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Morpho-systematic studies on *Collembola*

III. Body chaetotaxy in the first instars of several genera of the *Entomobryomorpha*

[Pp. 341-372, 8 text-figs., pls. XVI—XIX]

Badania morfologiczno-systematyczne nad *Collembola*

III. Chetotaksja ciała najmłodszych stadiów u kilku rodzajów *Entomobryomorpha*

Морфолого-систематические исследования над *Collembola*

III. Хетотаксия тела начальных стадий развития у нескольких родов *Entomobrymorpha*

Abstract. A description of the chaetotaxy of body in the first instars of *Isotomurus palustris* (MÜLL.), *Isotoma viridis* BOURL., *Tomocerus* (*Pogonognathellus*) *flavescens* (TULLB.), *Orchesella flavescens* BOURL., *O. bifasciata* NIC., *Heteromurus nitidus* WANKEL, *Entomobryoides myrmecophila* (REUT.), *Willowsia buski* (LUBB.), *Lepidocyrtus curvicollis* BOURL., *Pseudosinella alba* (PACK.) and *Cyphoderus albinus* NIC. is given. An attempt has been made to deduce the chaetotaxy of all the tergites from an initial pattern composed of 3 rows of 7, 7 and 6 setae, i. e., the pattern characteristic of most members of the *Poduromorpha*, and to homologize the setae of the genera under study with those of the *Poduromorpha*. A close homology of the setae has been established in the *Entomobryidae* s. l., which indicates the monophyletism of this group, and a close affinity has been demonstrated between the genus *Cyphoderus* NIC. and the *Entomobryidae* s. l.

INTRODUCTION

The *Entomobryidae* s. l. are certainly the most advanced group in the evolution of the *Collembola Arthropleona*. This is indicated, e. g., by their greatly heteronomic metamery of body, their passage to atmobiotic ways of living and the morphologic adaptations connected with it, and their colonization of different habitats, not excluding extremely dry ones. Evidence of this fact is also given by the marked differentiation of the setae in respect of both their shape (probably also their function) and their arrangement on particular tergites. The arrangement varies also from genus to genus and even from species to species, and constitutes an important taxonomic character.

The relatively poor diversity of chaetotaxy in the *Poduromorpha*, especially in the *Hypogastruridae* s. l., renders the homology of the setae within this group easy to observe and it was already described comparatively long ago (cf. SNIDER, 1967). This is not the case in so far as the *Entomobryomorpha* are concerned; nobody has hitherto dealt with this problem in the *Isotomidae*, probably because of the limited taxonomic application of chaetotaxy in this family, and only a few studies have been made on the homology of setae and the evolution of chaetotaxy in the *Entomobryidae*. These are as a rule studies given to the homology of setae and their evolution within one genus or, at the most, a group of closely related genera (e. g., GISIN, 1967a, b; SNIDER, 1967) and concern exclusively their imagines.

Studies on the evolution of chaetotaxy must be based on the fixed homology of the setae. Its determination, however, seems to be impossible for adult *Entomobryomorpha* because of the vast diversity of the patterns of setae in this group. This purpose may possibly be achieved by investigation of the postembryonic development of chaetotaxy. This method gave excellent results in acarology, but has hardly been used in studies on the *Collembola* (SZEPTYCKI, 1969). The present paper on the chaetotaxy of the first instars is a report of the initial stage of such studies.

In this paper I discuss the chaetotaxy of the first instars, i. e., specimens which having emerged from the eggs have not yet gone through a moult, belonging to the following species: *Isotoma viridis* BOURLET 1839 and *Isotomurus palustris* (MÜLLER 1776) of the family *Isotomidae*, *Tomocerus* (*Pogonognathellus*) *flavescens* (TULLBERG 1871) of the family *Tomoceridae*, *Orchesella flavescens* BOURLET 1839, *O. bifasciata* NICOLET 1841, *Heteromurus nitidus* (TEMPLETON, 1835), *Entomobryoides myrmecophila* (REUTER 1886), *Willowsia buski* (LUBBOCK 1869), *Lepidocyrtus curvicollis* BOURLET 1839 and *Pseudosinella alba* (PACKARD 1873) of the family *Entomobryidae* s. l. and *Cyphoderus albinus* NICOLET 1841 of the family *Cyphoderidae*.

Three of the species mentioned, *Entomobryides myrmecophila* (REUT.), *Pseudosinella alba* (PACK.) and *Cyphoderus albinus* NIC., come from the material collected by Docent Dr J. WIŚNIEWSKI at Zielonki near Poznań during his studies on anthills of *Formica polyctena* FÖRSTER (WIŚNIEWSKI, 1967), whereas the specimens of the remaining species were obtained by laboratory breeding. For breeding I used glass tubes filled with a mixture of gypsum and charcoal according to HALE (1965). All the specimens reared were derived from Ojców near Cracow. Preparations were mounted in glycerine at first and, later, in SWAN's fluid after NOSEK (1969); some preparations were stained with Chlorazol Black A.

I wish to express my hearty thanks to Prof. dr. J. RAFALSKI for his detailed criticism of this paper in typescript, to Docent Dr. J. WIŚNIEWSKI for the delivery of his rich materials of *Collembola*, and to the workers of the Biological Station of the Institute of Systematic and Experimental Zoology, Polish Academy of Sciences, at Ojców for their help in the breeding of the specimens.

THEORETICAL ASSUMPTIONS

In order to render the sensible discussion of the homology of setae within the order *Collembola* possible, it is necessary to make some assumptions concerning the evolution of this order, especially the morphologic evolution of chaetotaxy. These assumptions seem to be generally accepted, but they have not, as yet, been clearly expressed.

It must be assumed first of all that the evolution of the *Collembola* proceeded from more homonomic forms to more heteronomic ones, because they certainly derive from the primitive *Atelocerata*, which resemble recent myriapods in metamery, and the *Poduromorpha*, considered to be more primitive also for some other reasons, are characterized by a more homonomic metamery. Moreover, the evolution from more homonomic forms to those being more heteronomic occurs with small exceptions in most arthropods. In the *Collembola* the secondarily homonomic forms living in the soil (e. g., *Tullbergia* LUBB., *Isotomodes* AXELS., *Yosiiella* HÜTH.) are an exception in this respect. This phenomenon, however, never leads to the origin of fairly large systematic units, but may only favour the preservation of some primitive characters. The *Collembola* are undoubtedly a monophyletic group, as evidenced by a number of surprisingly uniform structural details such as their peculiar leaping apparatus, the almost identical structure of the antennae and eyes, the chaetotaxy of the labrum, etc.

Since in the insects with homonomic segmentation, e. g., the *Protura* or larvae of holometabolic insects, the chaetotaxy recurs at most with slight changes on the successive segments, it may be supposed that the chaetotaxy of the hypothetical ancestor of the *Collembola* was also remarkably homonomic.

The homonomic metamery of the *Collembola* is disturbed, above all, by the reduction of the appendages on abdominal segments II and V and their great transformation on segments I, III and IV. The formation and development of the leaping apparatus brings about the increasing integration of the abdomen, particularly conspicuous in the *Entomobryidae* s. l., expressed by the reduction (narrowing) of tergites I, II and V accompanied by the marked enlargement of tergite IV. In all the *Collembola* there occurs a reduction of thoracic segment I, which leads to the complete reduction of its tergite in the *Entomobryomorpha*.

The morphologic evolution of chaetotaxy consists chiefly in two phenomena, namely, in changes of the shape of setae and in changes of their arrangement. Evolutionary changes in the shape of setae are difficult to investigate, because the setae are very poorly differentiated in most *Poduromorpha*, whereas the differences between them are already distinct in the *Entomobryomorpha*, and there are no transitional forms in the material examined. Moreover, this problem needs closer knowledge of the morphology and function of different types of setae. For this reason I shall only touch on it perfunctorily in this paper The changes in the arrangement of setae are of the greatest importance to my considerations. They express the changes to which the whole segment, or more strictly its shape, has been subjected, being independent of the direct influence of environment. For closely related species living in very different ecological conditions have, for the most part, very similar chaetotaxy, which may be exemplified by the fact that in the studies on cave species chaetotaxy is regarded

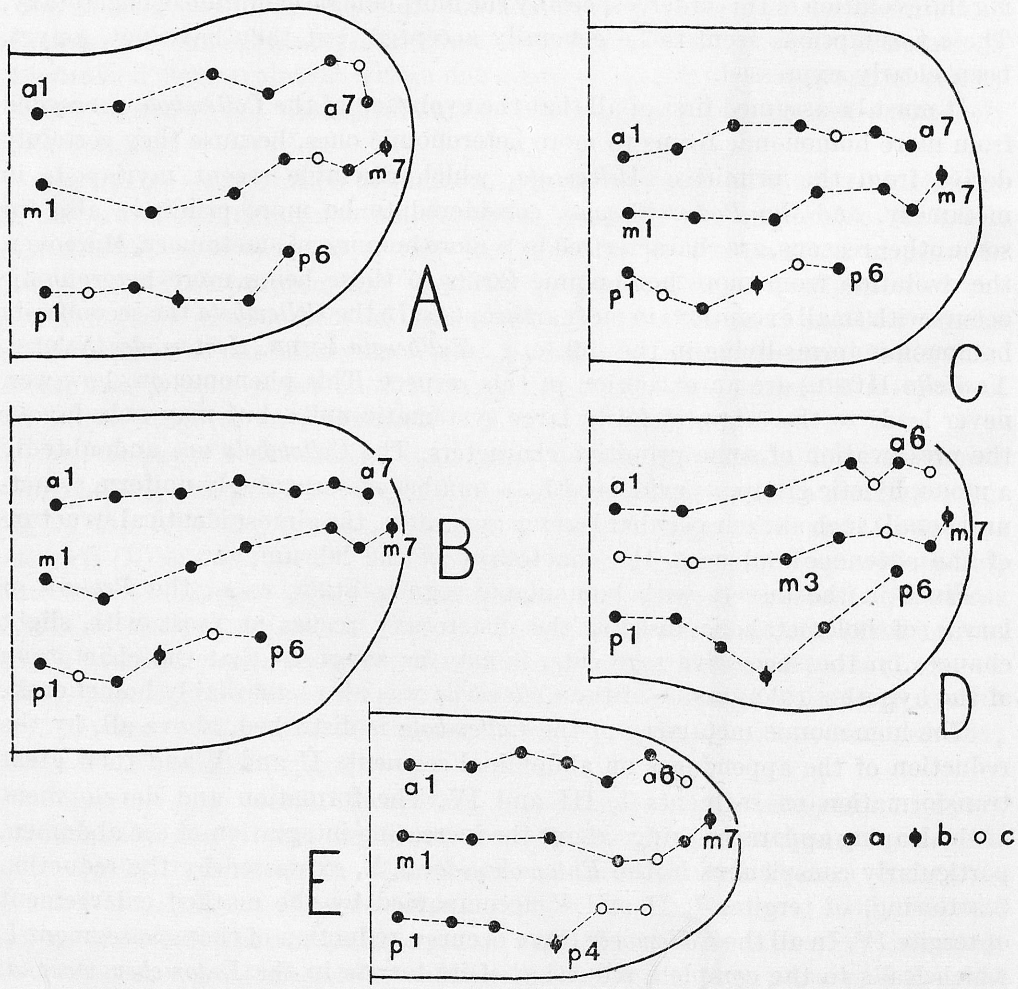

Fig. 1. Setal map of the chaetotaxy of thoracic tergites of *Hypogastruridae* (after THIBAUD, changed). A — *Ceratophysella bengtssoni* (ÅGR.); B — *Schaefferia coeca* CASS.; C — *Sch. willemi* (BONET); D — *Mesogastrura ojcoviensis* STACH; E — *Mesachorutes quadriocellatus* ABS.; a — normal setae, b — sensory setae, c — missing setae

as a „cave independent character“ (Christiansen, 1961). Thus, the arrangement of the setae observed on each segment is a modification of the original pattern and all the diversity of arrangement in particular segments can be reduced to one initial pattern. In addition to the phylogenetic homology of setae, i. e., the homology of the setae derived from a seta of the common ancestor, we may also deal with their serial homology, that is, the homology of the setae on different tergites derived from the setae recurring in the homonomic chaetotaxy of the initial form. Since the meso- and metathorax, as said above; underwent the smallest changes in the evolution of the *Entomobryomorpha*, it may be supposed that also the chaetotaxy of these segments shows the smallest changes.

In order to analyze the repeatedly described arrangement of the setae on the thorax in the *Hypogastruridae* I shall use the drawings presented by Thibaud (1967) in his paper, which contains descriptions and drawings of the chaetotaxy of 5 species: *Ceratophysella bengtssoni* (Ågren 1904) (Fig. 1B), *Schaefferia coeca* Cassagnau 1959 (Fig. 3B), *Sch. willemi* (Bonet 1930) (Fig. 4B), *Mesogastrura ojcoviensis* Stach 1918 (Fig. 5B) and *Mesachorutes quadriocellatus* Absolon 1900 (Fig. 5D). By complementing the patterns of chaetotaxy of individual species with the setae which do not occur in them but are present in the other species we obtain a „synthetic chaetotaxy“ (setal map) (Fig. 1). It consists of 3 rows (*a*, *m*, *p*) of 7, 7 and 6 setae, my designations differing somewhat from those used by Thibaud, i. e., the lateral *s.s.* is marked with the symbol *m7* instead of *m6* and the *s.s.* in the row *p* is designated as *p4*. The thoracic chaetotaxy of other hypogastrurids and probably that of most *Neanuridae* can be reduced to the same pattern too (cf. e. g. Yossi, 1961; Hüther, 1962; Gama, 1969).

