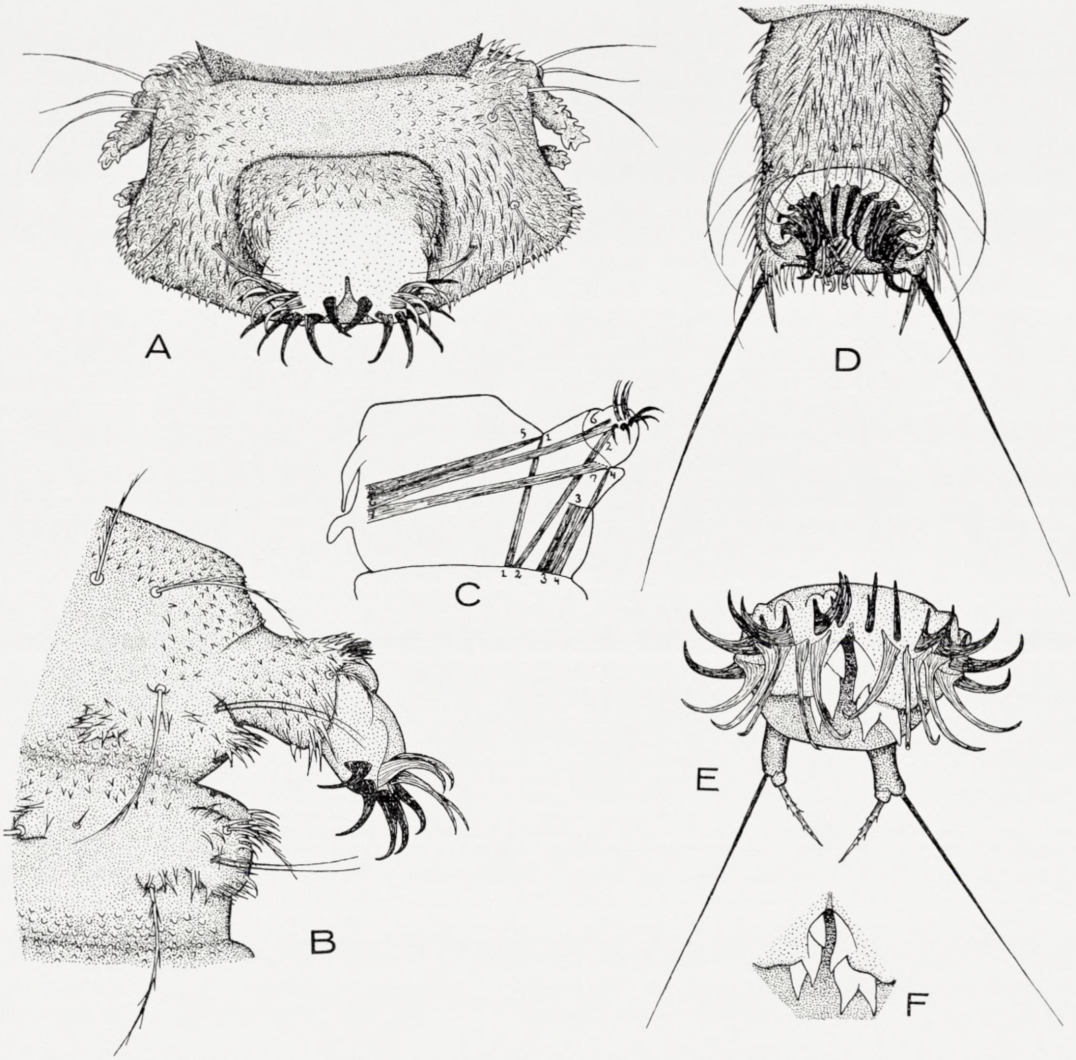


Fig. 16. A: *speculiger* or *dubius* larva; the prothorax and the most proximal part of the head in ventral view. B: *hexastichus* larva; ventral half of the pro- and the mesothorax in lateral view. C: same; muscles of the anterior proleg in lateral view. D: *alveolatus* larva; abdominal segment IX in ventral view; anal prolegs withdrawn. E: *hexastichus* larva; anal prolegs in ventral view. F: same; anal papilla in ventral view. *1—7*: muscles (see p. 48). A, B, and D—F: 125 ×; C: 64 ×.

dactylus, however, it is displaced orally. The lateroanal seta is always lacking on VIII. venter, but also on the other segments some of the setæ may be lacking.

On the thoracic venters of *Forcipomyia bipunctata* SAUNDERS (14, p. 177) describes "an anterior ventro-lateral pair of microchæta and behind them a group of three set very close together", i. e. in all four setæ like in *Atrichopogon*. On the abdominal segments he describes "three pairs of ventral microchæta".

The *abdominal segment IX* (fig. 16 D) approaches the cylindrical shape, though orally the dorsal side is a little bulging. (In *Forcipomyia* Saunders—14, p. 170—considers this segment as a subdivision of segment VIII. I do not see any reason for such an assumption). In its whole extent the segment is rather thick-walled, and the dorsal side is covered with an unpaired, light-coloured sclerite. The posterior end of the segment is cut off obliquely (the dorsal side being the longer), and through the opening a pair of short, thin-walled, *anal prolegs* (fig. 16E) may be protruded. Each proleg, like the lobes of the anterior proleg, carries two transverse rows of "claws", which, however, are curved forwards (or ventrally). In the posterior (or dorsal) row there are five light-coloured, slender claws, which are placed opposite the intervals between the six brown and more vigorous claws in the anterior (ventral) row.

The anal prolegs are only furnished with retractor muscles, which originate orally on the IX. venter and are inserted dorsally to the claws. By a weaker contraction these muscles may raise the claws from the substratum, by a stronger contraction invaginate the anal proleg. Rather anally on the IX. dorsum there originates a strong bundle of muscles, which is inserted into the dorsal side of the rectum; perhaps these muscles may also contribute to the movements of the anal proleg.

The anal prolegs, which are fused proximally, form the ventral limitation of the anus. On the side facing the anus each proleg carries three small, pointed *anal papillæ* (fig. 16EF), which are highly reminiscent of those of the Tanypodine larvæ, though much smaller. Saunders (14, pp. 176, 195, and 197; 15, pp. 258 and 271) describes anal papillæ in various other genera of the subfamily; they vary much both in number and shape, even among species of the same genus.

The setaceous equipment of segment IX is so different from that on the preceding segments that I do not dare to attempt a homologization. A light-coloured, strong, backward curved bristle stands laterally on the dorsum and anteriorly to the middle, on the edge of the sclerite or on a bulge of this edge; a little medially or medioanally to the seta there is a sensorial pit. Laterally and ventrally the posterior margin of the segment is surrounded by a semicircular or horseshoe row of setæ, seven on each side, of which the two outmost ones are placed on the posterior corner of the dorsum, in *sp. y* and *hexastichus* on a slender, backward directed process; the dorsal one of these two setæ is a strong, brownish spur, the ventral one a long, strong bristle, the longest and thickest of the larva. The five other setæ are smaller and light-coloured; the most ventral and the one next to the dorsal of these five setæ are removed somewhat farther from the posterior margin than the others. The concentration of setæ, tactile in function, along the posterior margin is easy to understand as to the function of the anal prolegs. In *polydactylus*, however, the number of setæ is reduced. Finally there is a seta rather orally on the IX. venter.

With the exception of the tergite on segment IX and occasionally some minute sclerites on the dorsa of the other segments the surface of the body is membraneous. As to the greater part it is covered with more or less conspicuous spinules or nodules. Generally it may be said that these—except in *polydactylus*—are longest and most slender on the ventral side.

Atrichopogon sp. x.

Only one, unfortunately a little damaged, specimen is at hand.

The larva resembles that of *speculiger* and *dubius* very much. The chief difference is the fact that the dorsal, oval, thin-walled, smooth areas are lacking, and the dorsa provided with an even cover of rather stout spinules (fig. 17).

Mediodorsal processes are not developed, but the area between the two mediodorsal setæ is raised somewhat over the rest of the dorsum. On the prothorax the laterodorsal process is small and especially short; on the mesothorax it is still shorter, but thicker; on the metathorax it is developed as on the abdominal segments. On the abdominal segments the dorsoanal process is quite short, merely a spiny elevation; on the prothorax it is developed almost as on segments I—VII, on the metathorax as well as on segment VIII it is smaller, and on the mesothorax it is entirely lacking. On segment VIII the mediodorsal and the laterodorsal seta are placed on a common, transverse sclerite.

Fig. 17. Larva of *A. sp. x.* Above right half of the prothorax in dorsal view, below left half of abdominal segment IV in dorsal view. 250 ×.

Atrichopogon speculiger & dubius.

I have been unable to find any morphological differences between the larvæ of these two species.

The head is developed as in the larva of *alveolatus* described below, except that the larval eye is far from being so high.

On the anterior abdominal segments the laterodorsal process is rather small (fig. 18 B). Posteriorly its size increases, so that the lateral process of segment VIII may nearly be called bifurcate. The laterodorsal seta, like the lateral setæ, is developed as a strong, but light-coloured and thin-walled, and somewhat curved bristle. The two subapical ones of the lateral setæ are both ventral in position (fig. 18 C). On segment VIII the central of the three lateral setæ is lacking. (Thus this seta corresponds to the dorsal, subapical seta in the other species). The mediodorsal seta is a small, but strong, faintly curved, brownish spur, placed on a small feebly developed sclerite. On segment VIII this sclerite is larger and also covers the dorsal surface of the laterodorsal process. There are no mediodorsal processes. The dorso-anal process is rather thick.

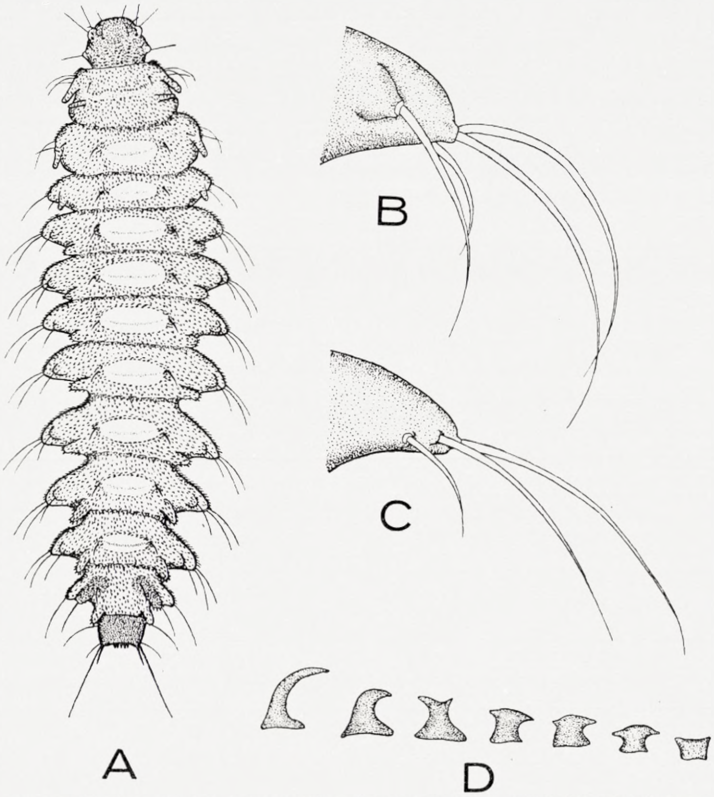


Fig. 18. *A. speculiger* or *dubius* larva. A: larva in dorsal view. B: distal half of right lateral process of abdominal segment III in dorsal view. C: distal half of left lateral process of abdominal segment III in ventral view. D: various types of spinules from the margin of the dorsal smooth areas; on the left a normal spinule (does not occur on the margin of these areas), on the right a rare, extreme type. In B and C the spinules have been omitted. A: 28 ×; B and C: 160 ×; D: 250 ×.

On the metathorax the lateral process is almost as big as on segment I, whereas on the mesothorax it is nearly lacking. On the thoracic segments the laterodorsal process is finger-like, directed posteriorly and laterally; it is biggest on the prothorax and smallest on the metathorax, where, however, it is much bigger and more slender than on segment I. The laterodorsal seta is placed proximally on the process. On the mesothorax the dorsoanal process is lacking.

The number and the development of the ventral setæ are as in the larva of *alveolatus* described below.

The most distinctive feature of the larva is some unpaired, transverse, oval, smooth areas on the dorsal side of the segments mesothorax—VII, between the two mediodorsal setæ (fig. 18A). The cuticle of the ovals is extremely delicate, so thin that its thickness cannot be measured, but anyway it is less than $\frac{1}{2}$ μ; (on the general body surface the cuticle is about 2.5 μ thick). They are very richly tracheated, each receiving a pair of tracheal branches, the diameter of which is about half that of the main tracheal trunks. Thus there cannot be much doubt that the ovals have a respiratory function. They are raised to a slightly higher level than the rest of the dorsal side.

Besides the ovals the following areas are smooth: On the dorsal side a narrow, transverse stripe on the prothorax and an unpaired, mediooral area on segment IX. On the ventral side the posterior side of the anterior proleg as well as the areas in front of and behind this proleg. The rest of the body is covered with cuticular processes. On the dorsal side they are developed as curved, brownish spinules, which are greatest on the dorsoanal processes of the metathorax and the abdominal segments. The spinules in the 2—3 "rows" nearest to the anterior and posterior margins of the ovals have a different shape: they are lower, but broad, and each furnished with two or three points or, more often, a single, asymmetrical point directed straight laterally (fig. 18D); many spinules in the internal "row" lack these points, their shape thus approaching that of the "incisors" of *cornutus* (p. 55). On the small abdominal sclerites the spinules are a little shorter, but more close-set. Low conical, or rounded nodules are found on the laterodorsal processes of the thoracic segments, on the slender dorsoanal process of the prothorax, on the posterior part of the lateral sides of pro- and mesothorax as well as on the posterior side of the lateral processes, and on the dorsal side of segment IX. On the latter segment there is, however, an unpaired group of very vigorous spinules on the posterior margin. On the ventral side the spinules are longer, slenderer, and light-coloured. Towards the intersegmental regions they merge into low conical or rounded nodules.

Length of the larva about 3.1 mm.

The larva seems to be very like that of *A. mülleri* Kieffer, described by Müller (11, p. 226).

Atrichopogon cornutus.

Besides exuviæ only one larva has been examined.

The larva resembles that of *speculiger* in possessing oval, smooth areas on the dorsal side of mesothorax—VII. (In the specimen mentioned the oval is lacking on the metathorax, which probably, however, is only an aberration. The exuviæ do not allow of any safe conclusion as to this point). Likewise the dorsal one of the three lateral setæ has been displaced ventrally, but in return the ventral one has an intermediate position, standing on the posterior side of the lateral process. In several other respects *cornutus* differs from *speculiger*.

The body is much broader, the width being 40 per cent. of the length, and since the height is almost the same, it is also much more flattened.

On the head (fig. 19 D) the larval eye is very high, as in the larva of *alveolatus* described below; its basal, non-hyaloid part is very dark-coloured. Setæ 4 and 10 are strong spurs. The former is the bigger one and complex, being covered with small spinules and having a more or less well developed lateral branch.

On the prothorax the dorsal of the three lateral setæ is much stronger than the other lateral setæ of the body and placed on a great process, which carries the semiglobular laterodorsal process on its anterior side, a foot-like process thus being formed. It is questionable whether this structure may be considered as homodynamous with the lateral processes of the following segments, from which it differs in shape and by only comprising a smaller part of the lateral side. Anally on this side there is a finger-like process of almost the same length as the lateral process of the mesothorax. The dorsoanal process is very short and very broad, a little less than semiglobular.

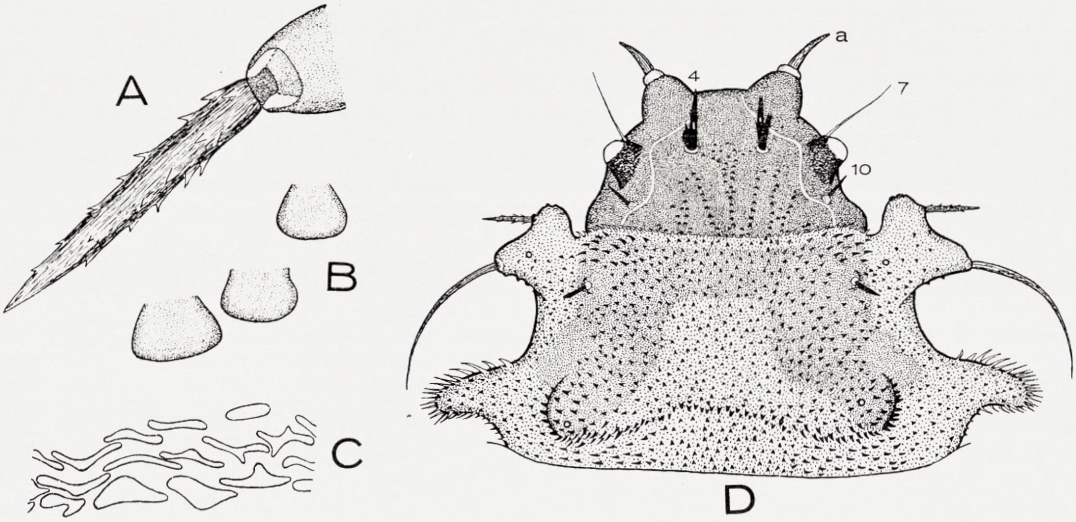


Fig. 19. *A. cornutus* larva. A: laterodorsal seta from the left side of abdominal segment I. B: incisor-like spinules from the margin of a dorsal, smooth area; seen from the flat side. C: the same, seen from the distal edge; optical, transverse section. D: head and prothorax in dorsal view. A: 615 ×; B and C: 250 ×; D: 105 ×.

On the mesothorax the rather big lateral process is bifurcated by a deep, vertical, V-like furrow, so that this segment at a first glance seems to consist of two. The anterior branch carries the setæ, the posterior one has the same shape as, but is longer than the lateroanal process of the prothorax. (Thus there is some similarity between the pro- and mesothorax, which may lead to the conclusion that the former actually is furnished with a bifurcated lateral process).