As the arrangements of setae extremely similar to this pattern recur in systematically remote species, e. g., in *Tullbergia krausbaueri* Börner 1901 (*Onychiuridae*), *Uzelia setifera* Absolon 1901 and *Yosiiella mira* Hüther 1967 (*Isotomidae*) (Yossi, 1961, Abb. 14, 17; Hüther, 1967, Abb. 1) and also in the first instars of *Isotoma viridis* Bourl. (Pl. XXX, 2) and *Isotomurus palustris* (Müll.), (Pl. XXXX, 1), I assume the arrangement of 7+7+6 setae to be the initial pattern of chaetotaxy for all the *Entomobryomorpha*.

ELEMENTS OF CHAETOTAXY IN *ENTOMOBRYOMORPHA*

On the surface of the tergites of the *Entomobryomorpha* there occur pseudopori and different types of setae. The pseudopori, described by Gisin (1963) from the members of the genus *Pseudosinella* Schäff. (Gisin, 1963) and later found in *Lepidocyrtus* Bourl. (Gisin, 1963) and *Seira* Lubb. (Gama, 1964), are certainly commoner structures than might be inferred from literature. In my material I found them in *Orchesella* Templ., *Tomocerus* Nic. and *Cyphoderus* Nic. and most likely they occur also in the remaining genera, because even in the species in which they have been observed they are not always well seen. I shall not deal with these structures in the further parts of my study.

I have distinguished two main groups of setae, setae proper, further termed setae for short, and setulae. Different types of setae may replace each other, i. e., they may be homologous with each other, whereas none of the types of setae ever replaces setulae or is replaced by them. For this reason setulae are regarded as a distinct group of structures.

Setulae are fine hairlike or spinous structures, as a rule, smaller than microchaetae and refracting light in a different manner. They seem to occur in all groups of the *Arthropleona*, as they have been observed in various genera, *Willemia* BÖRN. (HÜTHER, 1962), *Ceratophysella* BÖRN. and *Hypogastrura* BOURL. (ELLIS, 1967) of the family *Hypogastruridae*, *Anurida* LAB. (HÜTHER, 1964) of the *Neanuridae*, *Onychiurus* GERV. and *Mesaphorura* BÖRN. (ELLIS, 1967) of the *Onychiuridae*, and *Micrisotoma* BELLING. (BELLINGER, 1952), *Tetracanthella* SCHÖTT (CASSAGNAU, 1959), *Sensiterga* MURPHY (MURPHY, 1959), *Isotomodes* LINAN. (GAMA, 1963) and *Yosiiella* HÜTH. (HÜTHER, 1967) of the *Isotomidae*. They have also been recorded from a number of genera belonging to the *Entomobryidae* s. l., namely, *Orchesella* TEMPL. (STACH, 1960), *Lepidocyrtus* BOURL., *Pseudosinella* SCHÄFF. (GISIN, 1967a, b), *Microfalcula* BETSCH & MASS. (BETSCH & MASSOUD, 1968) and *Entomobryoides* MAYN. (SZEPTYCKI, 1969). Setulae were described as „fine hairs“ (BELLINGER, 1952), „sensillae“ (CASSAGNAU, 1959; ELLIS, 1967), „thin-walled sensillae“ (MURPHY, 1959), „Mikrosensilen“ (HÜTHER, 1962, 1964), „sensory hairs“ (STACH, 1960), „petites soies“ (BETSCH & MASSOUD, 1968) and „smooth microchaetae“ (SNIDER, 1967; SZEPTYCKI, 1969). They occur in varying numbers in all the species examined.

The chaetotaxy of each segment is distinguished by three characters, that is, the composition of setae and setulae, their shape and arrangement.

The differences in the composition of setae consist chiefly in the extremely frequent reduction of some setae and setulae. On the other hand, setae which have no homologues in other species or on other tergites (accidental setae) appear relatively rarely. Accidental setae generally appear in the proximity of common setae and for this reason I call their appearance a duplication of common setae without going into its histological mechanism. The duplication leads to the formation of two microchaetae (represented by the abbreviation „du“ in tables) or a macrochaeta and a microchaeta (represented by „MA+“ in tables). Duplication occurs also among setulae; here, however, accidental setulae independent of the common ones appear, in addition, very often.

The differences in the shape of setae discussed in this paper concern only the setae proper. Although the setulae are also differentiated in respect of both their shape and the strength of light refraction, these differences are rather hard to determine closely. Classification of setulae thus needs more precise instruments than the optic microscope.

The common setae are divided into four categories: microchaetae (represented by the abbreviation „mi“ in tables), scales (sc), macrochaetae (MA) and trichobotria (T). Microchaetae, scales and trichobotria are analogous with those in adult specimens and have been described repeatedly (e. g., STACH, 1960;

Snider, 1967). These setae are very much alike in all the species examined, only the microchaetae of *Tomocerus* Nic. differ somewhat from those in the other genera.

The macrochaetae have, however, developed differently in different families. In both genera of the family *Isotomidae* they are pointed and practically do not differ in shape from the microchaetae, only that they outsize these last by several times. In *Tomocerus* Nic. they are dagger-shaped, in *Cyphoderus* Nic. relatively short and broadened in a clublike manner. In the remaining genera they do not differ in shape from the macrochaetae of adult *Entomobryidae* (Stach, 1960, 1963; Snider, 1967). The types of setae are illustrated in Fig. 2.

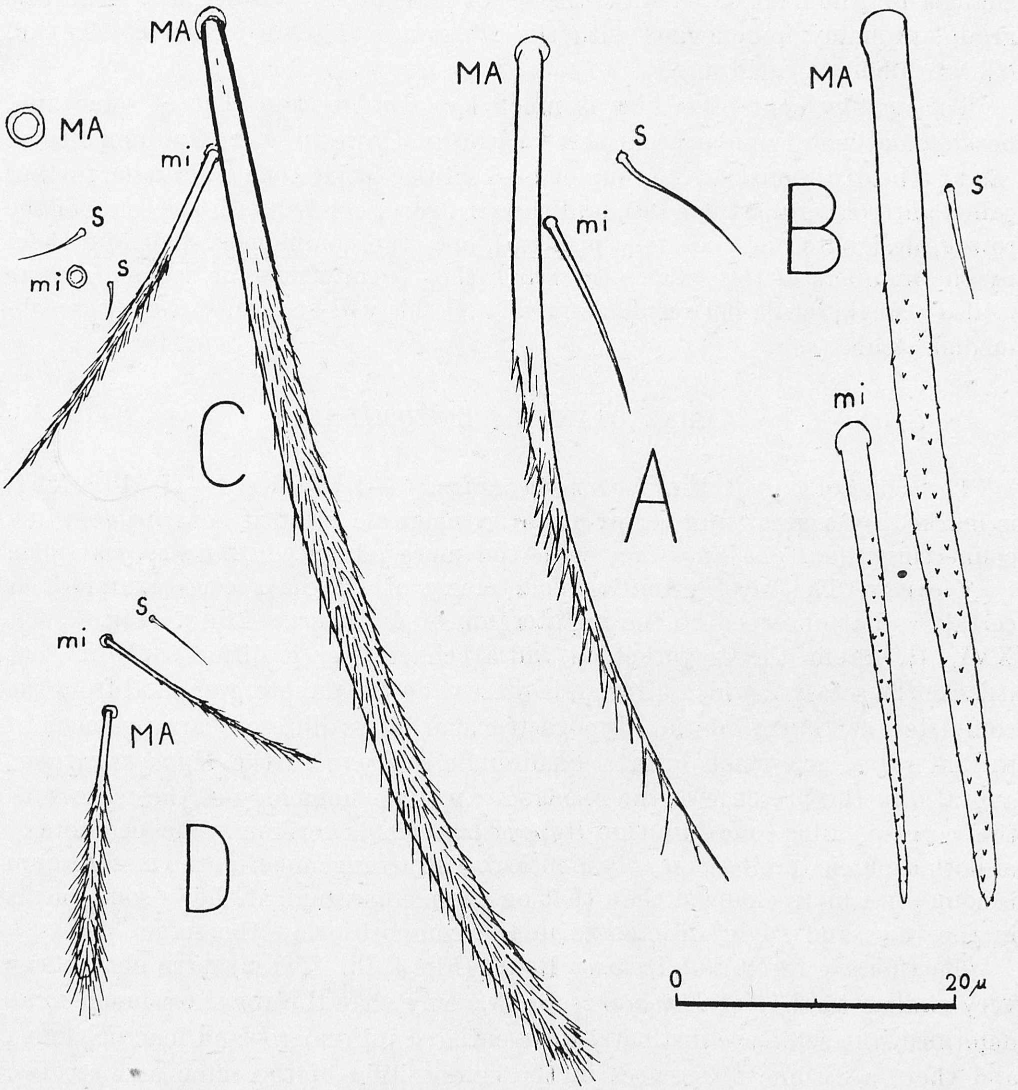

Fig. 2. Setae and setulae of *Entomobryomorpha*. A — *Isotoma viridis* Bourl.; B — *Tomocerus* (*Pogonognathellus*) *flavescens* (Tullb.); C — *Orchesella flavescens* (Bourl.); D — *Cyphoderus albinus* Nic.; MA — macrochaetae, mi — microchaetae, s — setulae

Finally, the last character of chaetotaxy is the arrangement of setae and setulae, in which two elements are distinguished: transverse rows and longitudinal columns. The initial pattern is composed of 3 rows, homologous with the corresponding rows in the *Hypogastruridae* and, as in this family, designated with the letters *a*, *m* and *p*, and seven columns. As is the common practice in the case of the *Hypogastruridae*, each seta is marked with a letter indicating the row and a figure symbolizing the column. Changes in the pattern of setae are most conveniently described by giving the changes in the shape of the rows and columns. A very characteristic trait of chaetotaxy, recurring with only small changes in a number of genera is the set of setae *a6*, *a7*, *m6* and *m7*. I call this group, probably homologous with the „*l*“ group of setae in *Xenylla* TULLB. (GAMA, 1969), a quadrangle.

The arrangement of setulae is much less regular than that of setae and, besides, accidental setulae occur here very often. However, some common setulae can also be distinguished. A group of 1—3 setulae inside the quadrangle, further called anterolateral setulae (*al*), and the setulae associated with the setae of the row *p*, designated as accessory *p* (*acc.p*), are the commonest. I denote them by the numbers of the setae *p* by which they occur. On some segments there is also a single setula between *a2* and *a3*, and this will be termed the anterosubmedial setula (*as*).

CHAETOTAXY OF *ISOTOMIDAE*

The chaetotaxy of the *Isotomidae* (Figs. 3—4, Tables I—II; Pl. XVI) is marked by a great number of primitive characters and it constitutes a link connecting the *Hypogastruridae* with the more advanced *Entomobryomorpha*.

Thorax. The most primitive chaetotaxy of all the species examined is certainly that observed on the metatergum of *Isotomurus* BÖRN. (Fig. 3, Pl. XVI, 1). From the hypothetical initial chaetotaxy it differs only in that it lacks the seta *m5*, which after all is present on the mesotergum, and from the complete chaetotaxy of the Hypogastruridae in its different arrangement of the lateral setae, which form a quadrangle, missing in the *Hypogastruridae*, and also in the presence of the setulae *acc.p*. The homology of the setae with the corresponding ones in the *Hypogastruridae* is striking. The chaetotaxy of both thoracic tergites is nearly identical. The arrangement on the mesotergum is somewhat more changed than that on the metatergum; it shows some bends in the rows and slight differences in the composition of the setae.

The thoracic tergites of *Isotoma* Bourl. (Fig. 4, Pl. XVI, 2) have chaetotaxy very similar to that of *Isotomurus* BÖRN., only that the rows are much more deformed, the setae are distinctly differentiated into micro- and macrochaetae, and there are some differences in the composition of the setae and setulae. These differences do not obscure their clear homology after all.

Abdomen. The chaetotaxy shows some major differences between *Isotomurus* BÖRN. and *Isotoma* BOURL. and for this reason these two genera will be discussed separately. Abdominal tergites I, II and V are strongly narrowed, which has changed the initial pattern to a high degree. The serial homology is very well seen on both tergites in each species, whereas the homology of setae between these genera is more difficult to determine. Tergites III and IV are far less narrowed and, as a result, their threerowed pattern generally remains undisturbed. On both these tergites *m6* is duplicated and, in addition, *p7*, which has no serial homologues on the previous tergites, is present. A large group of lateral setae is situated externally to column 7 on tergite III. The regular arrangement is disturbed, besides the above-mentioned accidental setae, by the lack of some setae and the deformation of the rows.

Isotomurus Börn. (Fig. 3; Pl. XVI, 1). The chaetotaxy of the first two abdominal tergites of this genus is undoubtedly more primitive than it is in *Isotoma* Bourl. Fig. 4; (Pl. XVI, 2). The three-rowed pattern is not, as yet, completely disturbed, although the disappearance of many setae and the heavy distortion of some columns, owing to which the setae of the row *m* enter into row *p*, make the homologization of the setae very difficult. The arrangement of setulae, very distinct on tergite II, is helpful in this respect. There are 6 setulae here, 5 of which may be homologized with the setulae of the *acc.p* group. This fact allows the determination of homology of the setae of the row *p* from *p3* to *p6*. The remaining setula is certainly homologous with one of the setulae *al*, which verifies the homology of column 6. On the assumption that 5 setae are lacking (see Table I) and so is column 7 on tergite I, the arrangement becomes quite clear.

On tergite III the serial homology in relation to the previous tergites is nearly completely obscured. The regular pattern is disturbed only by the abovementioned accidental setae and the reduction of some setae. The seta *p1* has developed into a macrochaeta and *m2* into a trichobotrium. The setulae, from *acc.p3* to *acc.p6* are present, the last one being duplicated. The position of both the setulae *acc.p6* is clearly changed as compared to that on the previous tergites, they both lie internally to the seta *p6*.

The chaetotaxy of abdominal tergite IV is heavily disturbed, chiefly by a bend in the row *p*, resulting in the position of the seta *p4* behind *p3*; a more or less analogous situation occurs on the mesothorax of *Isotoma* Bourl. (Fig. 4; Pl. XXXX, 2). The setae *a4*, *a6* and *p6* have developed into macrochaetae, *p3* into a trichobotrium. In the posterior part of the tergite there are 4 setulae: two *acc. p6*, situated, as on tergite III, internally to *p6*, and two others of obscure homology; one of them perhaps corresponds with *acc. p4*. One setula *as* occurs in the anterior part.

Abdominal tergite V is strongly narrowed and its chaetotaxy very much resembles that of the first abdominal segments. Some small differences exist in the shape and composition of the setae. Two lateral setae, perhaps serially homologous with the corresponding setae on tergite III, occur externally to column 7. There are, besides, 7 setulae of dubious homology.

Isotoma Bourl. (Fig. 4; Pl. XVI, 2). The initial chaetotaxy on the first abdominal tergites is nearly completely disturbed. Only the homology of columns 5, 6 and 7 is unquestionable. The columns situated farther to the inside have undergone a great transformation, namely, they are oriented obliquely to the body axis and, besides, many setae have been reduced. The correctness of the homologization is confirmed by the occurrence of the arrangement on tergite III, which is undoubtedly serially homologous with column 4 but less obliquely situated. The setula *acc.p4* and an accidental setula between *p5* and *p6* occur on both tergites and, in addition, *acc.p6*, *acc.p5*, *al*, and one accidental setula external to *m6* on tergite II.

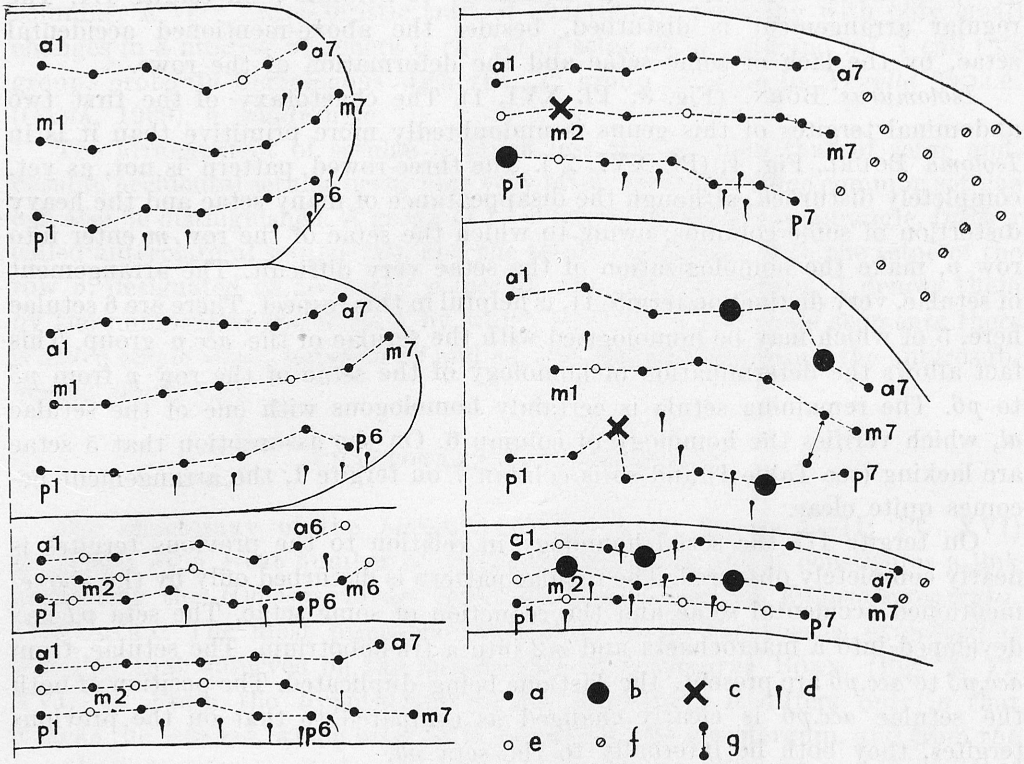

Fig. 3. Setal map of the chaetotaxy of *Isotomurus palustris* (MÜLL.). a — microchaetae, b — macrochaetae, c — trichobotria, d — setulae, e — missing setae, f — setae of incertain homology, g — duplication of setae

The homology of the setae on tergite III with those on tergite II is not so much obscured as it is in *Isotomurus* BÖRN. Here column 3 is lacking completely, but the macrochaetae are analogous. The setulae *acc.p4*, *acc.p5*, and two *acc.p6* are present.

The serial homology with the previous tergites is nearly entirely obliterated on tergite IV. Its only elements are the macrochaetae *m2* and *m5* and the dupli-

Table I

The chaetotaxy of *Isotomurus palustris* (Müller 1776)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. IV	Abd. V
a1	mi	mi	mi	mi	mi	mi	mi
2	mi	mi	—	—	mi	mi	—
3	mi	mi	mi	mi	mi	mi	mi
4	mi	mi	mi	mi	mi	MA	MA
5	—	mi	mi	mi	mi	mi	mi
6	mi	mi	mi	mi	mi	MA	mi
7	mi	mi	—	mi	mi	mi	mi
m1	mi	mi	—	—	—	mi	—
2	mi	mi	mi	mi	T	—	MA
3	mi	mi	—	—	mi	mi	mi
4	mi	mi	—	—	—	mi	mi
5	mi	—	mi	mi	mi	mi	MA
6	mi	mi	mi	mi	du	du	mi
7	mi	mi	—	mi	mi	mi	mi
p1	mi	mi	mi	mi	MA	mi	mi
2	mi	mi	—	—	—	mi	—
3	mi	mi	mi	mi	mi	T	mi
4	mi	mi	mi	mi	mi	mi	—
5	mi	mi	mi	mi	mi	mi	—
6	mi	mi	mi	mi	mi	MA	—
7	—	—	—	—	mi	mi	mi
setulae:							
as	—	—	—	—	—	+	—
al	2	—	1	1	—	—	—
acc. p3	+	+	—	+	+	+	?
4	+	+	+	+	+	?	?
5	+	+	+	+	+	?	?
6	du	du	+	du	du	du	?

mi — microchaeta; MA — macrochaeta; T — trichobotrium; du — duplication (two microchaetae or two setulae).

cation of *m6*. The chaetotaxy of this tergite very much resembles that on tergite III in *Isotomurus* Börn. (Fig. 3; Pl. XVI, 1), from which it differs only in the lack of some setae and the different distribution of the macrochaetae. The setulae *acc.p2* — *acc.p6* are present, *acc.p4* and *acc.p6* being duplicated.

The chaetotaxy of tergite V, as in *Isotomurus* Börn., exhibits distinct homology with the first abdominal tergites. Column 3 is quite reduced, as on tergite III. The setula *as* is in its normal position, other setulae are lacking.

The relatively large number of primitive characters of the chaetotaxy in *Isotomurus* Börn. is striking. They are the small number of macrochaetae, which here occur only on abdominal tergites IV and V, the very regular arrangement of setae on the thoracic tergites, the traces of the three-rowed pattern of setae on the first abdominal tergites, and perhaps the relatively large number

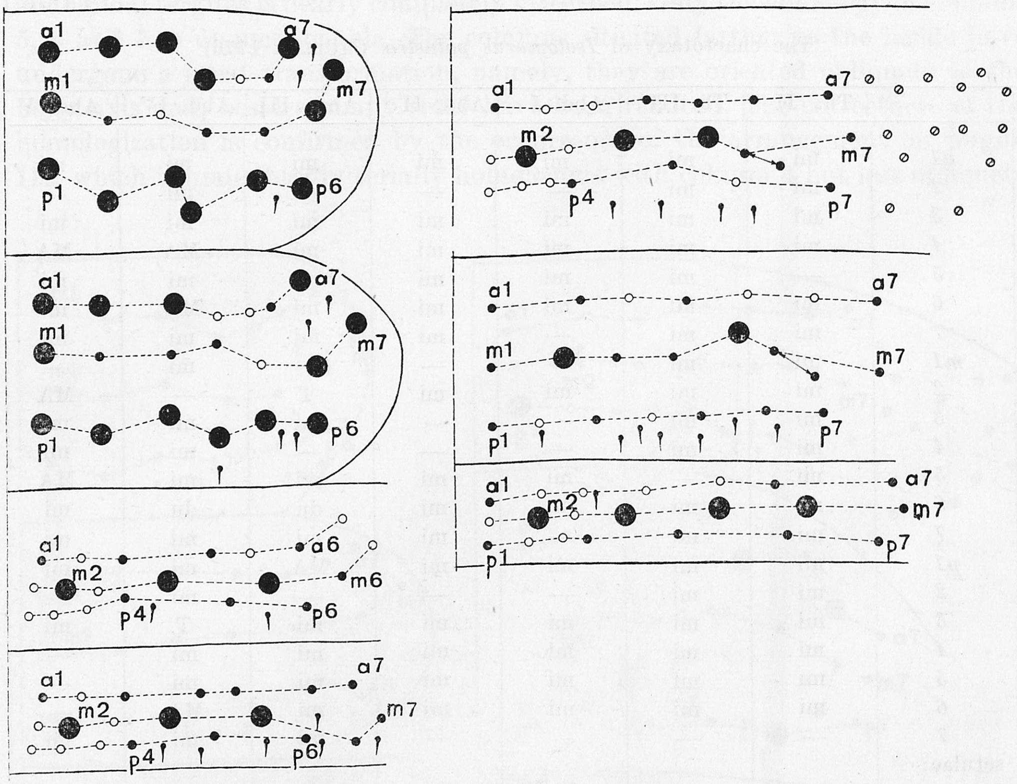

Fig. 4. The setal map of the chaetotaxy of *Isotoma viridis* Bourl. (symbols as in fig. 3)

of setulae of the group *acc.p*. On the other hand, the presence of trichobotria on abdominal tergites III (*m2*) and IV (*p3*) is certainly a progressive character. The homology of the first of them with the trichobotria of the other *Entomobryomorpha* deserves special emphasis; the other one, however, seems to have no homologues in the other genera examined. It is by all means an interesting fact that the distribution of the macrochaetae on abdominal tergite IV is similar in the first instars of *Isotomurus* Börn. and cretaceous *Protentomobrya walkeri* Folsom 1937 (cf. Delamare & Massoud, 1968, Fig. 2B).

In contradistinction to the previous genus, the chaetotaxy of *Isotoma* Bourl. is marked by a large number of progressive characters. These are, above all, the distinct differentiation of the setae into macro- and microchaetae and the complete obliteration of the three-rowed pattern of setae on the first abdominal tergites. The lack of trichobotria is a clear primitive character. It cannot be decided now whether the small number of setulae of the *acc.p* group is a primitive character or whether it is due to a secondary reduction of the originally larger number. It should be emphasized that the macrochaetae on the first abdominal tergites are homologous with those in *Tomocerus* Nic. and many members of the *Entomobryidae* s. l. However, it may well be that this homology results from a parallel evolution.

Table II

The chaetotaxy of *Isotoma viridis* Bourlet 1839

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. IV	Abd. V
a1	MA	MA	mi	mi	mi	mi	mi
2	MA	MA	—	—	—	mi	—
3	MA	MA	mi	mi	—	—	—
4	MA	—	mi	mi	mi	mi	—
5	—	—	—	mi	mi	—	—
6	mi	mi	mi	mi	mi	—	mi
7	MA	MA	—	mi	mi	mi	mi
m1	MA	MA	—	—	—	mi	—
2	mi	mi	MA	MA	MA	MA	MA
3	—	mi	—	—	—	mi	—
4	mi	mi	MA	MA	MA	mi	MA
5	mi	—	MA	MA	MA	MA	MA
6	MA	MA	mi	mi	du	du	MA
7	MA	MA	—	mi	mi	mi	mi
p1	MA	MA	—	—	—	mi	mi
2	MA	MA	—	—	—	—	—
3	MA	MA	—	—	—	mi	—
4	MA	MA	mi	mi	mi	—	mi
5	MA	MA	mi	mi	mi	mi	mi
6	MA	MA	mi	mi	—	mi	mi
7	—	—	—	—	mi	mi	mi
setulae:							
as	—	—	—	—	—	—	+
al	2	2	—	1	—	—	—
acc. p2	—	—	—	—	—	+	—
3	—	—	—	—	—	+	—
4	—	+	+	+	+	+	—
5	+	+	—	+	+	du	—
6	—	+	—	+	du	du	—

The abbreviations as in Table I.

CHAETOTAXY OF *TOMOCERUS (POGONOGNATHELLUS) FLAVESCENS*

(Tullberg 1871)

The chaetotaxy of *Tomocerus* Nic. (Fig. 5; Table III; Pl. XVII, 1) is clearly different from that of both the *Isotomidae* and *Entomobryidae*. In some respects, however, it is transitional between the chaetotaxies of these two families.

Mesothorax. Interpretation of the chaetotaxy of this tergite is difficult not only owing to the arrangement, different from that in the *Isotomidae*, but also because there are marked changes in the composition of the setae. The setae *a1*, *a3*, *a5*, *m5*, *p3* and *p5* are duplicated, the quadrangle is well seen, and there are three setulae *al*. In the vicinity of the seta *a3* there are 2 setulae, of which the internal one is most likely homologous with the setula *as*. There is still one setula in the proximity of the microchaeta *p5* and three other ones near the macrochaeta *p5*, but their homology is difficult to determine.