The mediodorsal setæ are developed as in *speculiger*. On the prothorax the sclerites which carry these setæ are very much enlarged and connected by a broad, oral "bridge". The laterodorsal seta is not developed as the lateral ones, but—also on the prothorax—as a strong, brown spur covered with small, scattered spinules (fig. 19 A). Moreover the laterodorsal process is much smaller than in *speculiger*; on the thoracic segments it is developed as on the abdominal ones. On segment VIII the dorsoanal process is lacking.

The spinules in the "rows" nearest to the ovals are developed as peculiar, thin-walled, incisor-like stuctures (fig. 19 B C).

On the abdominal segments there seems to be only one (on segment VIII none) ventral seta, probably corresponding to the lateral one of the two ventral setæ in *speculiger* and *alveolatus*.

The larva at least is very like that of *A. trifasciatus* Kieffer, described by Bangerter (2, pp. 350—52).

Atrichopogon alveolatus.

The head (fig. 9, right side, p. 30) is distinguished by the tall shape of the larval eye. All the setæ are developed as normal bristles.

On metathorax and the abdominal segments I—VIII the lateral process is distinctly bifurcate (fig. 20 ABC). The dorsal branch (= the laterodorsal process) again is bifurcate: its ventral branch carries the laterodorsal seta, its bigger dorsal branch is very thin-walled (fig. 21) and has a peculiar, alveolate structure, being

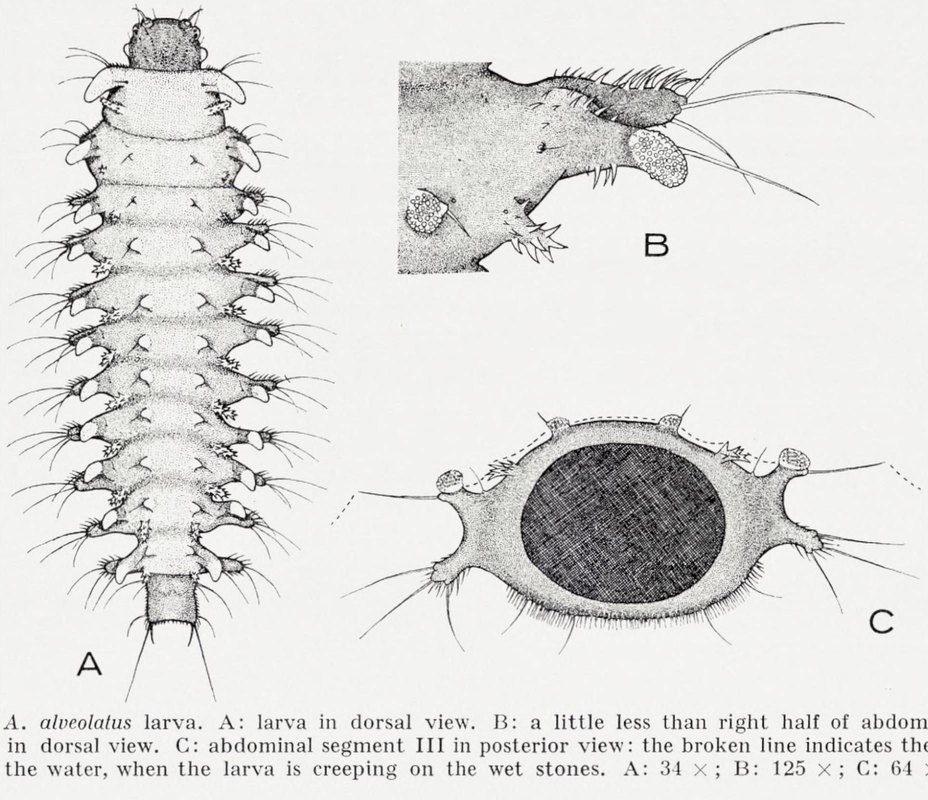


Fig. 20. *A. alveolatus* larva. A: larva in dorsal view. B: a little less than right half of abdominal segment II in dorsal view. C: abdominal segment III in posterior view: the broken line indicates the surface of the water, when the larva is creeping on the wet stones. A: 34 ×; B: 125 ×; C: 64 ×.

densely covered with rounded, still more thin-walled nodules. On the mesothorax the ventral branch of the lateral process is just indicated, on the prothorax it is—as in the other species—entirely lacking. On both these segments the laterodorsal process is developed as on the following ones, only the alveolate part is still bigger, especially on the prothorax. On the abdominal segments the mediodorsal seta is placed subapically on the lateral side of a well-developed mediodorsal process. The apex of the process has the same alveolate structure as the dorsal branch of the laterodorsal process. On meso- and metathorax the mediodorsal process is much smaller, and the alveolate part is feebly developed or entirely lacking. The alveolate structures are very richly tracheated; the diameter of the tracheal branch providing the laterodorsal process of the prothorax is about half that of the main trunk. There cannot be much doubt that we have to do with respiratory organs.


Fig. 21. *A. alveolatus* larva; longitudinal section through the cuticle of a laterodorsal process. 410 ×.

On the abdominal segments the dorsoanal process is finger-like, rather slender, and covered with strong spinules (fig. 20 B). On the mesothorax it is very short, merely a rosette of spinules; on the metathorax it is about half as long as on the abdominal segments.

The mediodorsal seta is a small, yellow spur. The laterodorsal seta and the lateral setæ are developed almost alike, as a little curved, very strong, but rather thin-walled, light-coloured bristles; the former is, however, a little shorter and stronger and straighter than the other three (fig. 20 B). On the abdominal segments there are only two ventral setæ, placed near the posterior margin. They possibly correspond to the oral one and the lateroanal one on the thoracic segments, the former being displaced anally. The lateral of the two setæ is the bigger one.

The whole ventral side, including the anterior and lateral sides of the basal part of the anterior proleg, is covered with slender, light-coloured spinules (fig. 16 D, p. 49), and similar ones are found on the anterior and—though on the middle and posterior abdominal segments only sparsely—on the posterior side of the lateral processes (fig. 20 B). Orally on the lateral side of pro- and mesothorax and dorsally on the posterior margin of segment IX there are short spinules; on the two former segments they are hook-like. Otherwise the cuticular processes are pale and little conspicuous nodules. Orally on the prodorsum, orally on dorsum VIII, as well as on dorsum IX they are, however, somewhat more strongly developed. On the margin of the alveolate areas on the prodorsum and the mediodorsal processes intermediates between the nodules of these areas and normal nodules may be seen. The following areas are quite smooth: on the prodorsum a transverse stripe, on the mesodorsum—dorsum VIII, a transverse, oval field between the medioral processes, and on segment IX a transverse stripe along the posterior margin.

Length of the larva about 2.5 mm.

The larva possibly cannot be distinguished from the larva of *A. thienemanni* Kieffer described by Lenz (9, p. 110).

Atrichopogon sp. y.

On the head (fig. 22 B) there is no antennal socle, and the antenna is not placed nearly so dorsally as in the preceding species. Seta 4 is bifurcate or coarsely penicillate. Seta 10 is a small, peculiar, club-shaped and plumose spur; it resembles a miniature poplar pollard. On the dorsal part of the frons there are only four fields of big nodules, which are pointed.

On the segments mesothorax—VIII the lateral process (fig. 22 C) is distinctly bifurcate. The dorsal branch (= the laterodorsal process) is developed as a long, filiform, silvery, tracheal gill, which at the base is directed dorsally, laterally, and posteriorly, but gradually bent, so that its distal part points straight backwards. On its anterior side it carries the laterodorsal seta, which on the mesothorax is placed a little proximally to the middle of the gill; on the following segments it is gradually displaced in a distal direction, so that on the posterior abdominal segments it stands on the middle of the gill. The slenderer part of the gill, especially, which lies distally to the seta is very thin-walled.

On the mesothorax the ventral branch of the lateral process is rather short, on the metathorax and the abdominal segments it is longer and finger-like. It carries the three lateral setæ, one apically, one subapically and dorsally, and one proximally and ventrally. The laterodorsal seta and the lateral setæ are developed alike, as light coloured, strong, faintly curved bristles; the subapical seta is, however, much shorter than the others. On the meso- and metathorax there is only one lateral seta, the apical one. On the prothorax the ventral branch is lacking as in the other species, and the laterodorsal process is reduced to a small, seta-bearing elevation.

A dorsoanal process is only found on the prothorax; it is rather short and thick.

The mediodorsal seta (fig. 22 D) is a dark, backward curved, and faintly plumose spur-like bristle. On mesothorax-segment VIII it is placed on a conical, mediodorsal process. On the mesothorax this process is rather small; posteriorly its size increases as far as segment VII; on segment VIII it is a little smaller again.

On segment IX the two posterior, dorsolateral setæ—the spur and the long bristle—are placed on the apex of a slender process.

The ventral setæ are developed almost as in the larva of *hexastichus* described below.

The dorsal side has a covering of slightly conspicuous, pale, rounded or low conical nodules, except on the areas between the mediodorsal processes, which are quite smooth. On the anterior margin of the prothorax they merge into stouter spinules. On the dorsoanal process of the prothorax and on the mediodorsal processes there are spinules, which are more conspicuous, especially owing to their brownish colour. Proximally on the anterior side of the dorsal as well as of the ventral branch of the lateral processes there is a group of spinules; on the dorsal branch they are brownish, on the ventral branch thinner and pale. The tergite on segment IX is covered with big, scale-like nodules, which are particularly distinct on the oral, bulging part; especially two very strong nodules on each side will be noted. On the ventral side of the body the cuticular processes are developed as in the larva of *hexastichus*.

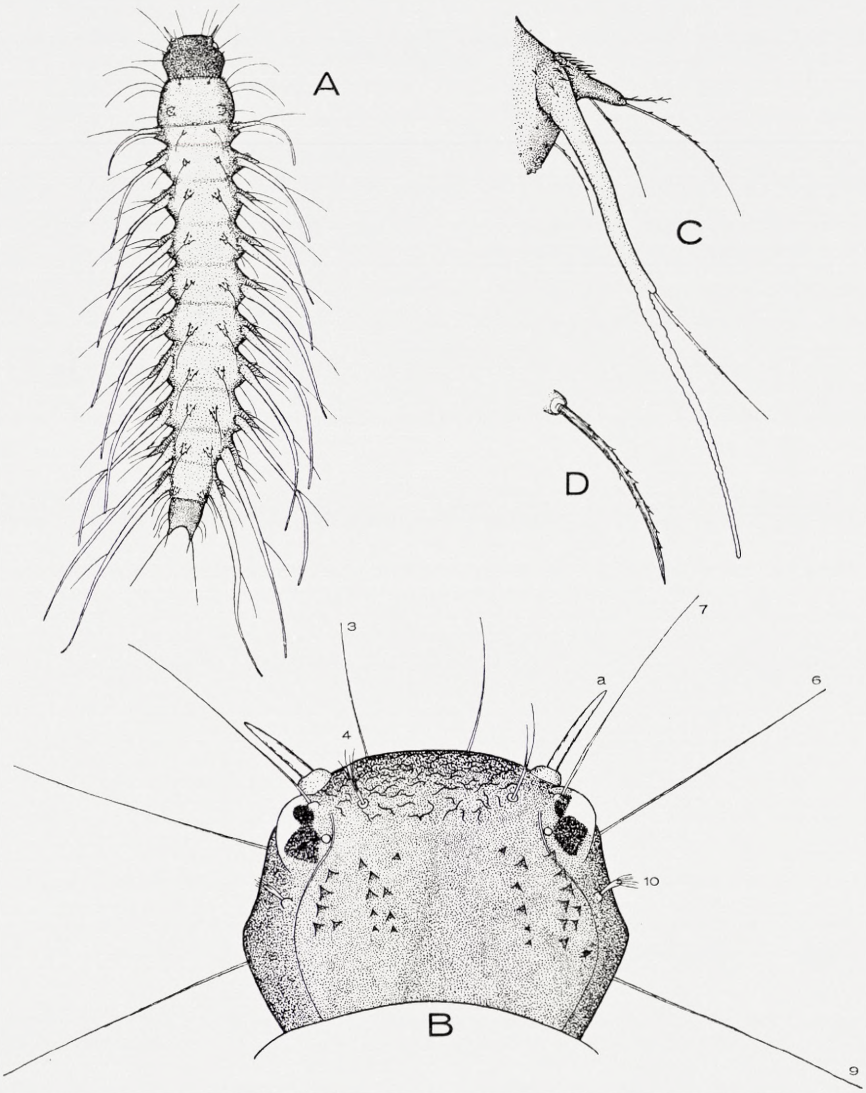


Fig. 22. Larva of *A. sp. y.* A: larva in dorsal view. B: head in dorsal view. C: lateral process from the right side of abdominal segment II in dorsal view. D: mediodorsal seta from abdominal segment II. A: 34 ×; B and C: 200 ×; D: 125 ×.

Length of the (perhaps not full-grown) larva about 1.9 mm.

The larva bears some resemblance to that of *A. peregrinus* Johannsen, described by Lilian C. Thomsen (22, Plate XIV, fig. 54).

Atrichopogon hexastichus.

On the head (fig. 9, left side, p. 30) the antennal socle is lacking, and the antenna has not so dorsal a position as in most of the other species. Setæ 4 and 10 are developed as small, penicillate spurs.

The respiratory apparatus of this larva (fig. 23A) may be considered a further development of the conditions found in *sp. y*. On the metathorax and the abdominal segments I—VIII both the dorsal and the ventral branch of the lateral process are developed as long, filiform, silvery, tracheal gills, and the same is the case with the dorsal branch on the mesothorax, whereas the ventral branch on this segment is but a small protuberance. On the abdominal segments a third gill is formed by the dorsoanal process; on the two thoracic segments this process is lacking. Thus there are one filiform gill on the mesothorax, two on the metathorax, and three on segments I—VIII. Posteriorly the length of the gills increases considerably. The dorsal and the intermediate (fig. 23EF) gill are evenly attenuated, whereas the ventral one (fig. 23G) has a thicker and abruptly cut-off apex. Proximally and orally the dorso-anal process carries one of the sensorial pits. The laterodorsal seta and the lateral setæ are normal, light-coloured bristles. The former is placed almost in the middle of the anterior side of the intermediate gill, the three latter on the ventral gill, one on the anterior side a little proximally to the middle, the two others on the apex; of the latter the dorsal one is much smaller than the ventral one. On the meso- and the metathorax as well as on segment VIII there is only one apical seta (the big one). On the two former segments the proximal seta is a small spur, which has a ventral position, on the mesothorax (fig. 16B, p. 49) at the base of the ventral branch of the lateral process, on the metathorax proximally on this branch.

The gills are backward curved. The ventral one lies in the horizontal plane and the two others are bent in such a way that they eventually also come to lie horizontally. The gills are very thin-walled, especially in their distal part (the intermediate one distally to the seta), and richly tracheated; the tracheal branch which provides the three gills is nearly half as wide as the main trunk. Thus there cannot be much doubt that the gills really are respiratory organs.

On the prothorax the short laterodorsal process carries the seta on the lateral side a little distally to the middle. Distally to the seta the process tapers rather abruptly to a finger-like appendage (fig. 23C); thus the laterodorsal process on the prothorax has a faint resemblance to the intermediate gill on the abdominal segments with which it is homodynamous. The dorso-anal process is short and finger-like (fig. 23D).

The mediodorsal setæ are brown, short, but stout, slightly plumose bristles. On the thoracic segments they are placed quite orally, on the abdominal segments they gradually move backwards. On the mesothorax the bristle is placed on a low process, on the metathorax and the abdominal segments on a high, slender, backward curved process (fig. 23H).

On the prothorax the "twin setæ" are placed on a small, pad-shaped elevation.