Metathorax. The chaetotaxy on this tergite is relatively least changed and the arrangement of the setae very much resembles that on the mesothorax in *Isotomurus* Börn. (Fig. 3; Pl. XVI, 1), which facilitates the homologization of the setae. The changes in the composition are the lack of some setae (Table III) and the duplication of the seta *a3*. The quadrangle is incomplete (*a7* missing) but distinct. There is one setula *al*, and, in addition, the setula *as*, *acc.p5* and two *acc.p6* situated as in *Isotomurus* Börn. Serial homology appears most distinct in the shape and arrangement of the setae of the row *p*.

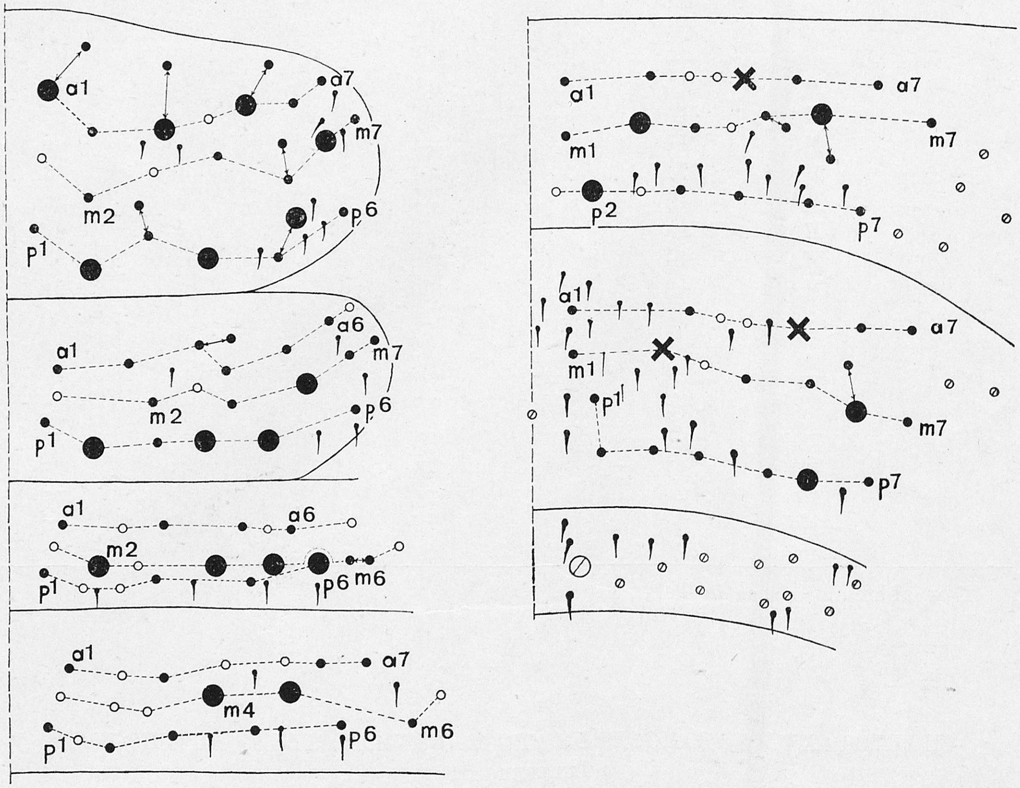

Fig. 5. The setal map of the chaetotaxy of *Tomocerus* (*Pogonognathellus*) *flavescens* (Tullb.). (symbols as in fig. 3).

Abdominal tergites I and II. The chaetotaxies of these tergites are very much alike and, at the same time, very similar to that in *Isotoma* Bourl., which makes the homologization of the setae easier. As in *Isotoma* Bourl. (Fig. 4; Pl. XVI, 2), the whole system has been narrowed, the setae of the row *m* nearly go in between the setae of the row *p*, and column 4 is oriented obliquely to the body axis. As in *Isotoma* BOURL. also, the setae *m2*, *m4* and *m5* have developed into macrochaetae. Both tergites bear the setulae *acc.p4* — *acc.p6* and, besides, abdominal tergite I has *acc.p2* and tergite II one setula *al* and one accidental setula situated between *m4* and *m5*, anteriorly to the row *m*.

Table III

The chaetotaxy of *Tomocerus* (*Pogonognathellus*) *flavescens* (TULLBERG 1871)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. IV
a1	MA +	mi	mi	mi	mi	mi
2	mi	mi	—	—	mi	mi
3	MA +	du	mi	mi	—	—
4	—	mi	mi	—	—	—
5	MA +	mi	—	—	T	T
6	mi	mi	mi	mi	mi	mi
7	mi	—	—	mi	mi	mi
m1	—	—	—	—	mi	mi
2	mi	mi	MA	—	MA	T
3	—	—	—	—	mi	—
4	mi	mi	MA	MA	—	mi
5	du	MA	MA	MA	du	mi
6	MA	mi	du	mi	MA +	MA +
7	mi	mi	—	—	mi	mi
p1	mi	mi	mi	mi	—	mi
2	MA	MA	—	—	MA	mi
3	du	mi	—	mi	—	mi
4	MA	MA	mi	mi	mi	mi
5	MA +	MA	mi	mi	mi	mi
6	mi	mi	MA	mi	mi	MA
7	—	—	—	—	mi	mi
setulae:						
as	+	+	—	—	—	—
al	3	1	—	1	—	—
acc. p2	—	—	+	—	—	—
4	—	—	+	+	—	—
5	?	—	+	+	?	?
6	+	+	+	+	?	?

MA + — duplication, macrochaeta and microchaeta; remaining abbreviations as in Table I.

Abdominal tergite III. The arrangement of setae on this tergite shows very close similarity to the arrangements on abdominal tergite III in *Isotomurus* BÖRN. (Fig. 3; Pl. XVI, 1) and on tergite IV in *Isotoma* BOURL. (Fig. 4; Pl. XVI, 2). As in those genera, it is changed chiefly by the somewhat oblique position of column 2 and an increase in the space between columns 1 and 2 in the anterior portion of the tergite. There are 5 lateral setae situated externally to column 7, probably homologous with the corresponding setae in the *Isotomidae*. The setae *m5* and *m6* are duplicated. There are 9 setulae, which I failed to homologize.

Abdominal tergite IV. The pattern of setae has been changed mainly by the displacement of columns 1 and 2. An additional microchaeta, situated medially (quite an exceptional character among *Entomobryomorpha*), and two lateral microchaetae are present. The seta *m6* is duplicated. There are numerous setulae of undeterminable homology.

Abdominal tergite V has its chaetotaxy quite different from those described above. It has 1 macrochaeta, 10 microchaetae and about 10 setulae. No homology can be determined.

The chaetotaxy of *Tomocerus* NIC. shows a number of specific characters, accompanied by both some primitive characters of the *Isotomidae* and some characters of the more advanced *Entomobryomorpha*. The specific changes are, in the first place, the changes in the composition of the setae, e. g., numerous duplications on the mesothorax and the presence of quite a number of accidental setulae. *Tomocerus* NIC. is related to the *Isotomidae* by its little changed arrangement of setae on the metathorax and the situation of the first abdominal tergites, very similar to that in *Isotoma* BOURL. The presence of the setula *as* on the thoracic tergites may also be a primitive character. The bend in the row *a* on the mesothorax forms a distinct transition between the regular arrangement in the *Isotomidae* and the greatly changed one in the *Entomobryidae* s. l. To this last group the chaetotaxy of *Tomocerus* NIC. is related chiefly by the presence of trichobotria on abdominal tergites III and IV. However, in contradistinction to *Isotomurus* BÖRN. the trichobotrium *a5* appears on abdominal tergite III and, in addition to it, the trichobotrium *m2* on tergite IV, where it is lacking in all the *Entomobryidae* s. l. examined. Generally speaking, the chaetotaxy of *Tomocerus* NIC. may be regarded as standing close to the chaetotaxy of the initial forms of the more advanced *Entomobryomorpha* in many respects, but not as identical with it. Consequently, it would be very instructive to examine the chaetotaxy of the first instars of the genus *Oncopodura* CARL & LEB., which in some respects is undoubtedly more primitive than Tomocerus NIC., though they are very closely related to each other.

CHAETOTAXY OF *ENTOMOBRYIDAE* s. l.

The chaetotaxies of the *Entomobryidae* s. l. (Fig. 6; Tables IV—X; Pls XVII, 2 — XIX, 1,) have many characters in common, hence the homologization of the setae within the family is fairly easy. The original three-rowed pattern of setae is generally heavily disturbed, but still it can be traced on all the tergites with the exception of abdominal segment IV.

Mesothorax. The chaetotaxy of this segment is very clearly related to that of the *Isotomidae* and, consequently, to the primitive chaetotaxy of the *Hypogastruridae*. The three-rowed pattern of setae, the distinct quadrangle and the occurrence of the setulae *al* belong certainly to these primitive characters. This allows the determination of the homology of the setae on this tergite with the corresponding setae of the *Poduromorpha* with great probability. The changes in the chaetotaxy in relation to the more primitive arrangements are limited to a strong deformation of the rows, especially the row *a* between *a1* and *a3*. A similar though somewhat less distinct phenomenon occurs also in *Cyphoderus* Nic. (Pl. XIX, 2) and, in a rudimentary form, appears in *Tomocerus* Nic. (Pl. XVII, 1). In all the genera examined the chaetotaxy of this tergite is extremely uniform. The differences in the composition of the setae boil down to the presence or absence of the setula *acc.p6* and the differences in shape concern exclusively the setae *m1*, *m2* and *m5* (Tables IV—VIII).

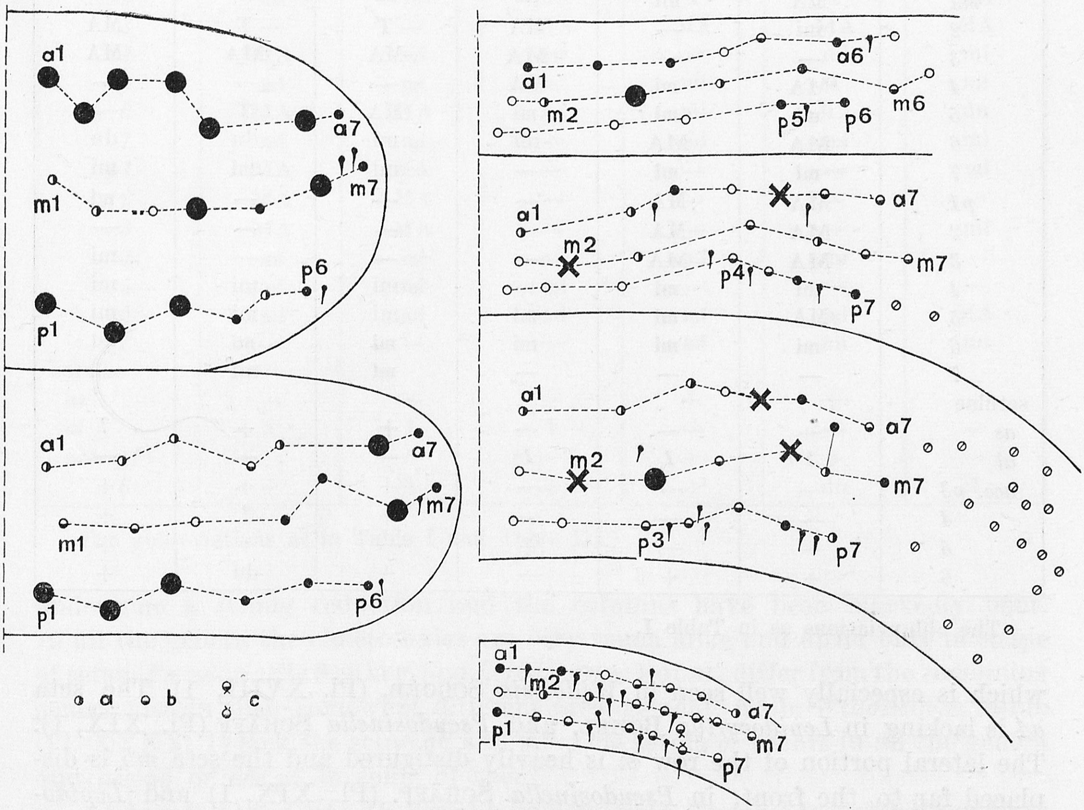

Fig. 6. The setal map of the chaetotaxy of *Entomobryidae* s. l.; a — setae developed as macrochaeta, microchaeta or scale, b — setae missing in some genera, c — setae duplicated in some genera; remaining symbols as in fig. 3

Metathorax. The chaetotaxy of thoracic tergite III of the *Entomobryidae* is characterized by its much greater diversity, especially in the shape and composition of the setae. The arrangement of setae differs chiefly in degree of the deformation of the initial pattern. In *Orchesella* Templ. and *Heteromurus* Wankel (Pl. XVII, 2; XVIII, 2) the row *a* is almost intact, in the other genera it has changed owing to the shifting of *a2* nearer to *a3* and *a4* nearer to *a5*,

Table IV

The chaetotaxy of *Orchesella flavescens* Bourlet 1839

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. V
a1	**MA**	MA	**mi**	mi	mi	**mi**
2	**MA**	MA	**mi**	mi	mi	**mi**
3	**MA**	mi	**mi**	**mi**	**mi**	—
4	**MA**	MA	—	—	—	mi
5	**MA**	MA	mi	**T**	**T**	MA
6	**MA**	**MA**	**mi**	mi	**mi**	mi
7	**mi**	**mi**	—	mi	mi	mi
m1	MA	mi	—	—	—	—
2	mi	—	MA	**T**	**T**	MA
3	—	—	**MA**	MA	**MA**	MA
4	**MA**	**mi**	MA	—	—	—
5	**mi**	**mi**	**mi**	MA	**T**	—
6	**MA**	**MA**	mi	mi	du	du
7	**mi**	**mi**	—	mi	**mi**	mi
p1	**MA**	MA	—	—	—	**mi**
2	**MA**	MA	—	—	—	—
3	**MA**	**MA**	—	—	—	mi
4	**mi**	**mi**	—	mi	mi	mi
5	MA	**mi**	**mi**	mi	mi	mi
6	**mi**	**mi**	**mi**	**mi**	**mi**	du
7	—	—	—	**mi**	mi	—
setulae						
as	—	—	—	+	+	?
al	*2*	*1*	*1*	—	—	—
acc. p3	—	—	—	+	+	+
4	—	—	—	+	?	+
5	—	—	+	—	+	+
6	+	+	—	+	du	+

The abbreviations as in Table I.

which is especially well seen in *Willowsia* Schoeb. (Pl. XVIII, 1). The seta *a4* is lacking in *Lepidocyrtus* Bourl. and *Pseudosinella* Schäff (Pl. XIX, 1). The lateral portion of the row *m* is heavily disfigured and the seta *m5* is displaced far to the front, in *Pseudosinella* Schäff. (Pl. XIX, 1) and *Lepidocyrtus* Bourl. even as far as in front of the row *a*. The row *p* and quadrangle are very similarly developed in all the genera and obviously serially homologous with the corresponding elements of the chaetotaxy of thoracic tergite II. In all the genera examined one setula *al* is present, in most of them the setula *acc.p6*.

Abdominal tergite I. In all the genera this tergite is very markedly narrowed, which has brought about the reduction of a number of setae and major changes in their arrangement. Homologization of the setae with the corresponding setae of the initial pattern is possible on the assumption that, as in *Isotoma* Bourl. (Pl. XVI, 2) and *Tomocerus* Nic. (Pl. XVII, 1), the row *p* has

Table V

The chaetotaxy of *Heteromurus nitidus* (Templeton 1835)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. V
a1	**MA**	mi	**mi**	mi	mi	**mi**
2	**MA**	mi	**mi**	mi	mi	**mi**
3	**MA**	mi	**mi**	**mi**	**mi**	—
4	**MA**	mi	—	—	—	mi
5	**MA**	MA	mi	**T**	**T**	MA
6	**MA**	**MA**	**mi**	mi	**mi**	mi
7	**mi**	**mi**	—	mi	mi	MA
m1	mi	mi	—	—	—	—
2	mi	—	MA	**T**	**T**	MA
3	—	—	**MA**	MA	**MA**	MA
4	**MA**	**mi**	mi	—	mi	mi
5	**mi**	**mi**	**mi**	mi	**T**	mi
6	**MA**	**MA**	mi	mi	MA +	du
7	**mi**	**mi**	—	mi	**mi**	mi
p1	**MA**	MA	—	—	—	**mi**
2	**MA**	MA	—	—	—	—
3	**MA**	**MA**	—	—	—	mi
4	**mi**	**mi**	—	mi	mi	—
5	mi	**mi**	**mi**	—	—	—
6	**mi**	**mi**	**mi**	**mi**	**mi**	MA
7	—	—	—	**mi**	mi	mi
setulae						
as	—	—	—	+	+	+
al	2	1	1	—	—	—
acc. p4	—	—	—	+	+	—
6	+	+	+	+	du	?

The abbreviations as in Table I and Table III.

undergone a strong reduction and the columns have been markedly bent. In all the genera the chaetotaxies are very much alike and differ only in shape of setae. *Pseudosinella* Schäff. and *Lepidocyrtus* Bourl. differ from the remaining genera also in their somewhat different arrangement, while *Willowsia* Schoeb. (Pl. XXXX, 1) lack the setae *a6* and *m6*. One setula *al* occurs in all the genera and *acc.p5* or *acc.p6* in some of them.

Abdominal tergite II. Serial homology with tergite I is generally distinct in the medial portion of this tergite, which makes it easier to homologize the setae. It is only somewhat obscured by a bend in the row *a* and the displacement of *a2* nearer to *a3*. An analogous situation occurs on tergite I in *Willowsia* Schoeb. As on tergite I, the row *p* is markedly reduced. The seta *p7* and two lateral setae are present in all the genera, and *m2* and *a5* have the form of trichobotria. The setulae *as* and *acc.p6* are also present in all the genera and *acc.p4* in some of them.

Abdominal tergite III very much resembles the previous one, but it is less shortened. The seta *p4* appears frequently and even *p3* is sometimes

Table VI

The chaetotaxy of *Willowsia buski* (Lubbock 1869)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. V
a1	**MA**	mi	**mi**	MA	MA	**mi**
2	**MA**	mi	**mi**	MA	MA	**mi**
3	**MA**	MA	**mi**	**mi**	**mi**	—
4	**MA**	MA	—	—	—	mi
5	**MA**	mi	—	**T**	**T**	—
6	**MA**	**MA**	**mi**	mi	**mi**	mi
7	**mi**	**mi**	—	mi	mi	mi
m1	mi	—	—	—	—	—
2	mi	mi	mi	**T**	**T**	MA
3	—	—	**MA**	mi	**MA**	MA
4	**MA**	**mi**	MA	mi	—	—
5	**mi**	**mi**	**mi**	mi	**T**	—
6	**MA**	**MA**	—	mi	du	—
7	**mi**	**mi**	—	mi	**mi**	—
p1	**MA**	MA	—	—	—	**mi**
2	**MA**	MA	—	—	—	—
3	**MA**	**MA**	—	—	—	mi
4	**mi**	**mi**	—	—	mi	mi
5	MA	**mi**	**mi**	mi	mi	—
6	**mi**	**mi**	**mi**	**mi**	**mi**	mi
7	—	—	—	**mi**	mi	mi
setulae						
as	—	—	—	+	+	+
al	2	1	1	—	—	—
acc. p3	—	—	—	—	—	+
5	—	—	—	—	—	+
6	+	+	?	+	du	—

The abbreviations as in Table I.

present (Tables IV—VIII). There are numerous lateral setae situated externally to column 7. As in the *Isotomidae* and *Tomocerus* Nic., the seta *m6* is duplicated; *m5* is as a rule developed into a trichobotrium. The setulae *as*, *acc.p4* and *acc.p6* are present, this last one being mostly duplicated.

Abdominal tergite V is different in different genera, though in general it resembles abdominal tergite I. Accidental setulae of undeterminable homology are here very frequent.

Abdominal tergite IV. The problems presented by this segment are quite different from those encountered in connection with the previous tergites, for this segment is much more elongated than the other ones and the number of its setae is considerably larger. These two changes completely obliterate the original arrangement and make it impossible to determine the serial homology with the previous tergites. As a result, it becomes necessary to apply „artificial" designations which do not determine the serial homology of particular elements but make it possible to establish the homology of the setae between

Table VII

The chaetotaxy of *Entomobryoides myrmecophila* (Reuter 1886)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. V
a1	**MA**	mi	**mi**	mi	mi	**mi**
2	**MA**	mi	**mi**	mi	mi	**mi**
3	**MA**	mi	**mi**	**mi**	**mi**	—
4	**MA**	MA	mi	—	—	—
5	**MA**	MA	—	**T**	**T**	—
6	**MA**	**MA**	**mi**	—	**mi**	—
7	**mi**	**mi**	—	mi	—	mi
m1	MA	—	—	—	—	—
2	mi	mi	mi	**T**	**T**	mi
3	—	—	**MA**	MA	**MA**	mi
4	**MA**	**mi**	MA	mi	—	—
5	**mi**	**mi**	**mi**	mi	**T**	—
6	**MA**	**MA**	mi	MA	MA +	mi
7	**mi**	**mi**	—	—	**mi**	mi
p1	**MA**	mi	—	—	—	**mi**
2	**MA**	mi	—	—	—	mi
3	**MA**	**MA**	—	—	—	—
4	**mi**	**mi**	—	—	mi	mi
5	mi	**mi**	**mi**	—	mi	—
6	**mi**	**mi**	**mi**	**mi**	**mi**	mi
7	—	—	—	**mi**	MA	mi
setulae						
as	—	—	—	+	+	—
al	2	1	1	—	—	—
acc. p3	—	—	—	—	—	+
4	—	—	—	—	—	+
6	+	+	—	—	du	—

The abbreviations as in Table I and Table III.

different genera. Such designations of macrochaetae have been introduced by Snider (1967) for the species of the genus *Lepidocyrtus* Bourl., but in our case his system is unfit for use, because the boundaries between the conventional areas „P", „M" and „L" are marked arbitrarily and it is impossible to find which seta belongs to which area in the genera with different arrangements. Moreover, Snider's system, created for macrochaetae in adult specimens, is not suited for the description of the full chaetotaxy of the first instars.

The division of the abdomen into conventional areas is possible after finding the elements of chaetotaxy which would be unquestionably homologous and present in all the genera examined. These elements are as follows (Fig. 7): a seta which lies somewhat anteriorly and laterally to the anterior trichobotrium (*l1*), the anterior and posterior trichobotria (*Ta* and *Tp*) and the intertrichobotrial seta situated between them (*it*), a seta positioned behind *Tp* on the extension of the line of trichobotria (*dp4*), and also an external setula in the posterior row setae and a seta lying near it (*dp9*). A system of 2—3 setae, situated more

Table VIII

The chaetotaxy of *Pseudosinella alba* (Packard 1873)

	Th. II	Th. III	Abd. I	Abd. II	Abd. III	Abd. V
a1	**MA**	mi	**mi**	mi	mi	**mi**
2	**MA**	mi	**mi**	MA	mi	**mi**
3	**MA**	mi	**mi**	**mi**	**mi**	—
4	**MA**	—	—	—	—	mi
5	**MA**	MA	mi	**T**	**T**	—
6	**MA**	**MA**	**mi**	mi	**mi**	mi
7	**mi**	**mi**	—	—	mi	mi
m1	MA	—	—	—	—	—
2	sc	MA	MA	**T**	**T**	MA
3	—	—	**MA**	MA	**MA**	MA
4	**MA**	**mi**	MA	mi	mi	mi
5	**mi**	**mi**	**mi**	MA	**T**	MA
6	**MA**	**MA**	mi	mi	MA +	MA
7	**mi**	**mi**	—	mi	**mi**	mi
p1	**MA**	MA	—	—	—	**mi**
2	**MA**	MA	—	—	—	—
3	**MA**	**MA**	—	—	mi	mi
4	**mi**	**mi**	—	mi	—	mi
5	MA	**mi**	**mi**	—	—	—
6	**mi**	**mi**	**mi**	**mi**	**mi**	mi
7	—	—	—	**mi**	mi	mi
setulae						
as	—	—	—	+	+	—
al	2	1	1	—	—	—
acc. p6	—	—	—	—	+	+

sc — scale; remaining abbreviations as in Table I and Table III.

or less in a line behind the seta *it* and perpendicularly to the line of trichobotria (*da9*, *da10*, *da11*), is also a common element. Lines drawn according to these setae, as in Fig. 7, divide abdominal tergite IV into three conventional areas, a dorsoanterior (*da*), a dorsoposterior (*dp*) and a lateral (*l*). In each of these areas I mark the setae with numbers, the setae which occur in one genus only or in genera with very similar chaetotaxies receiving the number of the nearest seta that is present in many genera provided with a coma, e. g., the seta *da6*' occurs only in *Orchesella* Templ. and lies near *da6* (Fig. 7A). The differences in composition and shape of the setae between individual species are listed in Table IX.

The chaetotaxy of the *Entomobryidae* s. l. differs between particular genera in minor details only. A number of important common characters (indicated by black letters in the tables IV—VIII) make this group extremely uniform in respect of chaetotaxy. On the other hand, however, a study of these small differences will certainly make it possible to go deeper into the problem of affinity between particular genera, but the material presented in this paper is too scanty for this purpose. Now it may only be stated that the genera examined belong to three groups.

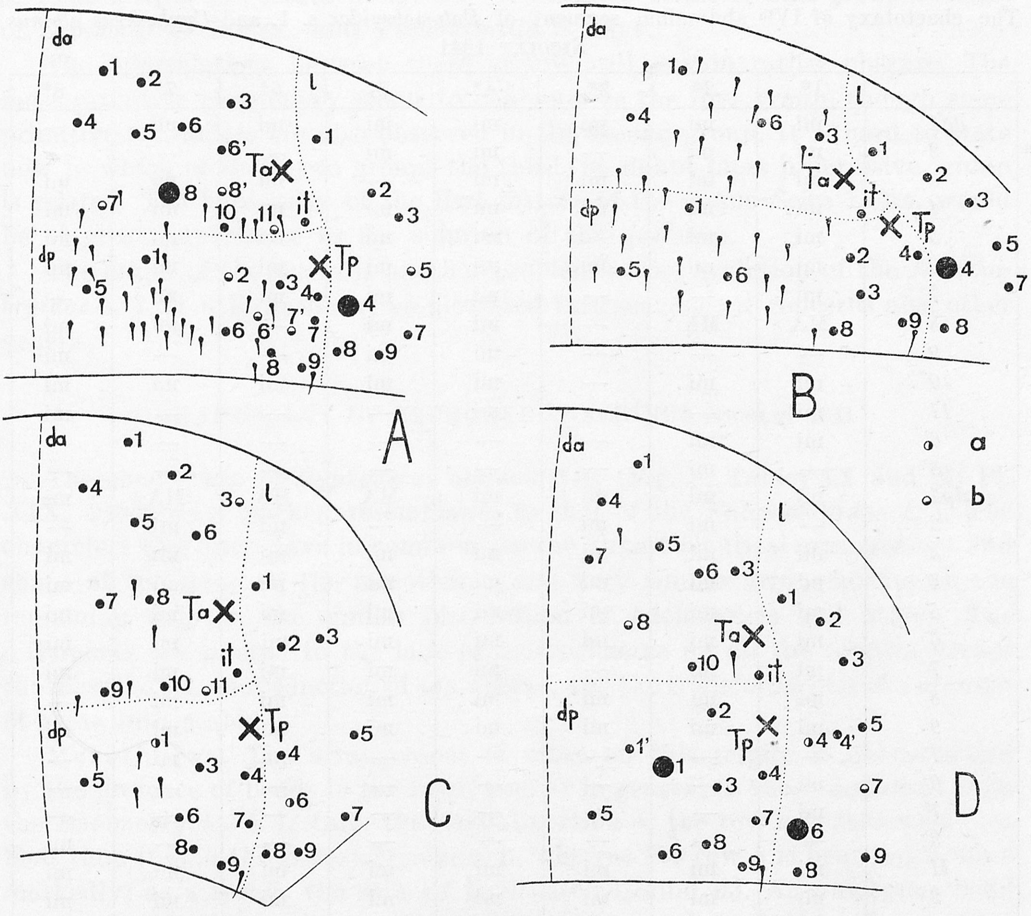

Fig. 7. Setal maps of the chaetotaxy of IVth abdominal tergites of *Entomobryidae* s. l. A — *Orchesella flavescens* (Bourl.) and *O. bifasciata* Nic.; B — *Heteromurus nitidus* (Templ.); C — *Entomobryoides myrmecophila* (Reut.) and *Willowsia buski* (Lubb.); D — *Lepidocyrtus curvicollis* Bourl. and *Pseudosinella alba* (Pack.); a — setae missing in one of species, b — setae developed either in form of macrochaeta or microchaeta, remaining symbols as in fig. 3

The first of them is characterized by the presence of the seta *m1* on the metathorax and *a5* on abdominal tergites I and V and the duplication of *m6* on tergite V. Abdominal tergite IV lacks *l6*, and the arrangement of the setae of the row *a* on the metathorax is regular. This group includes the genera *Orchesella* Templ. and *Heteromurus* Wankel and has some characters in common with the third group, but their importance to phylogeny is still unclear.