This "paired proleg", which also is found on the meso- and the metathorax (fig. 16 B, p. 49), seems to have some relation to the imaginal legs. The "neck" through which their peripodal cavities communicate with the hypodermis joins the latter just at the median margin of the "paired proleg". On the meso- and the metathorax the "paired proleg" also carries the mediooral seta. Immediately in front of the "twin setæ"

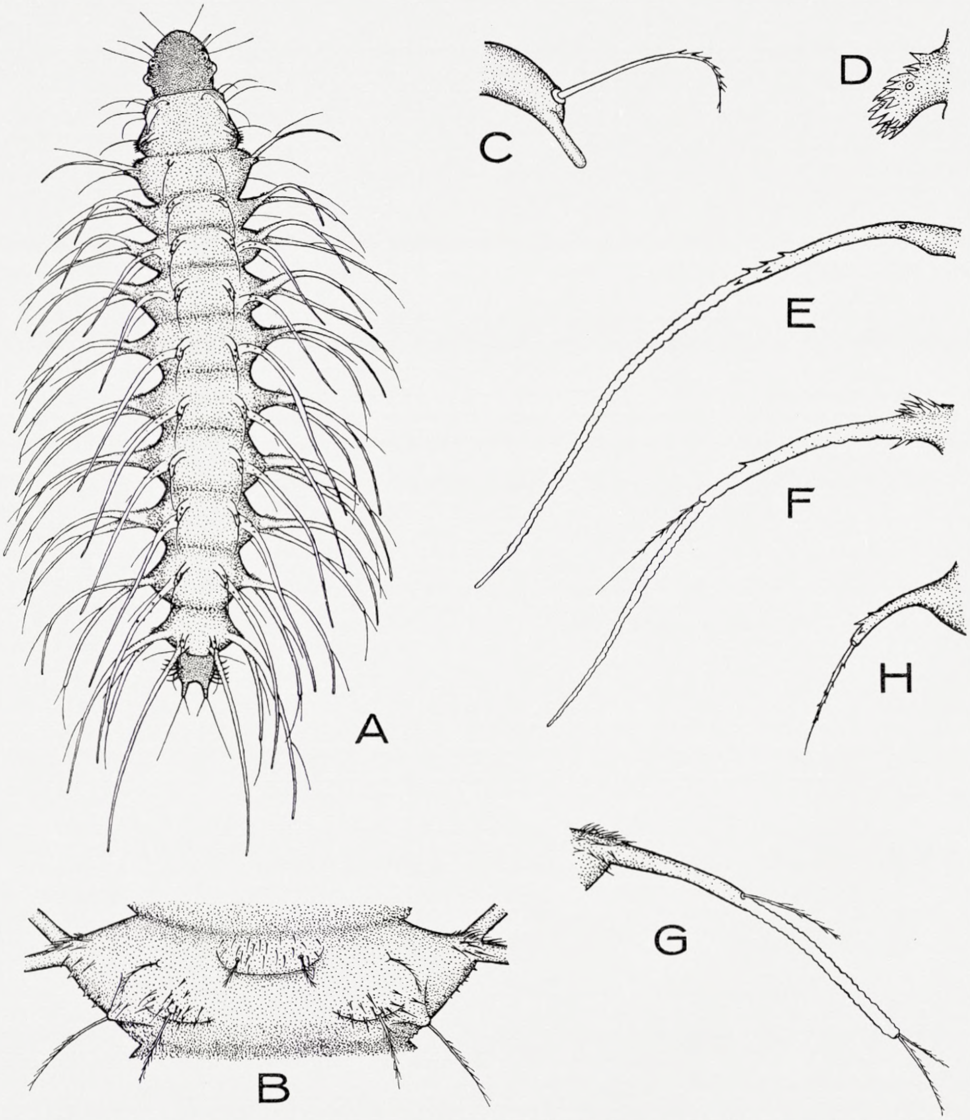


Fig. 23. *A. hexastichus* larva. A: larva in dorsal view. B: abdominal segment I in ventral view. C: right laterodorsal process of prothorax in dorsal view. D: right dorsoanal process of the prothorax in lateral view. E: right dorsoanal process of abdominal segment III in lateral view. F: right laterodorsal process of abdominal segment III in lateral view. G: ventral branch of lateral process from left side of abdominal segment II in ventral view. H: mediodorsal process and seta from abdominal segment III in lateral view. A: 28 ×; B and E—H: 80 ×; C and D: 160 ×.

a straight spinule is seen. On the abdominal segments there are, as on the thoracic segments, four pairs of setæ. One, homodynamous with one of the "twin setæ", is placed on a pad-like elevation, which corresponds to the "paired proleg" on the thoracic segments, and the two mediooral setæ are situated on an unpaired pad (fig. 23 B). All these pads, which probably play a part in locomotion, are rather densely covered with spinules; on segments VII and VIII the lateroanal fields of spinules fuse to an unpaired transverse field. On the abdominal segments the lateroanal seta is placed on a conical process.

On the posterior margin of segment IX the two laterodorsal setæ—the spur and the long bristle—are placed on a slender, backward directed process (fig.16 E, p. 49).

The dorsal side has a covering of scattered, rounded or low conical, pale, and slightly conspicuous nodules; towards the intersegmental regions the nodules become more close-set. Spinules are found distally on the anterior side of the mediodorsal processes (fig. 23 H; not on the mesothorax), on the dorsal side of the dorsoanal process of the prothorax (fig. 23 D), on the prominent posterior corner of the prothorax (fig. 16 B, p. 49), and at the base of the branches of the lateral processes (fig. 23 FG); finally there are a group of about five stout spinules on each side of the anterior part of segment IX. The following areas are quite smooth: an anal, transverse belt on the prodorsum, the area between the mediodorsal processes, the laterodorsal process on the prothorax, and the gills, apart from a ring-like belt on the dorsal gill (fig. 23 E) and some few and scattered spinules on the intermediate gill proximally to the seta (fig. 23 F). The greater part of the ventral side is smooth. Besides the spinules already mentioned there is a rather dense covering on the anterior and lateral sides of the anterior proleg and on a paired area in front of this proleg (fig. 16 B, p. 49), there are some few spinules on the processes which carry the lateroanal setæ, and finally some short spinules and nodules on segment IX.

Length of the full-grown larva up to 4.3 mm.

The larva bears some resemblance to that of *A. peregrinus* Johannsen, described by Lilian C. Thomsen (22, Plate XIV, fig. 54).

Atrichopogon polydactylus.

The most distinctive feature in the setaceous equipment of the head (fig. 24 B) is the fact that seta 10 is represented by two very close-set and very slender bristles. Seta 7 is diminutive, in return seta 3 is nearly as big as seta 6. Also as regards the cuticular processes the head differs from that of the other species. The dorsal side has the same sculpture as the anterior and lateral sides. Dorsally and anally on the lateral side a short, but stout, blunt, brownish spine will be noted.

On all the segments from the mesothorax to abdominal segment VIII the laterodorsal process protrudes into a big, distally tapering, tracheal gill (fig. 24 G). At their bases the gills are directed laterally, posteriorly, and rather much upward, but they are soon bent in such a way that they come to be placed horizontally. The size of the gills increases posteriorly. They are very thin-walled and richly tracheated; the diameter of the branch providing each gill is nearly half that of the main tracheal trunk. Thus there cannot be much doubt that we have to do with respiratory organs.

On the mesothorax a ventral branch of the lateral process is not developed. On the following segments (fig. 24E) it is a slender, finger-like process; on segment VIII it is, however, very much reduced. Apically the gill carries the rather thin and pale laterodorsal seta. The three lateral setæ are pale and faintly curved. One is placed on a small, conical process between the gill and the ventral branch, the two others on the latter, one apically, and one proximally and ventrally. On the meso- and the metathorax there are only two lateral setæ, the ventral one lacking.

Abnormality: On the right side of segment VI in one specimen there was an additional lateral seta; it was smaller than the others and placed subapically and orally on the ventral branch of the lateral process.

In dorsal view the prothorax and the mesothorax are constricted in the middle, the former by a rounded furrow behind which the segment is produced into a prominent corner, the latter by a sharp furrow in front of and behind which the lateral side of the segment is bulging. The laterodorsal seta of the prothorax is a small, club-shaped or chisel-like spur, placed apically on the short, finger-like, laterodorsal process (fig. 24C). The dorsal one of the lateral setæ on this segment stands on a small process (fig. 24D), as on the abdominal segments.

The mediodorsal seta is a small, pale seta, rather often of an aberrant shape (fig. 24H). On the segments from the mesothorax to segment VIII it stands on the apex of a high, distally tapering, mediodorsal process (fig. 24F), which is directed upwards, backwards, and laterally. One of the sensorial pits is found laterally on the base of this process.

A dorso-anal process is lacking on all the segments, also on the prothorax.

On the venters of the thoracic segment the "twin setæ" are lacking, whereas the abdominal segments have the full number of ventral setæ. The lateroanal one is displaced orally and stands at the base of the ventral branch of the lateral process.

On segment IX the number of setæ in the anal row is much reduced, only two of the five light bristles, corresponding to the dorsal and the next but dorsal ones in the other larvæ, being present.

Nearly the whole body has a very conspicuous covering of rather slender spinules. On the mediodorsal processes the spinules are smaller, and the proximal half of the posterior side and the distal half of the anterior side are entirely smooth. Likewise the spinules are smaller on the larger, distal part of the gills; on the dorsal side they are minute and scattered, on the other sides long and extremely slender. Anally on the prodorsum there is a paired, transverse, oval, smooth area. The greater part of dorsum IX is smooth, though on the oral half with three fields—an unpaired median one and a pair of laterals—of very robust, conical nodules.

Length of the full-grown larva about 4.1 mm.

The larva perhaps cannot be distinguished from that of *A. rostratus* Winnertz, described by Lenz (9, p. 110), and it seems to be very like those of *A.* (*Kempia*) *fuscus* Winnertz, described by Goetghebuer (5, pp. 174—80), and *A.* (*Kempia*) *hæsitans* Kieffer, described by Lenz (9, pp. 111—12). As regards *A. fuscus* cp., however, p. 88.

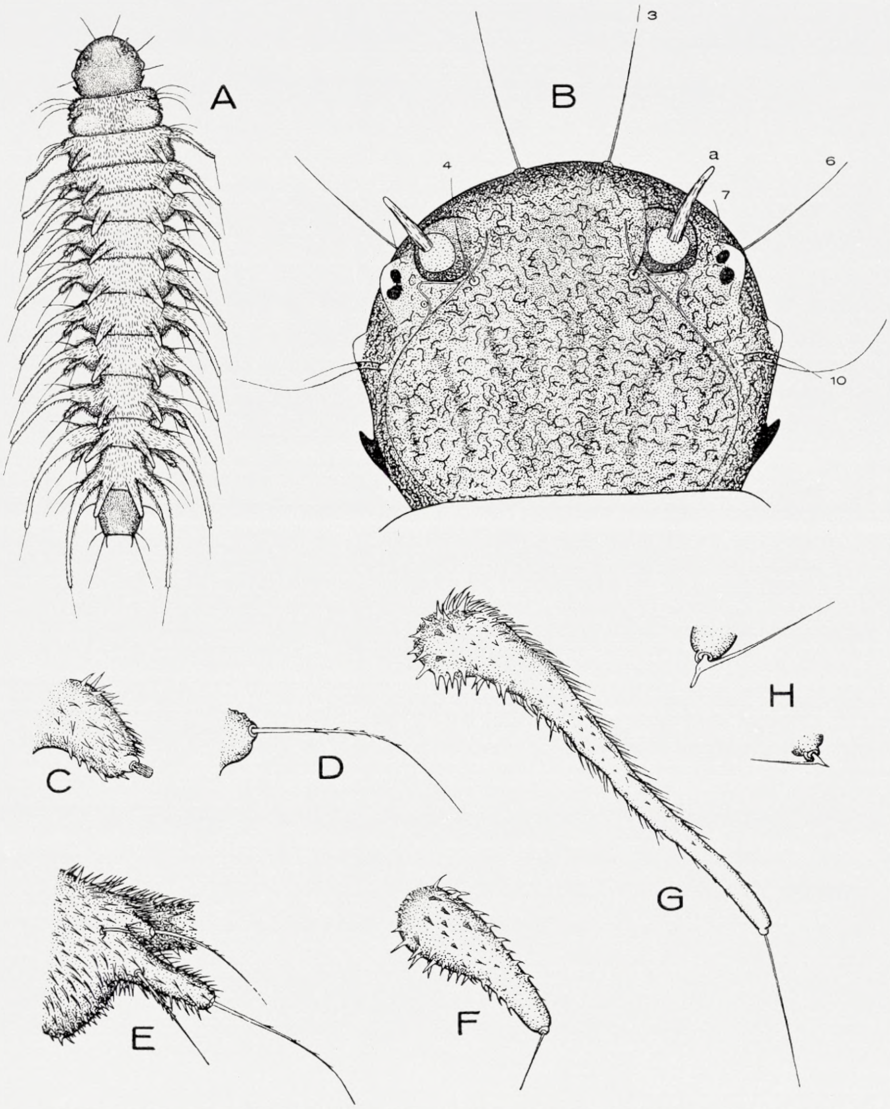


Fig. 24. *A. polydactylus* larva. A: larva in dorsal view. B: head in dorsal view. C: right laterodorsal process of the prothorax in dorsal view. D: the dorsal of the lateral setæ on the prothorax. E: left lateral process of abdominal segment III in ventral view; the greater part of the dorsal branch has been cut off. F: mediodorsal process and seta from right side of abdominal segment II in dorsal view. G: right laterodorsal process of abdominal segment III in dorsal view. H: two aberrant mediodorsal setæ. A: 22 ×; B—D, F, and G: 125 ×; E: 55 ×; H: 200 ×.

THE PUPÆ

Like the larvæ the pupæ are small beings, the length of *polydactylus* and *hexastichus*, which belong to the bigger species, being about 2.9 and 3.1 mm, respectively. The faintly flattened body is broadest across the posterior part of the thorax or abdominal segment I. From here it is only slightly attenuated towards the broadly rounded anterior end, but evenly and strongly tapering towards the pointed posterior end. Thus the body is streamlined (fig. 25), there being no constrictions between the head and the thorax or between the latter and the abdomen.

The pupa is of the obtect type. The sheaths of the mouth parts, legs, and wings cover the entire ventral surface of the thorax and abdominal segment I, the greater part of venter II, and the mediooral part of venter III. The coxæ are directed anteriorly and laterally, the rest of the legs posteriorly and medially. In their larger distal part the tarsi of the two forelegs adjoin each other closely in the median line of the body. The greater part of the middle coxa is concealed by the foreleg; femur, tibia, and the proximal part of the tarsus lie laterally to this leg; the distal part of the tarsus is concealed by the wing sheaths and the foreleg, except the extreme apex, which projects behind the foreleg. The wing-sheaths lie laterally to the fore and middle legs. The hind legs are covered by the wing-sheaths and the fore and middle legs, except the distal part of the tarsus, which is seen, pointing medially, behind the apex of the wing-sheaths. The rounded sheaths of the mouth parts lie in the triangular area between the anterior coxæ. Anteriorly the outline of the body (in dorsal or ventral view) is formed by the antennæ, which are only separated by a short interval; their distal ends wedge in between the wing-sheaths and the tibia-tarsus of the middle leg.

On the dorsal side the head is distinctly separated from the thorax, and the anterior margin of the latter projects a little over the posterior margin of the former. The meso- and the metathorax are separated by a fine furrow, which in the middle is shaped like a broad V, so that the short metadorsum is entirely bipartite. In the cuticle of the pupa there is, on the other hand, no boundary between the pro- and the mesothorax, and the distinction made in the following sections is quite conventional, the respiratory tube of Nematocerous pupæ being generally considered as belonging to the prothorax.

On the dorsal side of the head and thorax there is a Y-shaped line of weakness in the cuticle. The shaft stretches from the posterior end of the mesothorax to the posterior end of the head, the branches towards the bases of the antennæ; the branching point is concealed by the anterior margin of the thorax. The part of the Y which occurs on the head, no doubt, corresponds to the *coronal* and the *frontal sutures*.

The *frons* carries a spur-shaped seta, placed on a small process. In some specimens I found a sensorial pit medioorally to this process, but I have been unable to decide whether it is of constant occurrence. Anally on the frons there is a low, unpaired process, which, however, is lacking in *polydactylus*. On the *epicranium* a smaller spur or spur-like bristle is found near the middle of the frontal suture,

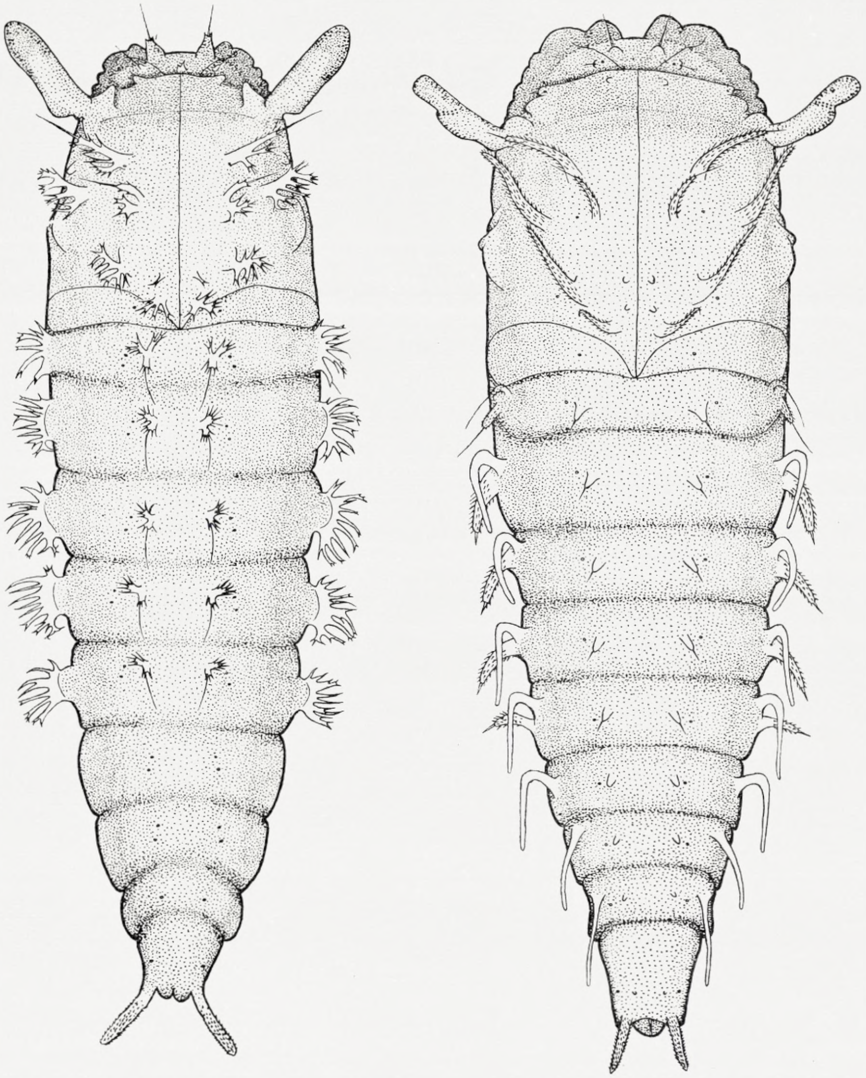


Fig. 25. Pupæ of *A. hexastichus* (left; 43 ×) and *A. polydactylus* (right; 55 ×) in dorsal view.

occasionally (*hexastichus, polydactylus*) placed on a small process, and between this seta and the frontal suture there is a sensorial pit. In *alveolatus* the seta is lacking, though the pit is present. Finally there are two sensorial pits on the base of the antenna.

The large *respiratory tube* (figs. 27 B, p. 69; 30 A, p. 71; 31 A, p. 73) is placed laterally on the prodorsum; it is directed laterally, anteriorly, and upwards. The tube, which is somewhat flattened and on the posterior side has a more or less pronounced hump, is double-walled. From the rounded distal end of the cylindrical inner tube two rows—a dorsal and a ventral one—of closely lying tubules are issued. The tubules grow a little wider distally and terminate on the distal end of the tube in a semicircular or U-shaped row of small, spiracular openings. The latter are arranged in groups of 2—9, each containing the same or almost the same number of dorsal and ventral tubules. The numbers of tubules in the two rows are almost, but not absolutely, equal. The proximal end of the tubules projects a little into the inner tube; each carries here a spinule, on the dorsal tubules dorsally, on the ventral ones ventrally to the internal opening; the ventral spinules are twice as big as the dorsal ones (the latter pictured in the figs. mentioned). The inside of the tube is often covered with thin-walled spinules, whereas the tracheal tænidia do not appear until proximally to the tube.—In *polydactylus* (which see) the tube is approximately cylindrical and also in other respects differing from the description given above.

Fig. 26. Diagram showing the position of the dorsal processes on the right half of the mesothorax in the pupa.

Immediately medioorally to the respiratory tube there is a small, semiglobular, conical, or finger-like, forward directed process; on the anterior corner of the prodorsum a small, but very strong spur. Medially to this spur and more or less removed from it there is, at least in some species, a sensorial pit. Finally a minute, rounded, laterally directed process is found on or near the anterior margin of the prodorsum.

Laterodorsally on the *mesothorax* and almost in the middle of the segment, i. e. above the wing-base, there is a flat, dome-shaped or sometimes slightly irregular bulge. The dorsal side of the segment is furnished with a number of very characteristic *processes*, which, for the sake of clearness, I shall designate with numbers; position and numbers will appear from the diagrammatic fig. 26. It will be noted that the processes are arranged approximately in two oblique rows, which posteriorly converge toward the median line of the segment. In both rows the size decreases medioanally; processes 1 and 4 are almost of the same size (cp., however, *cornutus*). In *polydactylus* processes 1, 2, 4, 5, and 6 are slender, finger-like to filiform, tapering, and covered with rather stout, distally directed spinules. In the other species these processes are styliform (fig. 27 C, p. 69), on the anterior and especially the posterior side covered with more or less branched spines, so that in extreme cases plumose or digitate structures will arise (fig. 31 B–D, p. 73). However, it is only in *hexastichus* that all the five processes are typically developed; in the other species some or all of the processes are more or less reduced. The five processes do not stand at right angles to the surface of the segment, but—also in *polydactylus*—are rather parallel to it. Process 3 is of a varying, but always rather simple shape. Processes 1 and 2 carry a distal, spur-shaped seta. Finally there are two sensorial pits on the mesodorsum, one laterally to process 2, sometimes at or on the base of process 1, and one laterally to process 5. The *metadorsum* does not carry either processes or setæ, but has one or two sensorial pits, placed rather medially; the number seems to vary within the same species.

The *abdominal segments* I—V are furnished with a *lateral seta*, which on II—V always and on I generally is developed as a short, but very stout spur. The lateral seta is placed on the apex of a *lateral process*. In *polydactylus* this process is slender, slightly conical, and covered with vigorous, distally directed spinules, thus suggesting the mesothoracic processes in the same species. Dorsoorally, at or on the base of the process on segments II—V, there is a finger-like gill, which also is present on segments VI—VIII, though the process itself is lacking on these segments. In all the other species the obliquely backward directed process carries more or less strongly dichotomously branched spines on the anterior side. The spines, which are placed particularly on the proximal, thicker part of the process, may reach or even exceed the latter in size. Thus digitate structures are formed, which are spread in the "horizontal plane". The lateral processes of the abdomen belong to the most characteristic features of the *Atrichopogon* pupæ. In *hexastichus* the lateral setæ are lacking, but still the processes are very well developed (fig. 31 G, p. 73). Lateral processes may also be found on segments VI and VII, but here they are much smaller and much simpler, just as their spurs, if present, are much smaller.

It will be noted that the thorax and the abdomen of the pupa are richly provided with branched processes, which will cause a not inconsiderable increase of the body surface. Apart from the gills in *polydactylus* they are not much more thin-walled than the body itself, but their cuticle has a more hyaloid character, which perhaps may be regarded as a sign of greater permeability. Thus they may possibly function as respiratory organs (cp. pp. 80—81).

On segments I—V there is a generally spur-shaped *mediodorsal seta* placed on a small process. This process may also (*polydactylus*) be found on segments VI—IX, but without a seta. Further there are on segments I—VII two (rarely only one), and on segments VIII and IX one dorsal pit. On segments I—V the pits are situated laterally or orally to the seta, on segment IX rather laterally and anally.

Ventral setæ. On the clypeal region of the head there are a generally rather small seta, sometimes placed on a small process, and medially, orally, or anally to this seta a sensorial pit. Further a rather big pit is found distally on the sheath of the mandible.

The abdominal segments I—VIII have three ventral setæ (see, however, below). The lateral one has a rather lateral position, and on segment I it is placed quite laterally, standing just behind (and possibly a little ventrally to) the lateral seta. On this segment it stands on a slender process, so that apparently there are two lateral processes and two lateral setæ (figs. 27 G, 28 A). Also on segments II—IV (except in *polydactylus*) and generally V this seta is placed on a smaller process. The two other setæ stand beside or (*hexastichus*) behind each other; they are smaller, or at least shorter, than the lateral one, and the median (resp. oral) one is the smaller (cp. however, *cornutus*). The lateral of the ventral setæ is lacking on segment VIII (and in *polydactylus* on VI and VII, too), the intermediate one on segments I and II (in *hexastichus* on VIII, too?), the median one on segments I, II, and VIII (and in *alveolatus* occasionally on some of the other segments?). Thus there is only one ventral seta (the lateral one) on segments I and II, and on segment VIII one (the intermediate one) or none (*hexastichus*?). In *polydactylus* I found a sensorial pit rather orally and laterally on venter IX; in the other species I did not succeed in finding any.

Segment IX terminates with a pair of diverging *anal rods*, more or less densely covered with forward directed spinules (figs. 29 I, p. 70; 30 E, p. 71; 31 H, p. 73). In the ♂ the sheaths of the genital appendages project behind the tip of the abdomen, between the bases of the anal rods.

The body has a more or less conspicuous covering of nodules and small spinules, the former especially anteriorly, the latter especially posteriorly. The sheaths of the wings, the legs, and generally also of the mouth parts, are smooth, as well as the greater, distal part of the sheaths of the antennæ.

A. speculiger (fig. 27). Only exuviæ have been examined.

On the frons the median process as well as the lateral ones (fig. A) are covered with spinules of the same kind as the rest of the frons. The inside of the respiratory tube (fig. B) is smooth, apart from some fine, transverse wrinkles in the proximal part. The process in front of the tube is finger-like, but often very short, covered with spinules and nodules like those on the dorsal side of the thorax. On the mesothorax processes 1 and 2 are styliform, tapering, and covered with bigger and smaller spinules or, especially distally, nearly smooth (fig. C D). Process 4 (fig. E) is curved forwards; on its posterior side there are simple or feebly branched spines. Process 5 is entirely lacking, and process 6 is reduced to quite an inconspicuous node. The shape of process 3 (fig. F) varies from a simple spine to a low process covered with spinules. All the ventral setæ of the abdomen are developed as spurs. The intermediate one is smaller than the lateral one, and the median one is quite minute and difficult to detect. The anal rods are like those of *alveolatus* (fig. 30 E); they taper gradually to a sharp point and have a rather scattered covering of spinules, which on the proximal half of the median side is backward directed, otherwise forward directed. The extreme apex of the anal rods is smooth.

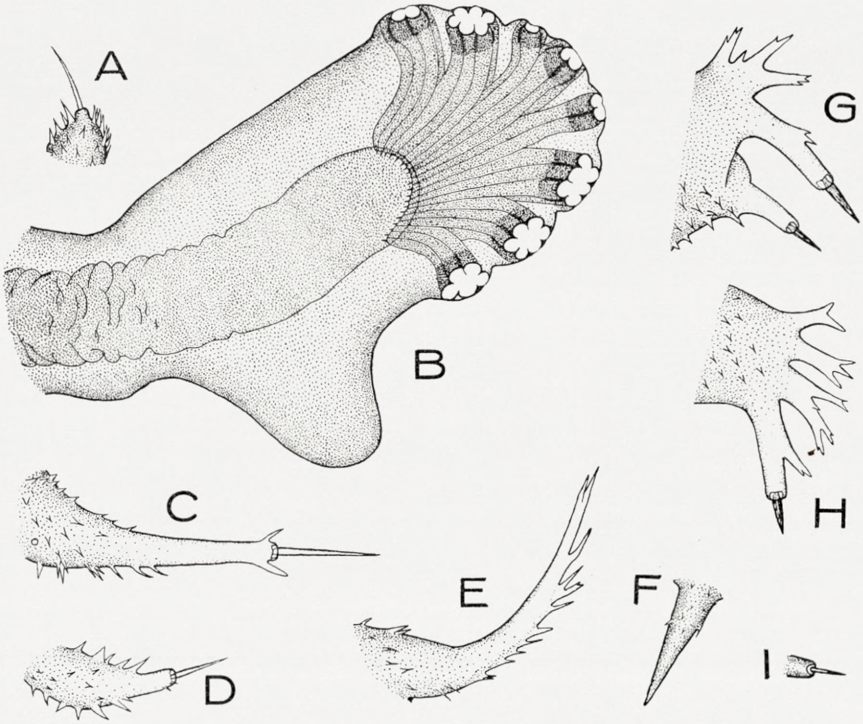


Fig. 27. *A. speculiger* pupa. A: right frontal process and seta. B: right respiratory tube in dorsal view. C: right mesothoracic process 1. D: right mesothoracic process 2. E: right mesothoracic process 4. F: left mesothoracic process 3. G: lateral process from right side of abdominal segment I. H: the same from right side of abdominal segment II. I: mediodorsal seta from right side of abdominal segment I. A and C—I: 250 ×; B: 400 ×.

A. dubius (fig. 28). Only exuviæ have been examined. The pupa is very like that of the preceding species, but may be distinguished by the abdominal segments VI and VII carrying small lateral processes (fig. CD), which are almost cylindrical and covered with spinules. Distally they carry small spurs, much smaller than those

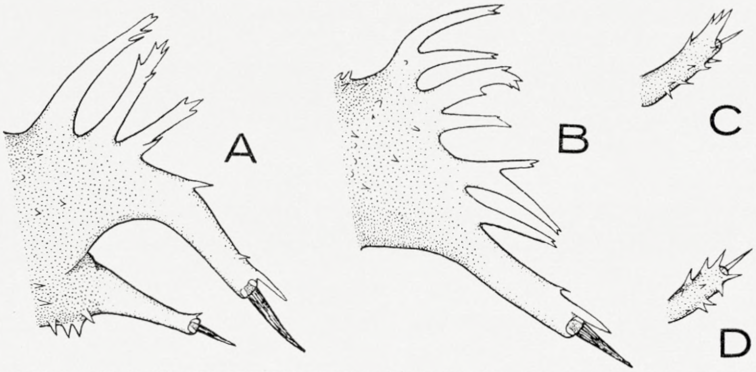


Fig. 28. *A. dubius* pupa. Lateral processes from the right side of abdominal segments I (A), II (B), VI (C), and VII (D). 250 ×.

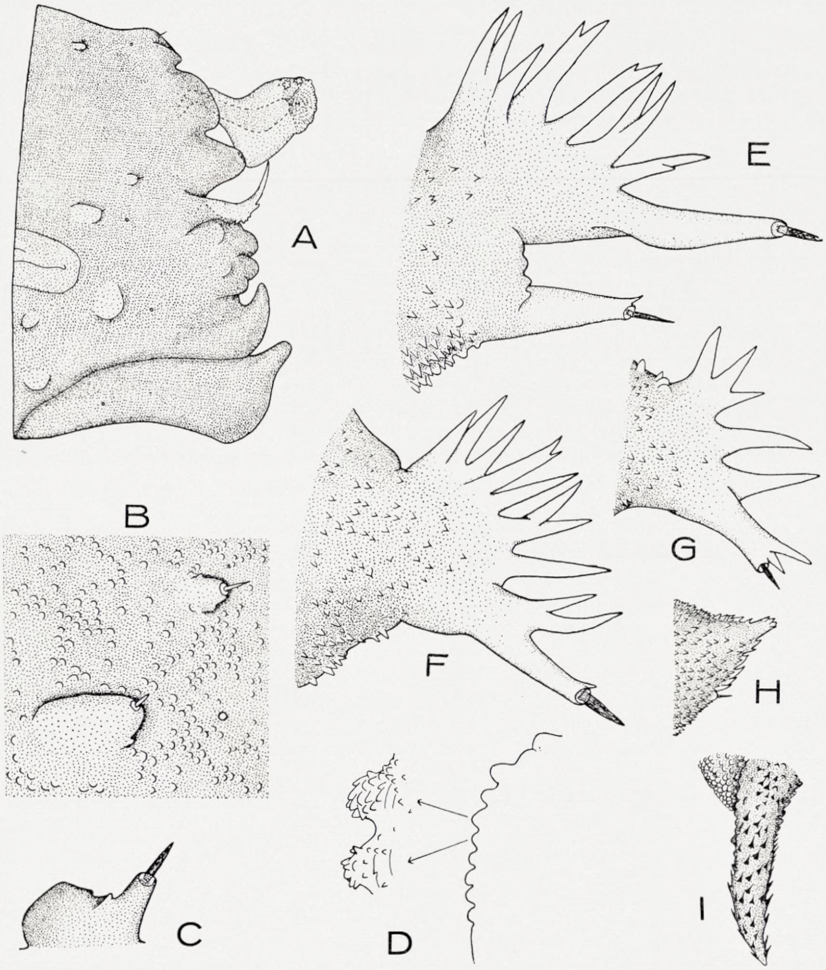


Fig. 29. *A. cornutus* pupa. A: right half of the thorax. B: setæ and anterior sensorial pit of the mesothorax. C: right frontal process and seta. D: outline of the proximal part of the left antenna (dorsal view) and detail of the same. E: lateral process from right side of abdominal segment I. F: the same, segment II. G: the same, segment V. H: the same, segment VI. I: right anal rod in dorsal view and also seen a little from the distal end. A: 64 ×; B, C, and E—I: 200 ×; D: 64 and 200 ×.

on segments I—V. (The lateroventral seta on segments VI and VII is of about the same size as the seta on the lateral process). Further the inside of the respitatory tube is covered with spinules, though not so densely as in the pupa of *alveolatus*, and the lateral processes of the abdomen seem to be a little bigger than in the preceding species; (length from the apex of the anterior branch to the point of the spur about 200 μ as compared with about 120 μ in *speculiger*, fig. 27 H).

A. cornutus (fig. 29). Only exuviæ have been examined. The pupa is rather different from that of the two preceding species. Especially characteristic is a clumsy, forward bent horn anally on the lateral side of the mesothorax (fig. A); a still more clumsy horn is found on the lateral side of the metathorax. The broad, respiratory tube is also characteristic. Its great width is due to the fact that the posterior hump is much widened, so that its lateral side is flush with the posterior side of the distal part of the tube. The inside of the tube is smooth. Just behind the tube, between it and process 4, there is a big, rounded process. The dome-shaped elevation above the wing-base is composite and much more pronounced than in the other species.

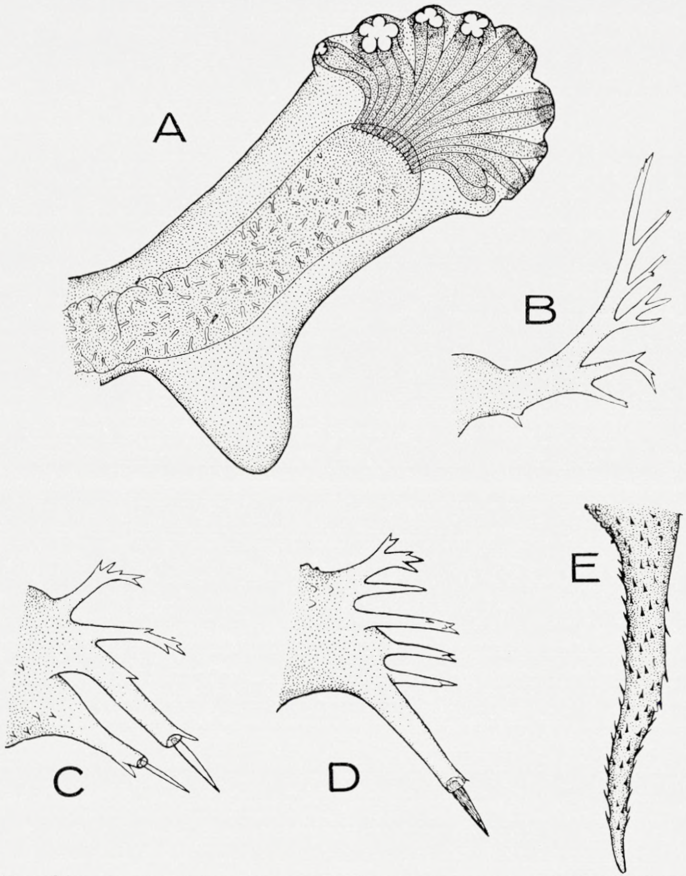


Fig. 30. *A. alveolatus* pupa. A: right respiratory tube in dorsal view. B: right mesothoracic process 4. C: lateral process from right side of abdominal segment I. D: same, segment II. E: left anal rod in dorsal view. A: 400 ×; B—E: 250 ×.

The frontal seta is placed on the lateral, approximately cylindrical branch of a bifurcate process (fig. C); the median branch is almost semiglobular. The lateral outline of the antenna (fig. D) is unusually sinuous, so that a row of small processes is formed. On the mesothorax processes 1 and 2 are developed as small, smooth elevations (fig. B). Process 4 is a forward bent horn, which on its posterior side only carries some few small spines or nodules. Processes 3, 5, and 6 are developed as small, flat, smooth elevations. On the other hand the lateral processes of the abdomen (fig. EF) are bigger and more richly branched than in the other species; on segment V, however, the lateral process (fig. G) and its spur is smaller than on the preceding segments. A still smaller spur is found on segment VI, placed in the middle of the posterior side of a small conical process (fig. H), densely covered with spinules. Such a process may also be developed on segment VII, but it does not carry a spur. The median ventral seta may be bigger than the intermediate one. In their proximal half the anal rods are almost cylindrical, in their distal half they taper to a sharp point and are slightly outward curved (fig. I). They have a rather scattered covering of forward directed spinules, which, however, on the proximal half of the median side are substituted by nodules.