The characters of the second group are the lack of *m1* and the presence of *m2* on the metathorax, the lack of *a5* and the development of *m2* into a microchaeta on abdominal tergite I, the presence of *da9* on tergite IV and the lack of *m4* and *m5* on tergite V. A bend in the row *a* on the metathorax is characte-

Table IX

The chaetotaxy of IV^th^ abdominal segment of *Entomobryidae* s. l. and *Cyphoderus albinus* Nicolet 1841

	1*	2*	3*	4*	5*	6*	7*	8*
da1	mi	mi	mi	mi	mi	mi	mi	—
2	mi	mi	—	mi	mi	—	—	—
3	mi	mi	mi	mi	—	mi	mi	mi
4	mi	mi	mi	mi	mi	mi	mi	mi
5	mi	mi	—	mi	mi	mi	mi	mi
6	mi	mi	mi	mi	mi	mi	mi	mi
7	mi	—	—	mi	mi	mi	mi	—
8	MA	MA	—	mi	mi	—	mi	mi
9	—	—	—	mi	mi	—	—	mi
10	mi	mi	—	mi	mi	mi	mi	mi
11	mi	—	—	mi	—	—	—	mi
6'	mi	mi	—	—	—	—	—	—
8'	—	mi	—	—	—	—	—	—
dp1	mi	mi	mi	mi	MA	MA	MA	mi
2	—	mi	mi	—	—	mi	mi	—
3	mi	mi	mi	mi	mi	mi	mi	mi
4	mi	mi	mi	mi	mi	mi	mi	mi
5	mi	mi	mi	mi	mi	mi	mi	mi
6	mi	mi	mi	mi	mi	mi	mi	mi
7	mi	mi	—	mi	mi	mi	mi	mi
8	mi	mi	mi	mi	mi	mi	mi	—
9	mi	mi	mi	mi	mi	mi	mi	mi
1'	—	—	—	—	—	mi	mi	—
6'	mi	—	—	—	—	—	—	—
7'	mi	—	—	—	—	—	—	—
9'	—	—	—	—	—	—	—	mi
l1	mi	mi	mi	mi	mi	mi	mi	mi
2	mi	mi	mi	mi	mi	mi	mi	mi
3	mi	mi	mi	mi	mi	mi	mi	mi
4	MA	MA	MA	mi	mi	MA	mi	mi
5	mi	—	mi	mi	mi	mi	mi	mi
6	—	—	—	mi	MA	MA	MA	mi
7	mi	mi	mi	mi	mi	mi	—	mi
8	mi	mi	mi	mi	mi	mi	mi	mi
9	mi	mi	—	mi	mi	mi	mi	mi
4'	—	—	—	—	—	mi	mi	—

1* — *Orchesella flavescens* Bourl.; 2* — *O. bifasciata* Nic.; 3* — *Heteromurus nitidus* (Templ.); 4* — *Willowsia buski* (Lubb.); 5* — *Entomobryoides myrmecophila* (Reut.); 6* — *Pseudosinella alba* (Pack.); 7* — *Lepidocyrtus curvicollis* Bourl.; 8* — *Cyphoderus albinus* Nic.

The abbreviation as in Table I.

ristic of this group in so far as the arrangement of setae is concerned. The genera *Willowsia* Pack. and *Entomobryoides* Mayn. belong in this group.

The third group is characterized by the development of *m2* into a scale on the mesothorax, the lack of *a4*, and *m1* and the presence of macrochaeta *m2* on the metathorax, the lack of *a7* on abdominal tergite II, the lack of *p4* and the presence of *p3* on tergite III, the presence of *dp1'* and *l4'* on tergite IV and the lack of the setula *acc.p6* on the thoracic tergites. This group consists of *Lepidocyrtus* BOURL. and *Pseudosinella* SCHÄFF.

The interrelations between these groups still remain rather obscure. The most primitive chaetotaxy seems to characterize the first group, though some primitive characters are also observed in the second group. It is hard to state now to which of these two groups the third, no doubt most progressive, group is related. The knowledge of the first instars of the genus *Seira* LUBB. would be of great importance to the solution of this problem.

The origin of the scales is another problem of the evolution of the *Entomobryidae* s. l. It will, however, be discussed further, since it concerns also other genera.

CHAETOTAXY OF CYPHODERUS ALBINUS NICOLET 1841

The chaetotaxy of *Cyphoderus albinus* NIC. (Fig. 8; Tables IX and X; Pl. XIX, 2) shows a marked resemblance to that of the *Entomobryidae* s. l. The characters that they have in common are the almost identical arrangement and shape of the setae on the mesothorax and very similar arrangements on the remaining tergites, the similar distribution of trichobotria and others. The differences are limited to the lack of macrochaetae on all the tergites except the mesothorax, the reduction of some setae, and the transformation of a number of setae into scales.

Mesothorax. The arrangement of setae on this tergite is characterized by the presence of bends in the rows, similar in general to those described from the *Entomobryidae* s. l. Only the medial portion of the row *a* is somewhat less bent than it is in the *Entomobryidae* s. l., whereas the row *p* is bent much more markedly; as a result, the seta *p4* is situated behind *p3*. An analogous bend occurs also in *Isotoma* BOURL. (Pl. XVI, 2). The quadrangle is well seen, there is one setula *al*, other setulae are lacking.

Metathorax. The arrangement of setae in the rows *a* and *p* is largely disturbed, whereas the row *m* is markedly bent in its lateral portion, owing to which the seta *m5* lies almost in front of *m4*. An analogous bend, though not so distinct, occurs also in the *Entomobryidae* s. l., especially in *Pseudosinella* SCHÄFF. (Pl. XIX, 1) and *Lepidocyrtus* BOURL. The quadrangle is well developed, the setae *a1*—*a4* are transformed into scales, *m1*—*m3* and *p1* reduced. The setula *as* and one *al* are present.

Abdominal tergite I. The arrangement of setae very much resembles that in the *Entomobryidae* s. l. only that much more setae have undergone a reduction. Columns 4 and 7 and the row *p* are completely reduced and, in addition, the seta *m1* is lacking. There is one setula *al*, other setulae are missing.

Tergites II and III. The chaetotaxy on these tergites does not differ from that in the *Entomobryidae* s. l. As in them, the setae *a2* and *a5*, and on tergite III also *m5*, are developed as trichobotria. The seta *a1* on tergite II has the form of a scale, on tergite III *m6* is duplicated and, in addition, there is only one lateral seta here. The setula *as* occurs on both tergites and, besides, one setula *al* is present on tergite II and *acc. p6* on tergite III.

The chaetotaxy of abdominal segment IV (Fig. 8; Pl. XIX, 2) very much resembles that in the *Entomobryidae* s. l. (Fig. 7), and it can be reduced to the same „artificial" pattern. It is composed of the same setae, except for *dp9'*, as the chaetotaxy in the *Entomobryidae* s. l. The occurrrence of the seta *da9* in *Cyphoderus* Nic., which has it in common with *Willowsia* Scheob. and *Entomobryoides* Mayn. (Fig. 7C), is noteworthy. However, the setae on abdominal segment IV are far more regularly arranged in *Cyphoderus* Nic. than they are in the *Entomobryidae* s. l.

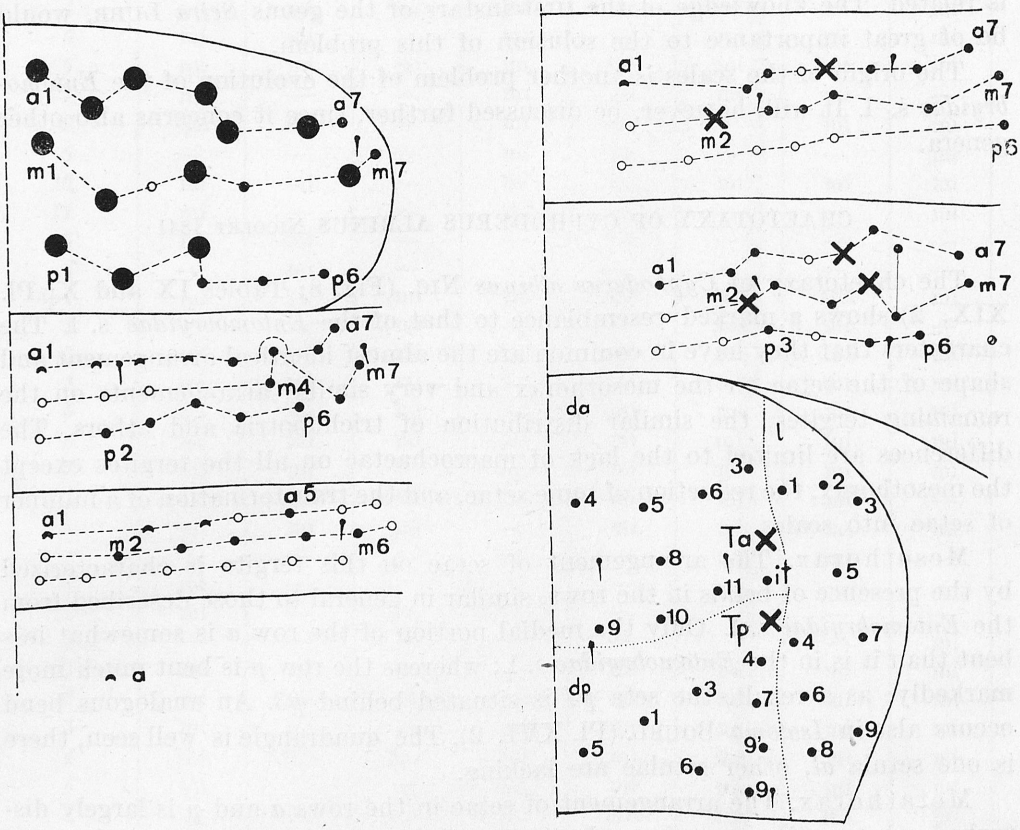

Fig. 8. Setal map of the chaetotaxy of *Cyphoderus albinus* Nic.; a — scales, remaining symbols as in fig. 3

Abdominal tergite V was not examined.

As has been mentioned above, the chaetotaxy of *Cyphoderus* Nic. comes very near to the chaetotaxy of the examined genera of the *Entomobryidae* s. l. It cannot be decided now whether this similarity should be regarded as an expression of close relationship, or whether it reflects a parallel evolution. An undoubtedly progressive character in relation to the *Entomobryidae* s. l. is the number of scales, larger than that in any other genus examined, the more advanced reduction and the more changed pattern of chaetotaxy on the tergites from thoracic II to abdominal III. On the other hand, a certainly primitive character is the presence of the setula *as* on the metathorax, where it also occurs in *Tomocerus* Nic. Now it cannot be found whether the lack of macrochaetae on all the tergites but the mesothorax is a primitive character or a result of the secondary simplification. Neither is it known how to interpret the regular arrangement of the setae on abdominal segment IV and the occurrence of the seta *da11* on this segment. It may well be that a close examination of the chaetotaxy of relative forms, especially that of the genus *Troglopedetina* Delam. and the members of the family *Paronellidae*, will make the answer to this question possible.

Table X

The chaetotaxy of *Cyphoderus albinus* Nicolet 1841

	Th. II	Th. III	Abd. I	Abd. II	Abd. III
a1	MA	sc	sc	sc	mi
2	MA	sc	sc	mi	mi
3	MA	sc	sc	mi	mi
4	MA	sc	—	—	—
5	MA	mi	mi	T	T
6	MA	mi	—	mi	mi
7	mi	mi	—	mi	mi
m1	MA	—	—	—	—
2	MA	—	mi	T	T
3	—	—	mi	mi	mi
4	MA	mi	mi	mi	mi
5	mi	mi	mi	mi	T
6	MA	mi	mi	mi	du
7	mi	mi	—	mi	mi
p1	MA	—	—	—	—
2	MA	mi	—	—	—
3	MA	mi	—	—	mi
4	mi	mi	—	—	—
5	mi	mi	—	—	mi
6	mi	mi	—	mi	mi
7	—	—	—	—	?
setulae					
as	—	+	—	+	+
al	1	1	1	?	—
acc. p6	—	—	—	—	+

The abbreviations as in Table I and Table VIII.