As far as can be judged from the description and figure of Müller (11, p. 227), the pupa cannot be distinguished from that of *A. mülleri* Kieffer, and perhaps the same is the case as regards the pupa of *A. trifasciatus* Kieffer, described by Mayer (10, pp. 214—15).

A. alveolatus (fig. 30). Only exuviæ have been examined. The pupa is very like that of *speculiger*. The chief difference is that the inside of the respiratory tube (fig. A), except quite distally, is covered with spinules, the majority of which are almost cylindrical with a rounded point. On the other hand the difference in shape which is seen by comparing figs. 27 B and 30 A is individual, not specific. (In the latter fig. a very unusual condition is pictured: The posterior group of spiracular openings is rudimentary, i. e. the tubules terminate in a club-shaped swelling without reaching the surface. In all the *Atrichopogon* pupæ examined it has only been seen in the specimen figured). In all the specimens examined the process in front of the tube was very long, finger-like; thus it generally seems to be longer than in *speculiger*. Process 4 (fig. B) is—at least generally—more richly branched than in *speculiger*. In rare cases a lateral seta may be found on segments VI and VII; if present it is minute, not more than half as long and one third as thick as the spurs on the preceding segments; it is placed on a small, cylindrical process, which can be distinguished from the corresponding processes in *dubius* by being smooth or only furnished with some very few spinules. As regards the presence of lateral setæ on segments VI and VII there are not only individual differences, but there may also be differences between the two sides of the body in the same specimen.

A. hexastichus (figs. 25 and 31). The pupa is distinguished by the very rich development of the branched processes on mesothorax and abdomen. The spines on the posterior side of processes 1 (fig. B) and 2 are big and richly branched, and on process 2 one of the spines, placed quite proximally, is almost as big as the process itself and abundantly branched. Thus process 2 is divided into two branches, of which the oral one, carrying the spur, is faintly plumose, whereas the anal one is digitate. The processes 4 (fig. C) and 5 (fig. D) resemble process 1, though without an apical spur and often more richly branched, whereas the smaller process 6 is digitate. Process 3 is a simple or feebly branched spine. A little in front of process 4 there is a small, finger-like process. On segments I—V the mediodorsal seta is developed as a slender spur or a spur-like bristle. It is placed on the apex of a short process (fig. E), which, besides some smaller spinules, carries a distal circle of spines round the alveole of the seta and, quite proximally on the anterior side, a digitate spine of about the same size as the process itself. Thus the mediodorsal process is divided into an oral and an anal branch, the latter bearing the seta. Lateral setæ are not found on the abdominal segments, but still the lateral processes are very well developed and richly branched (fig. G) on segments I—V. Or perhaps the explanation is rather that the seta has been transformed and without a boundary fused with the process. On segments I—V the lateral ventral seta stands on the apex of a small process (fig. F), which carries a distal circle of spines; on segment V, however, the latter

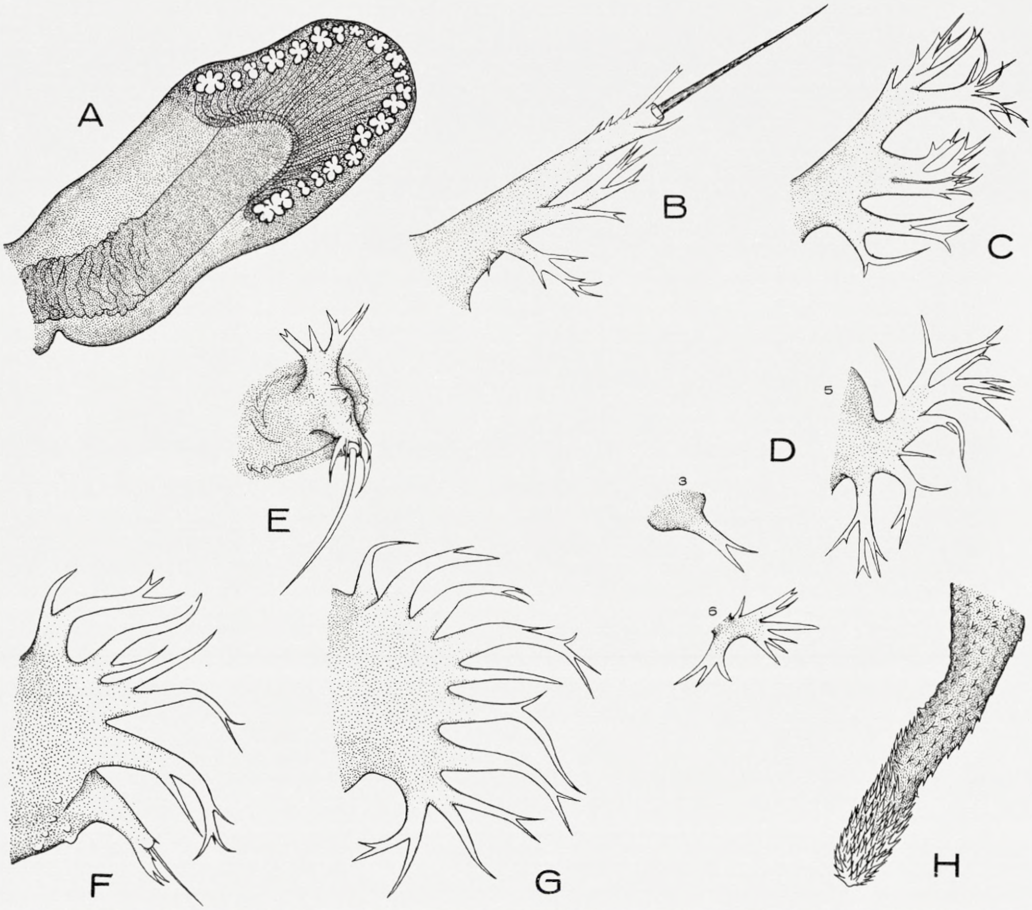


Fig. 31. *A. hexastichus* pupa. A: right respiratory tube in dorsal view. B: right mesothoracic process 1. C: right mesothoracic process 4. D: right mesothoracic processes 3, 5, and 6. E: mediodorsal process and seta from right side of abdominal segment I. F: lateral process from right side of abdominal segment I. G: same, segment II. H: left anal rod in dorsal view. A: 205 ×; B—H: 200 ×.

are lacking. On segments VI and VII this seta does not stand on a process and is shorter, but just as thick as on the preceding segments. The two other ventral setæ stand at a great mutual distance behind each other; they are small spurs, but the anal one is relatively thick.

The frontal processes are rather slender, conical, covered with scattered spinules. The epicranial seta is placed on a small process. The respiratory tube (fig. A) is rather slender, the anal bulge being only feebly developed. Apart from some fine, transverse wrinkles in the proximal part the inside is smooth. The anal rods (fig. H) are almost cylindrical with a rounded apex. The distal third is very densely covered with strong, forward directed spinules, which on the lateral side reach the middle of the anal rod. The rest of the surface is furnished with more scattered, backward directed spinules.

The pupa from which the aberrant imago described on p. 27 was reared showed some interesting abnormalities in the development of the mediodorsal processes and setæ on the abdomen (fig. 32). On segment I the processes have only one branch. The right one (fig. B) is conical and has on the apex a bigger and a smaller spinule beside the seta. The left one (fig. A) carries some bigger and smaller spinules on the thicker apex, but lacks the seta. The seta is also lacking on the left process on segment II (fig. C), which has the shape of a high, conical process tapering into a very slender appendage; or perhaps rather the seta has fused without boundary with the process itself. The latter possibility, which to me seems very likely, gives some support to the alternative explanation of the lateral processes of the abdomen mentioned above. The rest of the processes have two branches as in normal pupæ, but the oral one is of a more simple shape. On the right side of segment II (fig. D) it is a bifurcated, on segments III—V a simple spine. On the right side of segment III (fig. E) it is a little more complicated by carrying a small spinule.

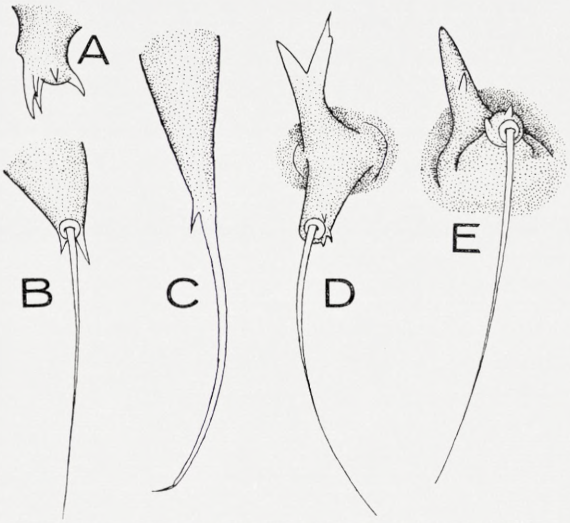


Fig. 32. *A. hexastichus* pupa, aberrant ♀. Mediodorsal processes from the left side of abdominal segment I (A), right side of segment I (B), left side of segment II (C), right side of segment II (D), and right side of segment III (E). 400 ×.

A. polydactylus (fig. 25). The pupa in several respects differs considerably from those of the other species. The respiratory tube (fig. 33) is approximately cylindrical and has no anal hump. As in the other species the distal end carries a U-shaped row of spiracular openings; but the oral part of this row stretches farther proximally than the anal end, and eventually bends across the dorsal side of the tube to continue in a proximal direction on the posterior side of the tube. Thus both ends of the spiracular row are on the posterior side of the tube, the proximal end at a more dorsal level than the distal one. The oral part of the row a little proximally to its middle has a more or less pronounced dorsal bend. The inside of the tube is quite shaggy with evenly tapering spinules. On the mesothorax processes 1, 2, and 4—6 are long, finger-like to filiform, tapering distally, and covered with rather strong, distally directed spinules. Process 3 is represented by two minute processes placed behind each other. The lateral processes on segment I—V are slender, unbranched, and covered with distally directed spinules. On segment I the process is rather small, at the base directed obliquely forwards, but curved almost semicircularly backwards. On segments II—IV the process is big, obliquely backward directed and slightly curved. On segment V it is smaller than on the preceding segments; at the base it is a little forward directed, but afterwards curved slightly backwards. On segment I the lateral seta is a spur-like bristle, on segments II—V a short, very strong spur. On segments II—V there is dorsally and orally, on or at the base of the lateral process, a finger-like, thin-walled process, which probably has a respiratory function. Basally it is directed obliquely forwards, but soon bent abruptly backwards. Though lateral setæ and processes are lacking on segments VI—VIII, the gills are present—strangely enough, since these segments are concealed within the larval exuviæ. The ventral setæ of the abdomen are spur-like bristles. On segment I the lateral one is placed quite laterally, behind and a little ventrally to the lateral seta and stands on an obliquely backward directed process, which resembles the lateral processes of segments II—V, though it is smaller than these. On segments VI—VIII (and of course IX) this seta is lacking. (A comparison between segment I and the following segments might lead to the conclusion that the gills of the the latter are homodynamous with the lateral process of segment I, and that the structure which above is called the lateral process should in reality be termed the process of the lateroventral seta. The fact, however, that segments II—V are furnished with three ventral setæ as in the other species disproves this assumption).

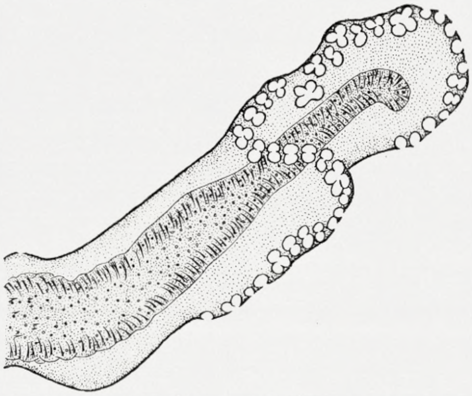


Fig. 33. *A. polydactylus* pupa. Right respiratory tube in dorsal view. 250 ×.

The epicranial seta is placed on a small process. The mediodorsal seta of the abdominal segments stands on a small, conical, smooth process. On segments VI—IX this seta is lacking, but the process is nevertheless present, though in posteriorly decreasing size; on segment IX it has a rather anal position. The anal rods are almost cylindrical in their greater, proximal part; distally they are much attenuated, though the apex itself is rounded. They are rather densely covered with strong, forward directed spinules.

At least as regards the lateral processes of the abdomen the pupa is very like that of *A.* (*Kempia*) *hæsitans* Kieffer, described by Lenz (9, p. 113, fig. 143).

BIOLOGY

The *Atrichopogon* fauna of the locality (cp. pp. 9—14 and Table I) may be divided into two ecological groups: the fauna on the stones in the rills and the fauna in the half submerged vegetation in *g* and *h*. (In this respect those parts of *g* which are situated immediately below the mouth of *c* and *e* agree with the rills). In the rills *e* and *f Atrichopogon* does not occur. This, as well as the fact that the genus is lacking in the typical springs of the district, will show that all the species are more or less thermophilous.

In the other rills the population may be very roughly estimated at 100 per sq.m., there being almost one larva on each stone of the size of a clenched fist. The great majority of the population belongs to the species *speculiger, dubius,* and *alveolatus.* Quite apart from the fact that the two former cannot be distinguished in the larval stage, it is not easy to say anything about the numeric proportion between the three species. This proportion varies, probably in connection with swarming seasons, and my material is not great enough to allow a statistical treatment. Roughly it may, however, be said that *speculiger + dubius* and *alveolatus* are of equal frequency, though the proportion is different in the various rills. In *a* and *b speculiger + dubius* dominate, in the lower part of *c* and in *d* the opposite is the case, and that—especially in *d*—to a rather pronounced degree. This indicates that *alveolatus* is not thermophilous to the same degree as *speculiger + dubius,* and this impression is corroborated by the fact that in a single collection from *i* (2-8 1944) I found a good number of specimens of *alveolatus,* but not a single one of the two other species. It may also of course play a rôle that *alveolatus* seems to be better adapted to aquatic life than the two other species and hence has an advantage in the competition in these rather well watered rills.

As regards the numeric proportion between *speculiger* and *dubius* the following particulars may be given: From pupæ which in the summer 1946 were collected in that part of *g* which lies below the mouth of the rills *c* and *e* four specimens of *speculiger* and two of *dubius* were reared. On the other hand larvæ which in the summer 1947 were collected in the rills *a* and *b* gave only two specimens of *speculiger,* but five of *dubius.* Though the material is very small, it may perhaps give a hint that *dubius* is more thermophilous than *speculiger.*

In the summer months the three larvæ mentioned above have not been found in *g*, and only once (24-7 1947) in *h*, namely a larva of *alveolatus* in the wet moss. This finding indicates also that this species is less thermophilous than the two others.

In the locality *cornutus* is a rare species, of which I have only found seven specimens, all in the rills *a—d*.

Nor can *polydactylus* be said to be common, though I have found a good many larvæ in the rills *a—d*. In the summer months only one specimen was found in *h* (23-7 1947; wet moss), and none in *g*.

The rarest species of the locality is, however, *sp. x*, of which only a single larva was found. It was taken on April 13th, 1944, on a stone in rill *a*. It is possible that its occurrence here was accidental, and that the species in reality lives in a terrestrial habitat (cp. p. 83).

In *g* (half submerged *Chara*) and in *h* (wet moss) the fauna is entirely dominated by *hexastichus*, which must be said to be very common here. In the moss the density of population is about 100 per sq.m., in the *Chara* it is somewhat smaller. (Owing to the fact that the sorting of the material from these habitats is rather difficult, the possibility that some larvæ have been overlooked cannot be excluded). That the species "prefers" these two habitats is in good agreement with its fine adaptation to aquatic life, and that it "prefers" *h* to *g* may indicate a less degree of thermophily. However, not a few specimens have been found in the rills *a—c* (but, strangely enough, not in *d*). Still, the balance of competition in the rills is possibly in favour of the other species.

The *sp. y* also shows a fine adaptation to aquatic life, and in good agreement with this it is restricted to *g* (*Chara*) and *h* (moss). But it is a rare species, which I have only found on three occasions in six specimens in all; (13-4 1946: one specimen in *h*; 24-4 1946: four specimens in *h*; 2-11 1942: one specimen in *g*). That *hexastichus* dominates so much over *sp. y*, may be due to the fact that the former is still better adapted to aquatic life than the latter. Still, it is very striking that all the findings of *sp. y* have been made in spring and autumn. Considering the small number of findings, one of the spring samples is remarkably rich, corresponding to a population of 40 per sq.m.

The larvæ lead a hygropetric life. Their familiarity with the dry element appears among other things from the fact that in captivity they will very soon escape, if they are kept in a container without a lid. On the other hand they do not object to descending below the surface of the water; this is especially true in *hexastichus* (and probably *sp. y*, too). The larvæ have some negative phototaxis. On the stones in the rills they are found on those surfaces of the stones which are in the shadow. In captivity they will, in the dusk or if the glass is placed in a shady place, often ascend to the upper surface of the chalk-pieces (see below) in order to eat; but if strong illumination is put on for observation, they will go down to the lower surface after the lapse of a short time.

In the laboratory I have made observations on the locomotion and the feeding of the larvæ. They were kept in small vessels ("solid watch glasses"), 33 mm wide and 9 mm deep, with lids upon them. In the glasses some pieces of chalk-incrustations, scraped off the stones in *a*, were placed, and at the bottom a thin layer of water in order to keep the chalk-pieces moist. Under these conditions the larvæ thrive excellently and may easily be brought to pupation. This is also the case with *hexastichus*; besides, this species was observed in small Petri dishes, 40 × 16 mm, with moss from *h*.

Locomotion (see also pp. 48 and 49). In the resting position the claws of the anterior as well as the posterior proleg are fastened to the substratum, the anterior proleg being stretched forwards. The movement is initiated by a wave, which runs from behind forwards and raises a couple of segments at a time from the substratum. The segments in question are lengthened, the posterior abdominal segments much, the anterior ones but slightly, the meso- and metathorax not at all. At the very moment the wave reaches the thorax the anterior proleg is carried backwards, at the same time being partly invaginated. When the anterior proleg reaches its hindmost position, the posterior proleg is drawn rapidly forwards; it lets go its hold on the substratum by retracting the claws in a manner like a cat. Finally the anterior proleg is carried forwards again, its claws being also raised from the substratum. The length of a "step" is about the same as the length of the two posterior abdominal segments. In this way the larvæ may creep about rather quickly, though in general they must be said to be sluggish animals. In *hexastichus* (and *sp. y*?) the wavy movement of the body is not so pronounced as in the other species, but otherwise the locomotion takes place in the same way. In this species it has also been observed that the head was used during the movements; the mandibles catch the edge of a moss-leaf, wherupon the larva nods.

Smaller alterations of the direction of locomotion are made by the larva curving the body to the side in question. Abrupt turnings take place on the spot, the anterior proleg working alone, independently of the anal prolegs. During this movement the larva occasionally raises the anterior segments high above the substratum and "throws" the forepart aside. If also the posterior end of the body is raised, the larva may turn round its vertical axis. The two ends are then raised alternately, never at the same time. Often it will be seen that the forepart of the body is raised high above the substratum and stretched from side to side in a searching way. In *hexastichus* the larva is frequently seen to wind its body around moss-stalks like a worm.

Feeding (see also pp. 32—42, and especially pp. 43—45). In captivity the larvæ feed upon the chalk incrustations, from which they scratch off the outmost layer with their mandibles, and after that chew it with their pharyngeal skeleton. That this material is their food in nature, too, will among other things appear from the fact that the contents of the intestine generate a copious amount of gas, if hydrochloric acid is added. Of course it must be the algal flora of the incrustations which constitutes the food proper. (There seems to be a physiological problem here: The activity of the digestive enzymes in insects is said to be dependent on an acid reaction, but in the *Atrichopogon* larvæ the abundance of chalk will certainly prevent any acidity). Also the larva of *hexastichus* thrives excellently on that diet. In the larvæ found in *g*, and especially in *h*, however, it cannot be the food. In captivity it proved impossible to keep it alive for a prolonged time, or, at least, it did not grow, in Petri dishes with moss from *h*. In the larvæ caught in nature the contents of the intestine were composed of fragments of diatom shells (and, strangely enough, also some few whole ones) embedded in a greenish-yellow to brownish substance. Other possible constituents were too finely divided to be determined.

That the mandibles besides their chief function also (in *hexastichus*) may be used during locomotion has been mentioned above. Further they seem to function as a sort of organs of touch. When the larva raises its forepart, searching, from the substratum, they are moved at a fast rate, almost like the tongue of a lizard.

Respiration. As in other Ceratopogonids the larvæ are apneustic and hence are under the necessity of cutaneous respiration. In moist air and in the case of small and sluggish animals, general cutaneous respiration will do, but in water and even in oxygen-saturated water conditions are somewhat more difficult, since the concentration of oxygen molecules is only a minute fraction of that in the air. Still, many developmental instars of aquatic insects (e. g. most stonefly nymphs) manage with general cutaneous respiration, and also in the larva of *A. sp. x* (p. 51) no special organs of respiration seem to be developed. It may be that this larva, which was only found on one occasion and only in one specimen, in reality is terrestrial (cp. p. 83).

In all the other species found in the locality respiratory organs have developed, though of different kinds. In *speculiger*, *dubius*, and *cornutus* they are represented by the thin-walled, oval areas on the dorsal side of the thoracic and abdominal segments (p. 53). When the larvæ are creeping in the thin film of water on the stones, these areas are in contact with the air. In *alveolatus* by the alveolated processes (p. 55), which, in the natural surroundings of the larva, project over the surface film as small, white knobs (fig. 20 C, p. 55). Thus in the four species mentioned above, the respiratory organs are generally in contact with the air, and the respiration may perhaps be said to be a mixture of aquatic and aerial respiration.

In the remaining species typical tracheal gills have developed (pp. 57, 59, and 61), and it will be noted that these structures are best developed in the larvæ (*sp. y* and especially *hexastichus*) which of all the *Atrichopogon* larvæ of the locality are found in the most aquatic habitat. Still, the distal part of the gills, which certainly plays the greater part in respiration, is placed rather dorsally, so also in these two species it will often be in contact with the air, and in *polydactylus* this will generally be the case.

I have made the simple experiment of confining larvæ of *speculiger* (or *dubius*) in a vessel with water which had been boiled for a prolonged time and thus probably was oxygen-free. It gave the rather surprising result that the larvæ under these conditions might survive for more than 24 hours in a lethargic state, from which they soon recovered, when placed under natural conditions.

The pupæ. Immediately before pupation the reaction of the larvæ to light is altered from a slight negative phototaxis to at least some degree of positive phototaxis, an alteration which perhaps has some connection with the fact that some of the ommatids of the imaginal eye have developed already at this time (p. 29). Hence the places in which the pupæ are found are more exposed to light than the places in which the larvæ live. In captivity it has even happened that they pupated on the lid of the vessel, and in nature they may be found in entirely dry situations, which does not seem to prevent emergence. Since the pupæ in contrast to the larvæ have an open (propneustic) tracheal system, it is of course of importance that for pupation places are chosen which are not too much exposed to floods (p. 8).

The prepupal stage is very brief; I have seen larvæ creep about lively before noon and pupate in the afternoon. In captivity the pupal stage lasts 2—5 days (exceptionally 7 days), if the animals are kept in vessels which—at least for some part of the day—are exposed to the sun, i. e. conditions very like those in which the pupæ of *speculiger, dubius, cornutus, alveolatus,* and *polydactulus* are found in nature. No doubt the duration greatly depends on the temperature. Pupæ may be reared at a temperature of 10—11°, but then the rearing takes a much longer time, up to several weeks.

As is well known, the four posterior segments of the pupa are enclosed in the larval exuviæ, and since the latter stick to the substratum, the pupa is in this way confined to the spot. The anal rods with their forward directed spinules (p. 68) no doubt serve to fix the posterior end into the exuviæ. The reduction of the setaceous equipment of the posterior segments is of course connected with the fact that these segments are covered by the exuviæ.

The pupa, however, is not motionless. If it is touched with a needle, it wriggles vividly, curving the forpart greatly upwards. In this way it is able to raise the anterior end high above the substratum, which probably is of importance as a means to keep the spiracles in contact with the air, in case the place of the pupa should be threatened by floods. Despite this measure the pupa will be rather exposed to total submersion for shorter periods, and although the larva, as mentioned above, may survive a period of oxygen-deficiency, it will possibly be more critical to the pupa, considering the intense histogenetic processes in this stage. Most probably, however, the abdominal gills in *polydactylus* (pp. 67 and 75) may serve as an emergency respiratory apparatus during submersion, and possibly the other species are also furnished with such an apparatus in the branched processes on the mesothorax and the abdomen (pp. 66—67). At least they will cause a not inconsiderable increase of the surface of the body, and it is difficult to give an alternative explanation. They might perhaps be interpreted as weapons of defence, which during the wriggles of the pupæ might wound smaller enemies in a way similar to that described by Hinton (8, p. 19) in some beetle pupæ. However, the lateral processes of the abdomen would seem to have an inadequate position for such a function; besides, the fact that the processes of the mesothorax are spread out in a "horizontal" plane speaks against this possibility. It will, moreover, be noted that the processes are best developed in that species (*hexastichus*; p. 72) in which the respiratory apparatus of the larva is best developed.

The emergence of the imago takes place by splitting up the Y-shaped line of weakness in the cuticle (pp. 64—65).

The imagines. It is a well-known fact that the imagines of *Atrichopogon* and some other Ceratopogonine genera are blood-suckers of other insects. In Finland Krogerus has made interesting observations (17, pp. 16—17; 18, pp. 256—57), which seem to indicate that these animals are very specific in their choice of hosts. I have practically not studied the biology of the imagines myself, but perhaps the three following, small observations are not without some interest: If the lid is removed from a vessel in which an imago has been reared, it will immediately fly towards the light. I have seen ♂♂ busily cleaning their antennæ, using both anterior tarsi at the same time. Also in the living ♂ the long setæ (the "beard") of the antennæ are directed nearly straight distally.

Annual cycle. I have found pupæ from the first days of May to the middle of August. In the remaining part of the summer I have not made so thorough searches, so it is probable that pupæ (and imagines) also occur in the rest of the summer proper, i. e. till September. A direct comparison between the stocks in spring and late summer indicates that a substantial decimation takes place during the winter months, and that not till the end of the summer the population reaches its former size. Together these facts seem to show that several generations are produced in the course of the summer. (Perhaps *sp. y* forms an exception in this respect; cp. p. 77.)

As regards studies of the wintering of the genus the small size of the animals causes some difficulties; in cold weather the attention of the investigator will inevitably be somewhat reduced, so that animals of that size may easily be overlooked. Hence I shall prefer first to give a brief account of my investigations on the wintering of *Eubria* and *Hermione* (cp. p. 15), and then mention those observations which indicate that the wintering of *Atrichopogon* takes place in the same way.

In the winter months, also in the case of thaw, one will search in vain for larvæ of *Eubria* and *Hermione* in those places of the rills where they live in the summer. Already in (the end of?) October the larvæ begin to disappear from the rills. Thus a very thorough search on 2-11, 1942, only gave one *Eubria* and three *Hermione* larvæ. But already in the early spring—e. g. 10-4, 1947, after the severe winter (pp. 9 and 12)—larvæ are again found in the rills. Only the early date for their reappearance speaks against the possibility that the wintering should take place in the imaginal stage, and this assumption is further disproved by the fact that already in the early spring larvæ of very different size are found, and among them also—at least nearly—full-grown larvæ, which cannot possibly have hatched from eggs laid in the same year.

Hence it must be considered as certain that the wintering takes place in the larval stage. The question is only where. In order to solve this problem I have carried out a series of investigations in the month of January. The 4-1, 1947, I found in the uppermost, ice-free part of rill *a* (p. 12) two small *Hermione* larvæ, and in the likewise ice-free rill *e* two *Eubria* larvæ. On the same day I sifted three samples (each of 1—2 litres) of frost-proof moss from various places at the edges of the rills *a* and *b*, by which I found: 7 specimens of *Eubria*, 30 of *Hermione*; 6 of *Eubria*, 16 of *Hermione*; 3 of *Eubria*, 6 of *Hermione*. The sample which gave the best result was taken at the uppermost end of rill *a*. Further I found four *Eubria* larvæ on a couple of smaller stones which I pulled out beneath the low cliff at the northern side of rill *a*. Finally I found on the 4-1, 1944, one *Hermione* larva between gravel and pebbles which I dug up from the bottom of an ice-free place in one of the rills (cp. p. 12).

Thus the larvæ winter in places where the outflow of subsoil water is great enough to prevent a danger of frost. The retreat to these places has already been made long before there is any danger of freezing of the rills, which of course is very appropriate; once danger of frost has occurred, the larvæ would not be able to migrate fast enough. The explanation is, no doubt, that the larvæ always seek out those parts of the rills where the temperature is highest. In the spring and summer the rills are warmer than the subsoil water, which is $7\frac{1}{2}$° (cp. Table I and p. 12). When in the autumn the temperature of the rills for the greater part of the day falls below $7\frac{1}{2}$°, the larvæ begin the migration towards their winter-quarters, led by the now warmer subsoil water. At least most of the larvæ carry the migration so far that in the winter they come to lead a subterranean life. In the spring the migration goes in the opposite direction.

Nor have *Atrichopogon* larvæ been found in the rills in the winter, any more than in *g* or *h*. In the latter half of April or in the beginning of May, depending on the severity of the winter, they reappear. The winter 1947 was a very severe one. On 3-5, 1947, a search for larvæ was started in the rills. After one and a half hour's intensive work, during which a very great number of stones were examined, I had found one larva of *alveolatus*. Then I went to the upper part of the rill *d*, and here larvæ of this species were very common, there being one or two on each stone. They seemed all to be practically full-grown; some few days later two of them emerged as imagines. Thus it seems very probable that the *Atrichopogon* larvæ winter in the same way as those of *Eubria* and *Hermione*. (The fact that I only found larvæ of *alveolatus* at this early date also indicates that this species is less thermophilous than the others; cp. p. 76). In *g* and *h* I have in late April also found larvæ of those species which in summer only occur in the rills. In the autumn possibly some of the larvæ will migrate to the moss in *h* and here winter together with *sp. y* and *hexastichus*, probably *sub terra*.

The thermic peculiarities of the locality may lead to the conclusion that its *Atrichopogon* fauna is of relict nature, viz. relicts from the Subboreal Period with its warm and continental climate. However, since nothing is known about the geographic distribution of the species in question, it is of course impossible to make any decision as to this point.

REMARKS ON THE EVOLUTION AND TAXONOMY OF THE GENUS

With the exception of *sp. x* all the larvæ treated in the present paper show respiratory adaptations to aquatic life (pp. 79—80). It is, however, a very striking fact that the adaptations are of three different kinds: in *speculiger, dubius,* and *cornutus* thin-walled, dorsal areas, in *alveolatus* alveolate respiratory processes, and in *sp. y, hexastichus,* and *polydactylus* typical, tracheal gills. This indicates definitely that originally the habitat of the *Atrichopogon* larvæ was terrestrial as in the other genera of the subfamily, so that we are concerned with an animal group, the larvæ of which are "going into the water". Only the fact that such adaptations are at all developed in so small animals points in the same direction. It is a general rule that change from truly aquatic to hygropetric life causes a reduction of the gill apparatus, since the respiratory conditions are much more favourable in the hygropetric habitat than in the purely aquatic one. However, the cuticle in terrestrial insects has probably other properties as far as permeability is concerned than that in aquatic insects, so that a development of a special respiratory apparatus becomes necessary when the former change to hygropetric life (cp. p. 79).

The larva of *A.* (*Kempia*) *pavidus* Winnertz is said to live beneath loose bark on trees (p. 6), and this habitat is perhaps that of the larvæ of the ancestors of the species treated here. In fact, it is not improbable that the larva of *sp. x* lives in such a habitat, and that the occurrence of a single specimen in the rills (p. 77) has been quite accidental. Many trees grow in the nearest vicinity of the rills. The flattened shape of body, characteristic of most larvæ (p. 29), may perhaps be interpreted as an adaptation to life in narrow crevices. The dorsoanal processes (p. 46) may be interpreted as auxiliary locomotory organs of importance when both sides of the body are in contact with the substratum, and thus be considered rudimentary organs in the forms treated here. At any rate, it is difficult to see which function they may have, and in *sp. y* and *polydactylus* they have indeed been obliterated, whereas in *hexastichus* they have taken over another function, as gills. (The ring-like belt of spinules on this gill—p. 61—indicates clearly that it has been derived from a process of a similar shape as in the other species).

In the class Insecta as a whole the original habitat is a terrestrial one. The larvæ of *Atrichopogon,* however, as well as the other Ceratopogonids have an apneustic tracheal system, which, no doubt, means that they descend from forms with aquatic larvæ. Thus the larvæ during the evolution of the genus have passed through the following changes: terrestrial—aquatic—terrestrial—aquatic (hygropetric). Quite an analogous case is found in the turtle *Dermochelys*, which during its evolution has made the changes: terrestrial—marine—terrestrial—marine, changes which have put their mark upon the structure of the carapace.

At a first glance one might be tempted to consider *polydactylus* (p. 61), *sp. y* (p. 57), and *hexastichus* as an evolutionary line. The first is furnished with gills, in the second the gills are longer and slenderer, and in the third their number has been increased. As far as *sp. y* and *hexastichus* are concerned, the interpretation is probably true: the gill-apparatus of the latter is a further development of that of the former. The two larvæ agree on several points (pp. 57—61): The position of the antenna and the lack of an antennal socle. The development of setæ 4 and 10 on the head capsule. The gill in *sp. y* appears to be strictly homologous with the intermediate gill in *hexastichus* by carrying the laterodorsal seta almost in the middle of the anterior side; the distal part of the gill is thus developed through an enlargement of the extreme apex of the laterodorsal process. The mediodorsal processes and setæ are developed nearly alike in the two species. The abdominal segment IX has a seta-bearing process on the posterior corner. The ventral side of the body is nearly alike in the two species and rather different from that of the other species. The lack of dorsoanal processes in *sp. y* is of course an evolution particular to this species.

Many things will, however, show that *polydactylus* is not closely related to *sp. y* and *hexastichus*. In the first place the pupa is of a type entirely different from those of the other species. Especially the structure of the respiratory tube (p. 74) as well as of the mesothoracic processes (pp. 66—67 and 74) and the lateral processes of the abdomen (pp. 67 and 74—75) must be emphasized. But also in the larva many features can be pointed out in which it differs from the larvæ of the other species: The sculpture of the head and the fact that seta 10 is developed as a "twin seta" (pp. 32 and 61). The development of the intermediate dorsal seta on the mesothorax (p. 47). The absence of a dorsoanal process on the prothorax (pp. 47 and 62) and of a "twin seta" on the thoracic venters (p. 62). Hence the gills must be supposed to have evolved independently in *polydactylus* on the one hand and *sp. y* and *hexastichus* on the other. (The position of the laterodorsal seta—p. 62—will also show that the gill in the former is not strictly homologous with the gills in the two latter). That is to say that within the genus we can trace not three, but four lines of evolution, one of which, represented by *polydactylus*, seems to be more distantly related to the three others.