DISCUSSION

Some characters common to the *Entomobryomorpha* and *Poduromorpha* can be distinguished in the chaetotaxy of the genera examined. They are the three-rowed arrangement of setae (at least on the thoracic tergites) and the presence of the setulae *al*. Since these last were described from so diverse forms as, e. g., *Onychiurus* GERV., *Hypogastrura* BORUL., *Anurida* LAB. and *Tetracanthella* SCHÖTT, and occur in all the genera under study, their presence is probably characteristic of all the *Arthropleona*.

In addition to these characters, a number of others such that are common to all the genera under examination but lacking in the *Poduromorpha* can be observed. These are, e. g., the arrangement of the quadrangle, the presence of the setula *as* and the setulae of the *acc.p* group, the differentiation of setae into macro- and microchaetae, and the occurrence of trichobotria (except the genus *Isotoma* BOURL.). The transformation of setae into scales also occurs in some genera. Unfortunately, the knowledge of the chaetotaxy of the lower *Isotomidae* is so fragmentary that only very little can be said about the origin of these characters.

The fact that the setula *as* was recorded even from the genus *Tetracanthella* SCHÖTT, which belongs to the primitive *Isotomidae* (CASSAGNAU, 1959, Fig. 4F), is of importance to the evolution of the pattern of setulae. Judging from the drawing in the paper quoted, the setula *as* occurs on all the tergites of this genus, maintaining close serial homology. Thus, it may be supposed that the regular arrangement of this setula on all tergites is a primitive character and its disappearance from many tergites in the genera under examination a secondary character. As for the setulae of the *acc.p* group, it cannot be decided now whether their relatively small number on many tergites is a primitive character or results from the reduction of an originally larger number. This last possibility would be indicated by the comparatively large number of these setulae in the genus *Isotomurus* BÖRN., which is primitive in many respects. Assuming this alternative, however, one should assume also the complete reduction of the setulae *acc.p* in the evolution of the *Hypogastruridae*.

In the family *Isotomidae* the differentiation of setae into macro- and microchaetae appears in such primitive *Anurophorinae* as, e. g., *Tetracanthella* SCHÖTT or *Uzelia* ABS. We do not know now whether the undifferentiated uniform chaetotaxy of many genera, e. g., *Folsomia* WILLEM and *Proisotoma* BÖRN. should be regarded as a primitive character or a result of the secondary simplification. Stress should be laid on numerous important points of resemblance between the arrangements of macrochaetae in *Isotoma* BOURL., *Tomocerus* NIC. and *Entomobryidae* s. l., but the scanty material does not permit the exclusion of parallel evolution in this case.

The origin of trichobotria was an important stage of the evolution of chaetotaxy. Only four setae (*a5*, *m2*, *m5*, *p3*) on abdominal tergites II—IV have been transformed into trichobotria in the forms examined (Table XI). In all

Table XI

Trichobotria in examined genera

	Abd. II			Abd. III			Abd. IV		
	a	b	c	a	b	c	a	b	c
a5	—	—	+	—	+	+	—	+	?
m2	—	—	+	+	—	+	—	+	—
m5	—	—	—	—	—	+	—	—	?
p3	—	—	—	—	—	—	+	—	—

a — *Isotomurus palustris* (Müll.), b — *Tomocerus* (*Pogonognathellus*) *flavescens* (Tullb.) c — *Entomobryidae* s. l. and *Cyphoderus albinus* Nic.

the *Entomobryidae* s. l. the trichobotria have developed identically and the same arrangement is observed also in *Cyphoderus* Nic. The table presented, however, shows that there are clear-cut differences in their distribution between *Isotomurus* Börn. and *Tomocerus* Nic. The phylogenetic significance of these differences is still unclear.

The last important step in the evolution of chaetotaxy was the appearance of scales. In this case parallel evolution is very probable; the genus *Tomocerus* Nic. is hardly related directly to the *Entomobryidae* „lepidosae" and its relationship to the genus *Cyphoderus* Nic. is also extremely problematic. Now it cannot be decided either whether the *Entomobryidae* „lepidosae" are a mono- or polyphyletic group and by what affinity they are related to the genus *Cyphoderus* Nic. An examination of more genera of this group will very likely make the answer to these questions possible. The genus *Araucanocyrtus* Mass. & Rap., which belongs to the *Isotomidae* but has setae resembling scales in shape (Massoud & Rapoport, 1968), may appear to be of great importance to the studies on the derivation of scales.

As will be seen from the foregoing considerations, the material described in this paper is too scanty to allow the determination of the course of phylogeny in the *Entomobryomorpha*. Nevertheless, it may be stated even now that the *Entomobryidae* s. l. are a monophyletic group, which is indicated by a number of significant similarities in chaetotaxy between the first instars of the examined genera of this group. Out of the genera examined, *Cyphoderus* Nic. is most closely related to them, whereas *Tomocerus* Nic. is far remoter. However, in order to establish the relationships between the genera within the *Entomobryomorpha*, it will be necessary to examine a great many genera of the family *Isotomidae* and the families poorly represented in the European fauna, such as the *Oncopoduridae*, *Cyphoderidae* and *Paronellidae*.

VALUATION OF RESULTS

Interpretation of the facts observed demanded the assumption of a number of hypotheses, in the first place, those concerning the homology of setae between different genera and the serial homology of setae. Not all these hypotheses are probable to the same degree.

The hypotheses concerning the homology of the setae on the thorax between the *Isotomidae* under study and the homology of setae between the genera belonging to the *Entomobryidae* s. l. are the most probable. The homology of the setae on the thoracic tergites between the *Isotomidae* and *Hypogastruridae* and the serial homology of the setae on the first abdominal tergites in particular species are very probable. Relatively less certain are the statements regarding the serial homology of setae between the thorax and the abdomen, the homology of setae between the *Entomobryidae* s. l. and the *Isotomidae*, and that in the genus *Tomocerus* Nic.

The verification of all these hypotheses will not be possible until more factual material has been collected, in particular, until chaetotaxy has been examined in a larger number of genera and the behaviour of setae in the postembryonic developement and also their innervation and function have been investigated.

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STRESZCZENIE

Autor opisuje chetotaksję ciała najmłodszych stadiów u: *Isotomurus palustris* (Müll.), *Isotoma viridis* Bourl., *Tomocerus* (*Pogonognathellus*) *flavescens* (Tullb.), *Orchesella flavescens* Bourl., *O. bifasciata* Nic., *Heteromurus nitidus* Wankel, *Entomobryoides myrmecophila* (Reut.), *Willowsia buski* (Lubb.), *Lepidocyrtus curvicollis* Bourl., *Pseudosinella alba* (Pack.) i *Cyphoderus albinus* Nic. W chetotaksji wyróżnia cztery typy szczecin: mikrochety, makrochety, trichobotria i łuski, oraz setulae — drobne, włosowate twory, z reguły mniejsze od mikrochet i odmiennie od nich łamiące światło.

Ponieważ *Collembola* wywodzą się niewątpliwie od form o bardziej homonomicznej segmentacji ciała i w ich ewolucji największym zmianom uległy segmenty odwłoka — najmniej zmienione pozostały segmenty tułowia, meso- i metathorax. Analizując chetotaksję na tergitach tych segmentów u kilku wybranych gatunków *Hypogastruridae*, autor dochodzi do wniosku, że wspólny dla nich wszystkich

układ szczecin składa się z trzech rzędów po 7, 7, 6 szczecin. Ponieważ podobne układy występują u odległych systematycznie form, autor uważa go za układ pierwotny i wyprowadza z niego chetotaksję wszystkich tergitów u zbadanych rodzajów, a w konsekwencji ustala też homologię szczecin u wszystkich zbadanych rodzajów. Do wspólnego schematu nie można na razie sprowadzić tylko chetotaksji silnie zmienionego IV segmentu odwłoka u *Entomobryidae* s. l. i u rodzaju *Cyphoderus* NIC. Dla chetotaksji tego segmentu autor wprowadza odrębne, „sztuczne“ oznaczenia szczecin.

Materiał opisany w niniejszej pracy autor uważa za zbyt ubogi dla rozważań filogenetycznych, zwłaszcza że w wielu wypadkach nie można wykluczyć ewolucji równoległej. Niemniej już teraz można stwierdzić, że zbadane *Entomobryidae* s. l. stanowią grupę niewątpliwie monofiletyczną, z którą bardzo blisko spokrewniony jest rodzaj *Cyphoderus* NIC.

РЕЗЮМЕ

Автор описывает хетотаксию тела начальных стадий развития у: *Isotomurus palustris* (MÜLL.), *Isotoma viridis* BOURL., *Tomocerus (Pogonognathellus flavescens* (TULLB.), *Orchesella flavescens* BOURL., *O. bifasciata* NIC., *Heteromurus nitidus* WANKEL, *Entomobryoides myrmecophila* (REUT.), *Willowsia buski* (LUBB.), *Lepidocyrtus curvicollis* BOURL., *Pseudosinella alba* (PACK.) и *Cyphoderus albinus* NIC. В хетотаксии различает четыре типа щетинок: микрохеты, макрохеты, трихоботрии, чешую и ворсинки — короткие щетинки, меньше микрохет и по-другому преломляющие свет.

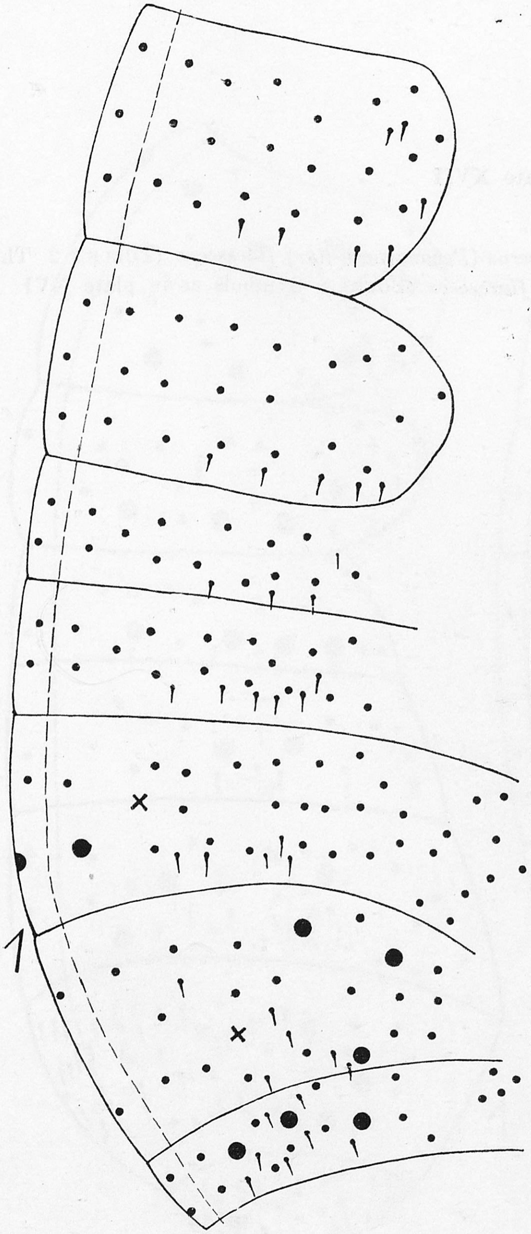
Так как ногохвостки происходят от форм с более гомономной сегментацией тела, в их эволюционном развитии наибольшим изменениям подверглись сегменты брюшка, а остались почти без изменения сегменты груди, средне- и заднегруди. Анализируя хетотаксию на тергитах этих сегментов у нескольких видов *Hypogastruridae*, автор констатирует, что общее для них расположение щетинок состоит из трёх рядов по 7, 7, 6 щетинок. Похожее расположение замечено у отделённых систематически форм. На этой основе автор считает это расположение первичным и выводит из него хетотаксию всех тергитов у исследованных родов, а в результате устанавливает также гомологию щетинок у всех исследованных родов. К общей схеме нельзя пока свести лишь хетотаксию, сильно изменённого IV сегмента брюшка у *Entomobryidae* s. l. и у рода *Cyphoderus* NIC. Для хетотаксии этого сегмента автор вводит отдельные „искусственные“ определения щетинок.

Описанный в настоящей работе материал, автор считает слишком скудным для филогенетических рассуждений, так как в ряде случаев нельзя исключить параллельной эволюции. Тем не менее, уже сейчас можно констатировать, что иседованные *Entomobryidae* s. l. составляют, несомненно, монофилетическую группу, из которой очень близко состоит в родстве род *Cyphoderus* NIC.