Apart from the development of the respiratory apparatus the *alveolatus* larva (pp. 55—56) in most respects is very like the larvæ of *speculiger*, *dubius*, and *cornutus* (pp. 52—55), whereas it is more different from the larvæ of *sp. y* and *hexastichus* (pp. 57—61). Based upon the larval morphology the following grouping of the species can therefore be made:

I. 1. a. *α. speculiger, dubius*
β. cornutus
b. *alveolatus*
2. *sp. y, hexastichus*
II. *polydactylus*

When *cornutus* is placed in a subdivision of its own and not together with *speculiger-dubius,* it is according to the development of setæ 4 and 10 on the epicranium, and especially to the structure of the pro- and mesothorax (p. 54), which seems to indicate that this species represents a special line of evolution.

It has already been mentioned that *polydactylus* in the pupal morphology deviates very much from the other species, so much that it indicates a very early branching off from the three other evolutionary lines. There is good reason for believing that the pupa of this species in the development of the processes of the thorax and the abdomen represents a primitive condition, though in the development of unquestionable gills (pp. 67 and 75) it shows adaptation to aquatic life. In contrast to the larvæ the pupæ of the other species exhibit a great uniformity. If the branched processes on the thorax and abdomen really are respiratory in function (pp. 67 and 80—81), it means that the aquatic adaptation is considerably older in the pupæ than in the larvæ. Nor is it surprising if such adaptations have had a greater selective value in the sedentary pupæ than in the mobile larvæ. In the case of unfavourable conditions (p. 8) the latter may move to more favourable places, or they may survive these conditions in a lethargic state (pp. 79—80), whereas the pupæ—at least in certain periods of their development—probably are more sensitive.

Based upon the pupal morphology we may thus distinguish the same two main groups as based upon the larval morphology, but within the first of these groups the arrangement will be somewhat different. The *alveolatus* pupa (p. 72) shows a very close agreement with the pupæ of *speculiger* and *dubius* (pp. 68—70), and the pupæ of these three species again are rather like that of *hexastichus* (pp. 72—73), whereas the *cornutus* pupa (pp. 70—71) differs more, especially through the meso- and metathoracic horns and through the feeble development of the mesothoracic processes. Hence the grouping of the pupæ will be as follows:

I. 1. a. *speculiger, dubius, alveolatus*
b. (*sp. y*?), *hexastichus*
2. *cornutus*
II. *polydactylus*

The only thing which might be said to be inconsistent with this grouping is the presence or absence, respectively, of spinules on the inside of the respiratory tube. This, however, is a very small character. The covering with spinules is possibly a primitive feature, which may have been of some importance in the terrestrial ancestors, and which is now independently reduced in the various species.

The imagines of the genus are extremely uniform, This, however, is not surprising. The imagines have not been affected by the change to aquatic life of the developmental instars, and—apart from the fact that they probably differ in the choice of host (p. 81)—the various species certainly lead a very uniform life. Thus there does not exist much cause of divergence in this instar, and the small differences which may be traced between the various species are probably pleiotropic effects of mutations, important to the larvæ and pupæ. (There is even a possibility that such pleiotropic effects to some extent have been counteracted through the selection of modifiers). Still, a grouping, though less sharp, can be made on the basis of the imagines. The most deviating species is *cornutus* through the development of the "hypopygium" (pp. 25 and 26) and the antennæ (pp. 17 and 26) in the ♂. Among the other species *polydactylus* (pp. 21 and 27) and—to a less degree—*alveolatus* (pp. 21 and 26) occupy a special position through the development of the empodium. The grouping of the imagines will then be:

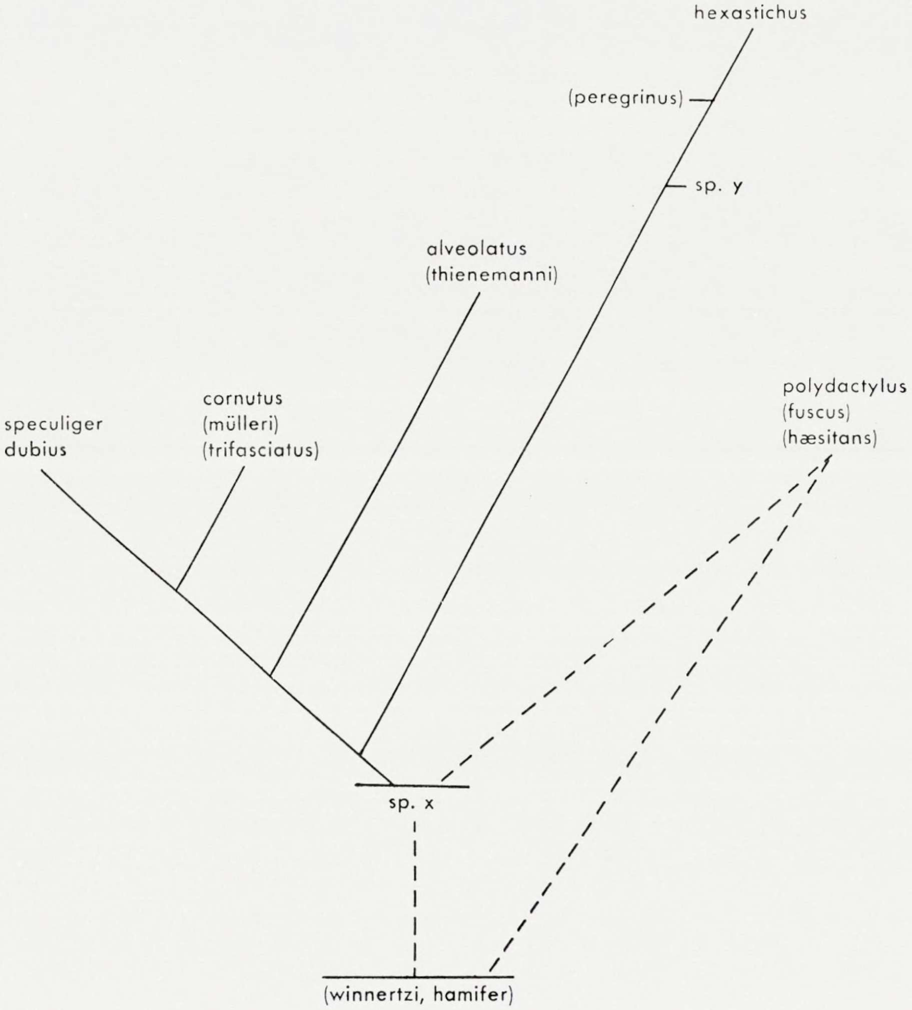
I. 1. a. *speculiger, dubius* (*sp. y*?), *hexastichus*
  b. *alveolatus*
 2. *polydactylus*
II. *cornutus*

If an ancestral tree is constructed for the species in question on the basis of the larvæ, it will be as shown in the diagram. (The very great deviations in pupal morphology may lead to the conclusion that *polydactylus* has been adapted to aquatic life independently of the other species). The question now is if those groupings which must be carried out on the basis of the pupæ and the imagines can be brought into agreement with this diagram.

As far as the imagines are concerned, this does not cause any difficulties. The character which distinguishes *polydactylus* may seem small (for which reason this species has been entered as a subdivision of main group I), but it may also be of a fundamental nature. The species *speculiger, dubius* (*sp. y*?), and *hexastichus* seem to belong to the type prevailing within the genus, i. e. that possibly they are very like the imagines of the primitive *Atrichopogon* species with terrestrial larvæ. The characters which distinguish *cornutus* and *alveolatus,* respectively, may be explained as evolutions particular to these two species. It is true that they seem to remove them from the groups in which they should be placed according to their larvæ, but they do not connect them with other groups.

As regards the pupæ, we have the same two main groups as in the larvæ, but the arrangement within the first of these groups is somewhat different, chiefly due the fact that the *cornutus* pupa differs rather much from the pupæ of the other species within this group. This may, however, also be explained as an evolution special to *cornutus* (and perhaps pleiotropic correlated with the special evolution of the imago), since it does not connect it with any group to which its larva would be a stranger. One of the characters which distinguish the *cornutus* pupa is the very feeble development of the mesothoracic processes. We are probably here concerned with a reduction, a reduction which, at least to some degree, seems to be compensated by a stronger development of the lateral processes of the abdomen. (As mentioned above, also the larva of this species bears the mark of a special evolution).

The ancestral tree based upon the larvæ may thus be considered fairly reliable.



In the ancestral tree some species have also been included the metamorphosis of which has been described by other authors, as far as these descriptions are copious enough to allow any conclusions about the affinities of the species in question. When *mülleri* is placed at *cornutus* and not at *speculiger-dubius*, it is due to Müller's description of the pupa (p. 72). Also in the imaginal morphology (7, pp. 18, 21, and 23) this species, as well as *trifasciatus*, seems to join *cornutus*. That *thienemanni* Kieffer really is specifically different from *alveolatus* among other things appears from the fact that its larva and pupa live in a habitat which, especially in a thermic respect, is very different from that of *alveolatus*. For those localities in which THIENEMANN (21, p. 3) found it must be characterized as typical springs (20, pp. 151—90). The metamorphosis of *A. peregrinus* Johannsen has been described by THOMSEN. According to her figure (22, Plate XIV, fig. 54) the abdominal segments of the larva carry two filiform gills on each side, one of which seems to be the dorsoanal process, the other the laterodorsal process. Thus this species forms a connecting link between *sp. y* and *hexastichus*. The terrestrial species *winnertzi* Goetghebuer and *hamifer* Goetghebuer, the metamorphosis of which has been described by SPEISER and BANGERTER, respectively, seem, in the larval as well as in the pupal stage, to have a considerably greater likeness to the developmental instars of the other genera of the subfamily than is the case with the species treated in the present paper. They may perhaps be considered representatives of the most primitive *Atrichopogon* species, a possibility which has been considered in the ancestral tree. Allowance has also been made for the possibility that *polydactylus* may descend direct from these primitive species, so that its aquatic adaptation is quite independent of that in the other species. The fact that the dorsoanal process is lacking, also on the prothorax (cp. pp. 47 and 83), perhaps points in this direction. Altogether *polydactylus* (and related species) in the larval as well as especially in the pupal stage is (are) so different from the other species that it (they) seem(s) to deserve at least subgeneric rank. The same is the case with the primitive species mentioned above. Thus the genus should be divided into three subgenera. However, KIEFFER's subgenera *Atrichopogon*, *Kempia*, and *Gymnohelea* can hardly be upheld (cp. 7, p. 17 and 9, p. 112).

GOETGHEBUER (5, pp. 176—80) has described the metamorphosis of *A. fuscus* Winnertz. The larva (5, p. 177, fig. 2), seems to have a great similarity to that of *polydactylus*, whereas the pupa (5, p. 179, figs. 4 and 5) should be of the same type as in the other species treated in the present paper. I find such a combination very unlikely and suppose that there has been some mistake. Perhaps the larva described by GOETGHEBUER does not belong to the species *fuscus* at all.

The present investigations may also contribute to throw some light upon the question of the reliability of those characters which are employed in distinguishing the *Atrichopogon* species (cp. pp. 5 and 6). In figs. 3—5 (pp. 17 and 19) a graphic representation is given of the proportion in length between the club and the funicle of the antenna. It will be seen that, especially in the ♀♀, there is a distinct statistical difference, but also a very great individual variation. In the ♂♂, except *cornutus*, there is so much overlapping that they are of very little use in this respect. In the ♀♀ it will be impossible to distinguish between *speculiger*, *hexastichus*, and *polydactylus* as well as between *dubius*, *alveolatus*, and *cornutus* in this way. With the exception of the *cornutus* ♂ the shape of the antennal joints in the species treated here is very uniform, so it does not give us any help. Turning to the wings (Tables IV and V, pp. 22—24) we shall see that neither in these organs any difference can be seen between *speculiger* and *hexastichus*, whereas there is a distinct difference between these two species and *polydactylus*, as well as between *dubius* and *alveolatus*; between *dubius* and *cornutus*, again, there is only a slight difference. These statements refer to the ♀♀, in the ♂♂ conditions will in most cases be even worse. From the above it will appear that by means of these characters it may—to put it mildly—be very difficult to distinguish between species which on the basis of the larvæ can be said with certainty to be specifically different. On the other hand, if due attention is not paid to the great individual variation, it may easily lead to the establishment of too many species. The endeavours ought to be directed towards a rearing of larvæ and finding of qualitative distinctive marks between imagines reared from different larval types.[1] The probable specificity of the imagines in choice of host may also be of use in this respect (p. 81).

Here there may be some reason to discuss if *speculiger* and *dubius* really are specifically different. From Table IV it appears that the wing of the ♀ in *dubius* is generally better equipped with macrotrichia than in *speculiger*, without there being any certain difference. Fig. 3 shows that the club of the antenna in *dubius* is comparatively longer than in *speculiger*. If a greater number of specimens, however, had been investigated, it is highly probable that an overlapping had also been found here. *A. dubius* (p. 25) is a little larger than *speculiger*[2], and it is possible that the characters mentioned, length of the club and number of macrotrichia, are correlated with the body-size, though probably also influenced by other (genetic) factors. The most certain differences between the two species are found in the pupal instar, viz. the lateral processes of the abdomen and the covering of the respiratory tube with spinules (pp. 69—70). These characters may simply be phenotypically correlated with body-size. An either-or, however, seems to assert itself, which indicates that they are of a genetic nature. Still, even in the latter case it does not necessarily mean that the characters are specific. We may also have to do with a dimorphic species, which has two alleles of a gene for process, etc., a gene which then also should exercise some influence upon body-size, club-length, and number of macrotrichia. A decision of the question can possibly only be made through breeding experiments, which, no doubt, will be very difficult to carry out. It caused MUNSTERHJELM (12, p. 159) considerable difficulties to obtain egg-laying of *A. rostratus* Winnertz in captivity, and it will probably be still more difficult to obtain mating.

The aberrant *hexastichus* ♀ mentioned above (pp. 27 and 74) exhibits an interesting example of pleiotropic effects of a mutation. The mutation has affected different organs in the pupa and the imago, in the former the mediodorsal processes of the abdomen, in the latter the antenna and the pretarsus. As regards the mediodorsal processes, it is of special interest that the mutation in the left process of seg-

---

[1] I have tried myself to find such marks, but—apart from some minor colour differences, which may be dependent on the age of the imagines—I only found four: the distinct colour-pattern and the genital appendages in *cornutus*, as well as the pretarsal characters in *alveolatus* and *polydactylus*, of which the two latter need use of oil-immersion to be seen. The first two are almost certainly common to several species, and the same is probably the case with the fourth and maybe with the third, too. We are perhaps in the peculiar situation to be forced to base the taxonomy to a great extent upon the developmental instars.

[2] The—as compared with the ♀—big size of the single *speculiger* ♂ examined is rather surprising.

ment II seems to have caused a condition which is also found in the lateral processes of normal pupæ. It is very difficult to explain the fact that the mutation in the pretarsus has produced characters, and even a very special character (the spinules of the empodium), which otherwise distinguish *alveolatus*. One might be tempted to believe that there has been a mistake. Hence I made new preparations (right middle and left hind tarsus) of the specimen in question, which, however, gave the same result as the old preparation (right hind tarsus). A confusion must be considered to be very unlikely. One possible explanation is that the shape which distinguishes the spinules of the empodium in *alveolatus* is a very primitive character, which has been lost independently in the other species, and that the mutation in this respect has been of an atavistic nature. Atavistic mutations are known in the animal kingdom, e. g. a mutation tending to restore the pentadactyl foot in *Cavia* (Pictet, Wright). There seem to be some difficulties in explaining the mutation as simply a loss mutation. Very probably it has also caused morphological changes in the larva. It was impossible, however, to find such in the larval exuviæ.

SUMMARY

The metamorphosis of eight (cp., however, below) *Atrichopogon* species has been treated from morphological and biological points of view. I did not succeed in rearing two of the species, which only occurred in small numbers; they are designated as *sp. x* and *sp. y*, respectively. The other six are described as new species: *speculiger, dubius, cornutus, alveolatus, hexastichus,* and *polydactylus.*

Most larvæ are rather flattened, but in *sp. y* and *hexastichus* the body approaches the cylindrical shape, though with long, filiform processes and—as in the other species—deep constrictions between the segments.

The field observations were made in a hygropetric locality in the forest Rold Skov in Himmerland, a province in northern Jutland. The locality is situated on the lower part of the western slope of the Lindenborg Aa valley and consists of a moist to swampy meadow from which the water flows to the river in stony rills. Generally the flow of water is constant and small, so that all stones over the size of a walnut emerge, but during and after heavy rain showers the rills will become torrents. Owing to the wind-sheltered and sun-exposed position of the locality the water of the rills is heated very much in the summer; it may assume temperatures up to 9° C. above the air temperature. On the other hand, in periods of frost the rills will freeze over almost entirely.

On the stones of the rills, in the boundary between water and air, the larvæ of *speculiger, dubius. cornutus, alveolatus,* and *polydactylus* live. The stones are covered with chalk incrustations, due to the activity of bluegreen algæ, and the larvæ feed on these incrustations (or, more correctly: their algal flora). The mandibles scratch off small particles of the incrustations and convey them, assisted by the labrum and epipharynx, into an elaborate pharyngeal skeleton, which has taken over the chewing process.

Between the foot of the slope and the river there is a level, swampy ground, covered with alder trees and rich in slow-flowing rills and puddles with partly emerging moss. In the moss the larvæ of *sp. y* and *hexastichus* live. They seem to feed chiefly on diatoms.

The locomotion of the larvæ is brought about by an undulating movement of the body, during which the posterior proleg serves as a point of fixation, and a swinging

movement of the anterior proleg. The more worm-like larva of *hexastichus* will often wind its body around moss-stalks. In this species it has also been seen that the head may assist during locomotion.

Several generations are, no doubt, produced in the course of the summer. The wintering takes place in the larval stage, in places where there is a more copious outflow of subsoil water, and—at least in most cases—subterranean. The migrations of the larvæ are directed by the temperature. In late autumn and in winter the subsoil water is warmer than the summer habitat of the larvæ, in spring and summer the opposite is the case.