PLATES

Plate XVI

1. The scheme of the chaetotaxy of *Isotomurus palustris* (MÜLL.) 2. The scheme of the chaetotaxy of *Isotoma viridis* BOURL. Symbols: a — microchaetae, b — macrochaetae, c — trichobotria, d — scales, e — setulae, f — pseudopori



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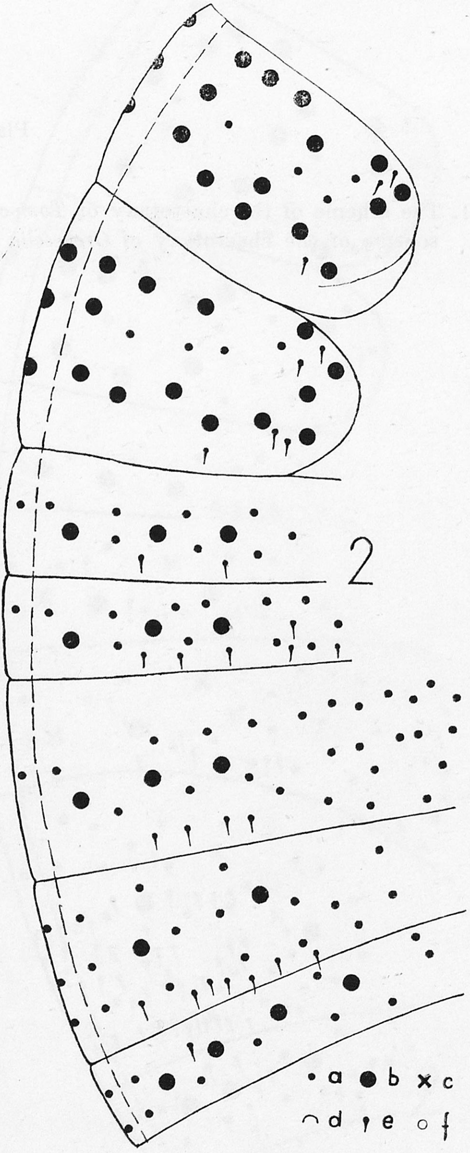

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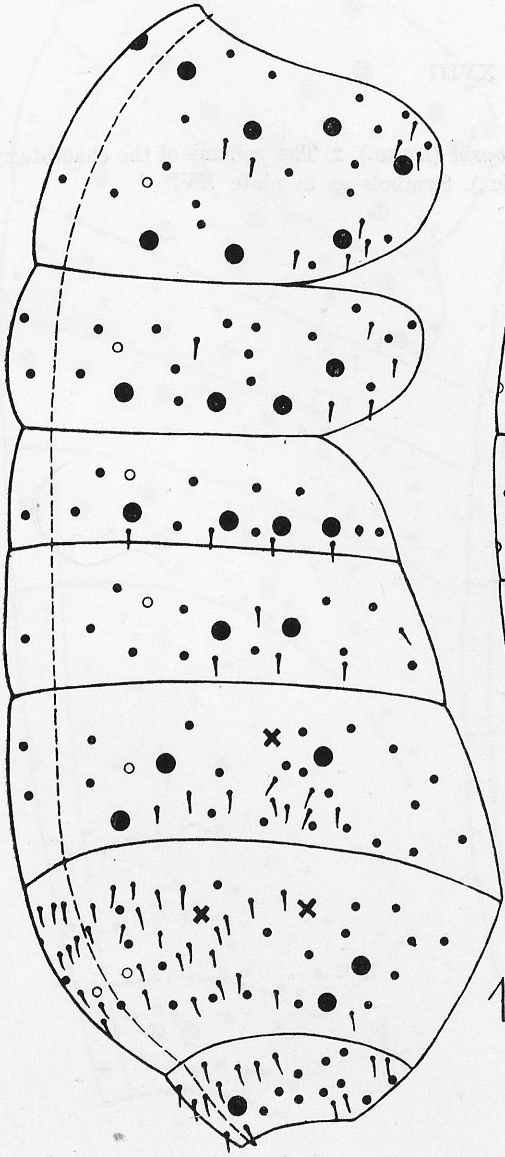
Plate XVII

1. The scheme of the chaetotaxy of *Tomocerus* (*Pogonognathellus*) *flavescens* (TULLB.) 2. The scheme of the chaetotaxy of *Orchesella flavescens* (BOURL.). Symbols as in plate XVI



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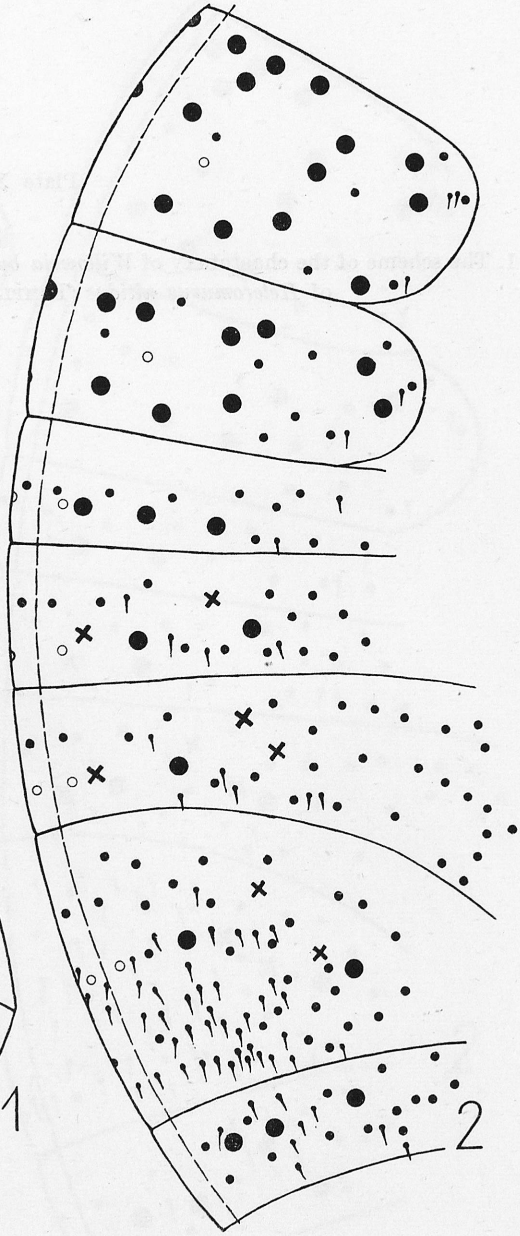
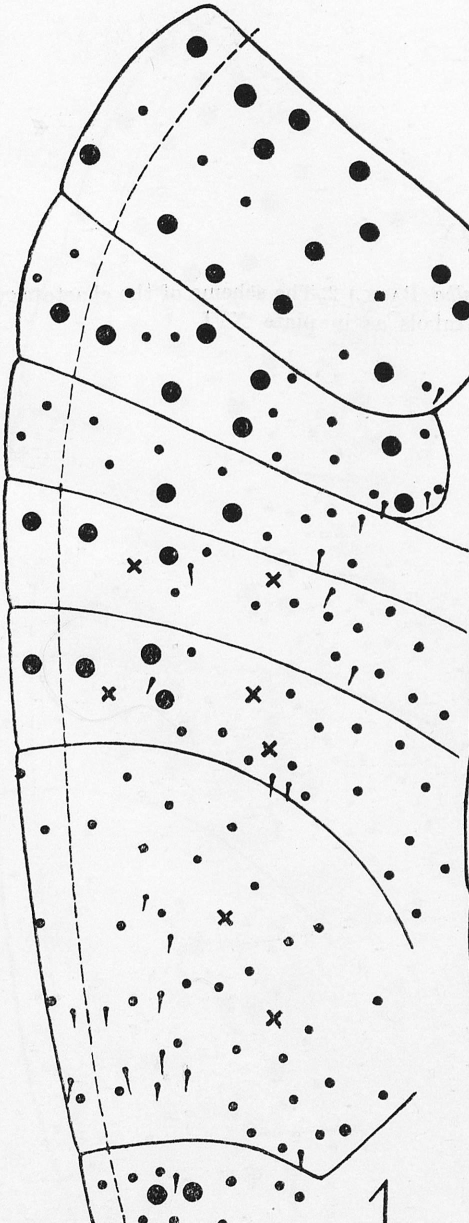


2

A Szeptycki

Plate XVIII

1. The scheme of the chaetotaxy of *Willowsia buski* (Lubb.). 2. The scheme of the chaetotaxy of *Heteromurus nitidus* (Templ.). Symbols as in plate XVI



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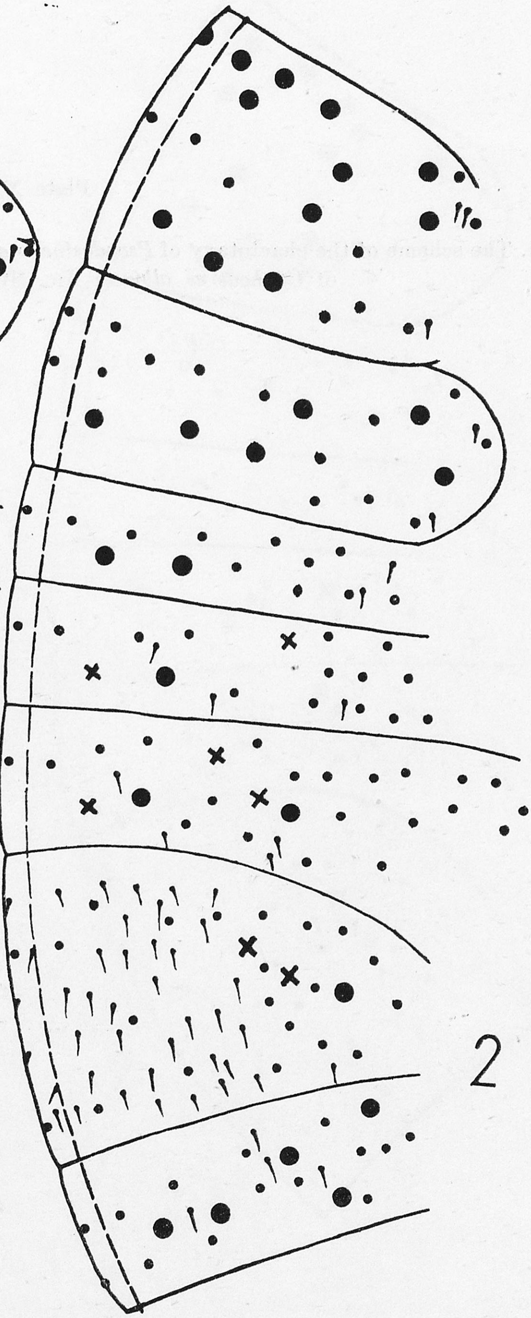

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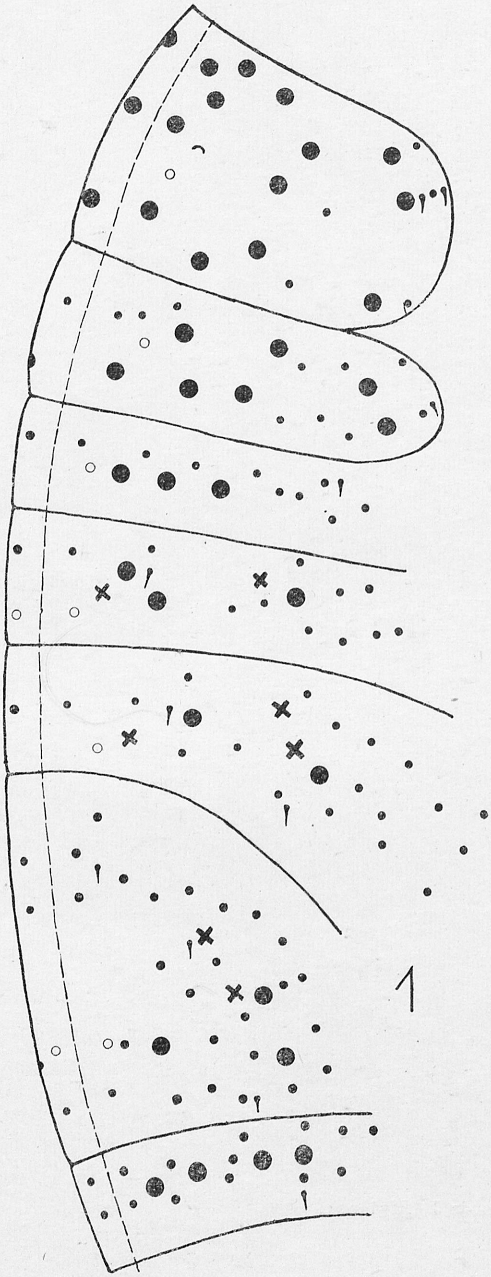
Plate XIX

1. The scheme of the chaetotaxy of *Pseudosinella alba* (Pack.) 2. The scheme of the chaetotaxy of *Cyphoderus albinus* Nic. Symbols as in plate XVI



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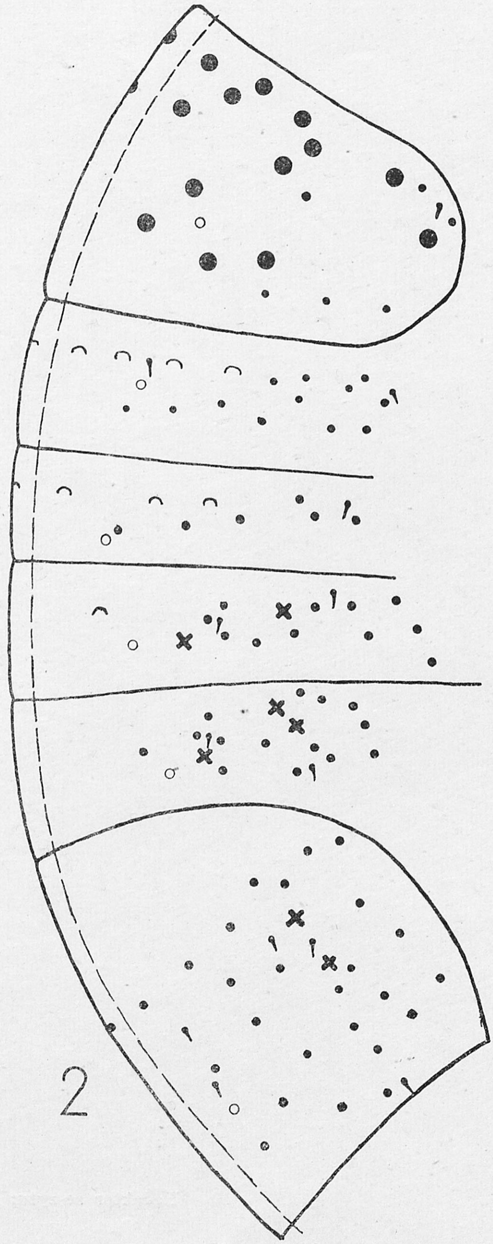

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A. Szeptycki