The thermic peculiarities of the locality might lead to the conclusion that its *Atrichopogon* fauna is of a relict nature, viz. relicts from the Subboreal Period with its warm and continental climate. Since nothing, however, is known about the geographic distribution of the species in question, it is of course impossible to make any decision as to this point.

The *Atrichopogon* species treated here probably descend from forms the larvæ of which led a terrestrial life, beneath loose bark on trees. It is not unlikely that the larva of *sp. x* lives in such a habitat, and that the occurrence of a single specimen in the rills has been quite accidental. The flat shape of body, characteristic to most species, may be interpreted as an adaptation to life in narrow crevices, and segmentally arranged, spiny processes (dorsoanal processes) as auxiliary locomotory organs of importance when both sides of the body are in contact with the substratum. Within the genus four evolutionary lines with different respiratory adaptations to aquatic life in the larval stage can be traced: (1) *speculiger*, *dubius*, and *cornutus* with thin-walled, smooth, and richly tracheated, dorsal areas. (2) *alveolatus* with alveolate, respiratory processes. (3) *sp. y* and *hexastichus*, and (4) *polydactylus* with filiform, tracheal gills. In *sp. x*, which possibly is representative of the ancestral form, there are no adaptations of this kind.

In the pupæ two main groups can be distinguished. One, represented by *polydactylus*, shows adaptation to aquatic life in possessing finger-like, tracheal gills. In the other main group the pupæ, in contrast to the larvæ, are very uniform. They are richly provided with branched processes, which perhaps are respiratory in function. This being the case means that the adaptations to aquatic life are considerably older in the pupæ than in the larvæ. It is also quite natural that it should be so. Such adaptations are, no doubt, of greater selective value in the sedentary pupæ, which may be subjected to submersion during floods, than in the mobile larvæ.

The most primitive *Atrichopogon* species are probably represented by *winnertzi* Goetghebuer and *hamifer* Goetghebuer, the metamorphosis of which has been described by Speiser and Bangerter. In the larval as well as in the pupal stage they lead a terrestrial life and are considerably more like the developmental instars of the other genera of the subfamily than is the case with the species treated here. *A. polydactylus* perhaps descends direct from such a primitive form.

Based upon the larval and pupal morphology an ancestral tree has been constructed (p. 87). On the same basis the genus may be divided into three subgenera. Kieffer's subgenera *Atrichopogon, Kempia,* and *Gymnohelea,* however, can hardly be upheld.

The taxonomy of the genus is a very difficult problem. Most of the characters employed in distinguishing the species are of a quantitative nature and subject to a very great individual variation. On the one hand it may be difficult or impossible to distinguish between species which on the basis of the larvæ and pupæ can be said with certainty to be specifically different. On the other, if due attention is not paid to the great individual variation, it may easily lead to the establishment of too many species. The endeavours ought to be directed towards a rearing of larvæ and finding of qualitative, distinctive marks of imagines reared from different larval types. If such characters cannot be found—and my investigations seem to point in this direction—we are in the peculiar situation to be forced to base the taxonomy to a great extent upon the developmental instars.

It is questionable whether *speculiger* and *dubius* really represent two species or we are concerned with one dimorphic species.

An aberrant ♀ of *hexastichus* furnishes an interesting example of pleiotropic effects of a mutation, which has affected different organs in the pupæ and in the imago. It is very surprising that in the pretarsus it has produced a character which otherwise distinguishes *alveolatus*. Whether the mutation had also manifested itself in the morphology of the larva could not be decided with certainty on the larval exuviæ.

REFERENCES

1. Anthon, Henning, 1943: Der Kopfbau einiger Nematoceren Dipterenfamilien. Spol. Zool. Mus. Haun. **3**.
2. Bangerter, H., 1933: Mücken-Metamorphosen V. Konowia, Wien. **12**.
3. Bischoff, W., 1933: Über die Kopfbildung der Dipterenlarven. Arch. Naturgesch. Berlin. **88**. Abt. A, H. 6.
4. Boesel, M. W. & E. G. Snyder, 1944: Observations on the early stages and the life history of the grass punky, *Atrichopogon levis* Coquillet. Ann. Ent. Soc. Amer. Columbus. **37**.
5. Goetghebuer, Maurice, 1922: Larves et nymphes des Ceratopogonines. Ann. Biol. Lacust. Bruxelles. **11**.
6. —, 1922: Étude critique des Ceratopogonides de la collection Meigen. Bull. Soc. Ent. Belg. Bruxelles. **4**.
7. — , 1934: Heleidae, die Imagines. Lindner Flieg. Pal. Reg. **13a**.
8. Hinton, H. E., 1946: The "gin-traps" of some beetle pupæ; a protective device which appears to be unknown. Trans. Roy. Ent. Soc. London. **97**.
9. Lenz, Fr., 1934: Die Metamorphose der Heleidae. Lindner Flieg. Pal. Reg. **13a**.
10. Mayer, Karl, 1934: Die Metamorphose der Ceratopogonidae. Arch. Naturgesch. Berlin. N. F. **3**.
11. Müller, G. W., 1905: Die Metamorphose von *Ceratopogon Mülleri* Kieffer. Z. wiss. Zool. Leipzig. **18**.
12. Munsterhjelm, Gust., 1920: Om Chironomidernas äggläggning och äggrupper. Acta Soc. Fauna Flora Fenn. **47_2**.
13. Nielsen, Anker, 1948: Postembryonic development and biology of the Hydroptilidæ. D. Kgl. Danske Vidensk. Selskab. Biol. Skr. **5_1**.
14. Saunders, Leslie G., 1924: On the life history and the anatomy of the early stages of *Forcipomyia*. Parasiotology, Cambridge. **16**.
15. — , 1925: On the life history, morphology, and systematic position of Apelma Kieff. and Thyridomyia n. g. Ibid. **17**.
16. Speiser, P., 1910: Beiträge zur Kenntnis der Dipteren-Gruppe Heleniae. Zool. Jahrb. Jena. Suppl.-Bd. **12**.
17. Storå, Ragnar, 1937: Mitteilungen über die Nematoceren Finnlands. Acta Soc. Fauna Flora Fenn. **60**.
18. — , 1939: Mitteilungen über die Nematoceren Finnlands II. Notul. Ent. Helsingfors. **19**.

19. Søgaard Andersen, F., 1949: On the subgenus *Chironomus*. Vidensk. Medd. Naturhist. Foren. Køb. **111**.

20. Thienemann, August, 1924: Hydrobiologische Untersuchungen an Quellen. Arch. Hydrobiol. Stuttgart. **14**.

21. —, 1926: Hydrobiologische Untersuchungen an Quellen VII. Insekten aus norddeutschen Quellen mit besonderer Berücksichtigung der Dipteren. Deuts. ent. Z. Berlin.

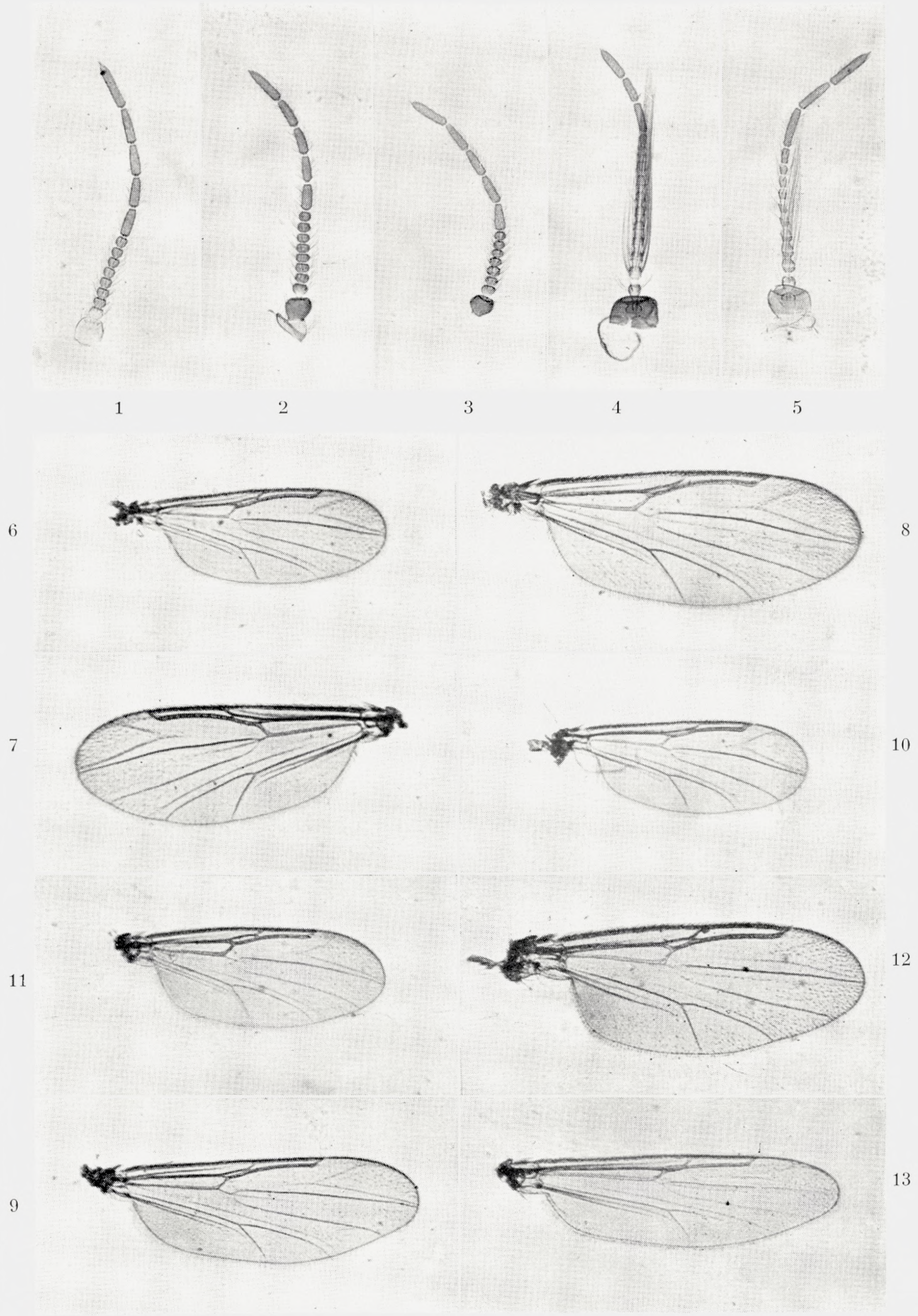
22. Thomsen, Lillian C., 1937: Ceratopogonidae. O. A. Johannsen: Aquatic Diptera V. Ithaca N. Y.

Indleveret til selskabet den 30. januar 1950.
Færdig fra trykkeriet den 7. marts 1951.

Fig. 1. View towards SSW over the hygropetric locality at Stubberupvad. The rills are seen as depressions in the ground; the narrow stripe in the foreground is rill *f*, the next one is rill *a*.

Fig. 2. The rill *a* seen from the lower end.

PLATE II.



1—5: antennæ; $^{50}/_{1}$. In 2, 4, and 5 the first joint is seen, especially distinctly in 2; the point which forms the articulation with the antennifer should be noted. 1: *cornutus* ♀; 2: *hexastichus* ♀, normal; 3: *hexastichus* ♀, aberrant; 4: *alveolatus* ♂; 5: *cornutus* ♂. 6—13: wings; $^{25}/_{1}$. 6: *speculiger* ♀; 7: *dubius* ♀; 8: *cornutus* ♀; 9: *cornutus* ♂; 10: *alveolatus* ♀; 11: *hexastichus* ♀; 12: *polydactylus* ♀; 13: *polydactylus* ♂.

DET KONGELIGE DANSKE VIDENSKABERNES SELSKAB

BIOLOGISKE SKRIFTER

Bind II (kr. 61.00):

		kr. ø.
1.	Böcher, Tyge W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. I. Über die Flechtenheiden und Dünen der Insel Läsö. 1941	4.00
2.	Sørensen, Thorvald: Untersuchungen über die Therophytengesellschaften auf den isländischen Lehmflächen (*»Flags«*). 1942	3.00
3.	Orla-Jensen, S.: The Lactic Acid Bacteria. Die echten Milchsäurebakterien. Ergänzungsband. 1943	18.00
4.	Westergaard, M.: Cyto-Taxonomical Studies on *Calamagrostis Epigeios* (L.) Roth, *Ammophila Arenaria* (L.) Link, and their Hybrids (*Ammophila Baltica* (Flügge) Link). 1943	8.00
5.	Nielsen, K. Brünnich: The Asteroids of the Senonian and Danian Deposits of Denmark. *Opus posthumum* edited by Th. Mortensen and Alfred Rosenkrantz. 1943	9.50
6.	Rosenvinge, L. Kolderup, and Lund, Søren: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. II. Corynophlaeaceæ, Chordariaceæ, Acrothrichaceæ, Spermatochnaceæ, Sporochnaceæ, Desmarestiaceæ, Arthrocladiaceæ. With supplementary Comments on Elachistaceæ. 1943	6.00
7.	Böcher, Tyge W.: Studies on the Plant Geography of the North-Atlantic Heath Formation. II. Danish Dwarf Shrub Communities in Relation to those of Northern Europe. 1943	12.50

Bind III (kr. 60.50):

1.	Olsen, Sigurd: Danish Charophyta. Chorological, Ecological and Biological Investigations. 1944	22.00
2.	Jessen, Knud, and Helbæk, Hans: Cereals in Great Britain and Ireland in Prehistoric and Early Historic Times. 1944	8.50
3.	Gram, K., Jørgensen, C. A., og Køie, M.: De jydske Egekrat og deres Flora. 1944	26.00
4.	Orla-Jensen, S., Olsen, Erik, and Geill, Torben: Senility and Intestinal Flora. A Reexamination of Metchnikoff's Hypothesis. 1945	4.00

Bind IV (kr. 72.00):

1.	Böcher, Tyge W.: Beiträge zur Pflanzengeographie und Ökologie dänischer Vegetation. II. Über die Waldsaum- und Graskrautgesellschaften trockener und halbtrockener Böden der Insel Seeland mit besonderer Berücksichtigung der Strandabhänge und Strandebenen. 1945	20.00
2.	Sørensen, Thorvald, and Gudjónsson, Gudni: Spontaneous Chromosome-Aberrants in Apomictic Taraxaca. Morphological and Cyto-Genetical Investigations. 1946	10.00
3.	Böcher, Tyge W., Christensen, Tyge, and Christiansen, M. Skytte: Slope and Dune Vegetation of North Jutland. I. Himmerland. 1946	12.00
4.	Böcher, Tyge W.: *Dichothrix gelatinosa* sp. n. Its Structure and Resting Organs. 1946	2.00

		kr. ø.
5.	Rosenvinge, L. Kolderup, and Lund, Søren: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. III. Encoeliaceæ, Myriotrichiaceæ, Giraudiaceæ, Striariaceæ, Dictyosiphonaceæ, Chordaceæ, and Laminariaceæ. 1947	14.00
6.	Ravn, J. P. J.: Om Nyker-Omraadets Kridtaflejringer. 1946	4.00
7.	Knisely, Melvin H., Bloch, Edward H., and Warner, Louise: Selective Phagocytosis. I. Microscopic Observations concerning the Regulation of the Blood Flow through the Liver and other Organs and the Mechanism and Rate of Phagocytic Removal of Particles from the Blood. 1948	10.00

Bind V (kr. 82.50):

1.	Nielsen, Anker: Postembryonic Development and Biology of the Hydroptilidæ. A Contribution to the Phylogeny of the Caddis Flies and to the Question of the Origin of the Case-Building Instinct. 1948	30.00
2.	Jørgensen, Erik G.: Diatom Communities in Some Danish Lakes and Ponds. 1948	18.00
3.	Lemche, Henning: Northern and Arctic Tectibranch Gastropods. I. The Larval Shells. II. A Revision of the Cephalaspid Species. 1948	18.00
4.	Sørensen, Thorvald: A Method of Establishing Groups of Equal Amplitude in Plant Sociology Based on Similarity of Species Content and its Application to Analyses of the Vegetation on Danish Commons. 1948	7.50
5.	Nilsson, Tage: On the Application of the Scanian Post-Glacial Zone System to Danish Pollen-Diagrams. 1948	9.00

Bind VI (under pressen):

1.	Orla-Jensen, S., Orla-Jensen, Anna D., and Snog-Kjær, Agnete: Biological Researches on the Silage Process. 1948	2.00
2.	Lund, Søren: The Marine Algæ of Denmark. Contributions to their Natural History. Vol. II. Phæophyceæ. IV. Sphacelariaceæ, Cutleriaceæ, and Dictyotaceæ. 1950.	10.00
3.	Tuxen, S. L.: Über den Lebenszyklus und die postembryonale Entwicklung zweier dänischer Proturengattungen. 1949	10.00
4.	Paulsen, Ove: Observations on Dinoflagellates. Edited by Jul. Grøntved. 1949.	9.00
5.	Thomsen, Mathias: Weismann's Ring and Related Organs in Larvae of Diptera. 1951.	15.00
6.	Nielsen, Anker: Contributions to the Metamorphosis and Biology of the Genus Atrichopogon Kieffer (Diptera, Ceratopogonidæ). With Remarks on the Evolution and Taxonomy of the Genus. 1951	16.00
7.	Böcher, Tyge W.: Cytological and Embryological Studies in the Amphi-Apomictic *Arabis Holboellii* Complex. 1951	9.00

Bind VII (under pressen):

1.	Nygaard, Gunnar: Hydrobiological Studies on some Danish Ponds and Lakes. Part II: The Quotient Hypothesis and some new or little known Phytoplankton Organisms. 1949	40.00
2.	Christensen, Paul J. Holst: Studien über die postembryonale Entwicklung bei *Cochlidion Limacodes* Hufn. (Fam. *Cochlididae, Lepidoptera*). 1950	10.00

PRINTED IN DENMARK
BIANCO LUNOS BOGTRYKKERI