Homology and morphology in Poduromorpha (Hexapoda, Collembola)

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Abstract. The detailed external morphology and general anatomy of the majority of families and subfamilies of Poduromorpha were investigated and compared. This examination was done in relation to the three remaining orders of Collembola: Entomobryomorpha, Symphypleona and Neelipleona. Within Poduromorpha, homologies among the different families and subfamilies are established for general chaetotaxy, and chaetotaxy of head, buccal cone, sensilla of fourth antennal segment, anal valves and tibiotarsus. A consistent and comprehensive nomenclature is proposed for these morphological features unifying those applied in scattered existing studies. Observations on first instars are reported. Comparison of first instars and adult chaetotaxy suggests a possible paedomorphic trend in the evolution of Poduromorpha.

INTRODUCTION

The external anatomy of springtails (class Collembola) has been investigated for a long time (e.g., Bourlet, 1839; De Geer, 1743; Lubbock, 1873), starting consistently with the work of Börner (e.g., Börner, 1901, 1906, 1913). Since then, our knowledge of springtail morphology has increased significantly. However, most studies have focused on single groups of different levels: Subfamily (e.g., Rusek, 1976), genus (e.g., Yosii, 1962) or even a single species (e.g., André, 1988). Almost no attempts have been made to generalize to the other groups, with the exception of a comprehensive work on the labial palps (Fjellberg, 1999). Consequently, several nomenclatures exist for the same structures according to different groups and usually the homologies have not been clarified.

The main goal of the present work is to establish homologies of the morphological features among the different groups in Poduromorpha, and to do this in relation to the other orders when possible. It is also my intention to provide a comprehensive nomenclature unifying the scattered and incomplete studies available in the literature.

Springtails are a diverse group with more than 6500 species described to date (Rusek, 1998), This probably represents a small part of their total specific diversity, a diversity that could reach more than 50 000 species (Hopkin, 1997; Hopkin, 1998). Poduromorpha comprises more than a third of the described species of springtails with about 2500 species in approximately 260 genera.

The class Collembola is traditionally divided in two groups (e.g. Börner, 1906; Cassagnau, 1990; Gisin, 1960; Hopkin, 1997; Massoud, 1971b; Uchida, 1971), Arthropleona and Symphypleona *sensu lato*. The Symphypleona s.l. are comprised of the orders Symphypleona *sensu stricto* and Neelipleona. Members of this group are globular in shape with fused abdominal segments. Arthro-

pleona are characterized by possession of an elongate body with abdominal segments 1–4 clearly separated from each other by an intersegmental membrane. Arthropleona is comprised of the orders Poduromorpha and Entomobryomorpha. The Poduromorpha have a distinct prothorax that bears dorsal setae and third and fourth abdominal segments that are similar in size. Generally Entomobryomorpha have a greatly reduced prothorax that never bears setae, as in Symphypleona s.l., and the fourth abdominal segment is two to four times longer than the third segment. Exceptions to this are Isotomidae, Oncopoduridae and Tomoceridae, which have similar sized abdominal segments as in Poduromorpha.

MATERIAL AND METHODS

To carry out the present study, the collections of the Muséum National d'Histoire Naturelle (MNHN, France) were studied as well as institutional loans and personal field collecting. Thirteen species covering the diversity of Poduromorpha were also kept in culture for several years in order to study first instars and postembryonic development: *Tetrodontophora bielanensis* Waga, 1842 (Tetrodontophorinae), *Onychiurus ambulans* Linné, 1758, *Kalaphorura paradoxa* Schäffer, 1900, and *Protaphorura armata* Tullberg, 1869 (Onychiurinae), *Mesaphorura macrocheta* Rusek, 1976 (Tullbergiinae), *Ceratophysella gibbosa* (Bagnall, 1940) and *Xenylla tullbergi* Börner, 1903 (Hypogastruridae), *Podura aquatica* Linné, 1758 (Poduridae), *Friesea mirabilis* (Tullberg, 1871) (Frieseinae), *Anurida granaria* (Nicolet, 1847) (Pseudachorutinae), *Morulina verrucosa* Börner, 1903 (Morulinae), *Monobella grassei* Denis, 1923 and *Neanura muscorum* Templeton, 1835 (Neanurinae) and an Entomobryomorpha, *Folsomia candida* Bourlet, 1839 (Isotomidae). In total, more than one hundred species were examined for this study. These species represent all families and subfamilies of Poduromorpha and some major groups in the three remaining orders (Entomobryomorpha, Symphypleona, and Neelipleona).

Specimens were preserved in 95% ethyl alcohol; dissections of mouthparts and other structural features were made in that medium. They were cleared in successive 10% potassium

hydroxide solution and Amann's Lactophenol (lactic acid-glycerol-phenol: 25–50–25). The Lactophenol medium was slightly warmed up for the most pigmented specimens. Specimens were mounted on microscope slides using Marc André II mounting medium (see Massoud, 1967). The slides were slightly warmed up with an alcohol burner in order to improve specimen position in the slide for a favorable observation (slight inflation).

Specimens were examined using a compound microscope with differential interference contrast optics at magnifications ranging form 250 to 1250 (oil immersion lens for the higher magnifications). Drawings were made with a drawing tube.

RESULTS

General aspects

Poduromorpha are elongate springtails with a clearly segmented body, cylindrical in shape or slightly flattened. Contrary to other springtails, the prothorax is always developed and bears dorsal setae. Members of this group are generally small, with some species as small as 0.4 mm in length (e.g. in the genera *Mesaphorura* Börner, 1901 and *Willemia* Börner, 1901). However, some species can grow to a centimeter in length (e.g. in the genera *Tetrodontophora*, *Holacanthella* Börner, and *Caledonimeria* Delamare Deboutteville & Massoud, 1962).

Poduromorpha are usually uniformly pigmented: many are white (Onychiurinae, Tullbergiinae, *Willemia*, some *Anurida* Laboulbène, 1865 etc.) while most of the others present a monochromatic pigmentation limited to blue or red. The degree of pigmentation is correlated to latitude and altitude; the number of dark species increases near the poles and in mountains (Rapoport, 1969). Rapoport (1971) considered that the darker species warm up more quickly in the sun and are more active than the lighter colored species. However, dark species are actually found on sun-exposed places as the littoral seashore (e.g. the dark-blue *Anurida maritima* (Guérin-Méneville, 1836), and the dark Actaletidae) and several studies showed that Collembola were sensitive to UV radiation and suggested that dark pigmentation plays a protective role in exposed species (Verhoef et al., 2000; Zinkler & Wilking, 1989). Species with patterns of different colors are exceptional: there are a few bi-colored species that are usually dark blue and yellow (Arlé & Rufino, 1976; Mendoça & Fernandes, 1999), occasionally red and yellow or rarely tri-colored red, yellow and white (Cassagnau & Deharveng, 1984). More generally, pigmentation in Poduromorpha is much more uniform than in Entomobryomorpha and Symphypleona. However, knowledge on pigmentation of Collembola remains very fragmentary insofar as it has not been studied extensively (e.g. Bouthier & Thibaud, 1974).

Cuticle. Examination of the surface of the cuticle using a scanning electron microscope indicates a characteristic granulation (Dallai, 1973; Lawrence & Massoud, 1974; Massoud, 1969; Massoud & Barra, 1980; Massoud & Betsch, 1973). The ornamentation of the cuticle presents mainly three degrees of complexity:

1. Primary granules: elementary granules, generally triangle-shaped, that are regularly distributed and linked to one another by ridges and thus forming a hexagonal pattern (Massoud, 1969). Sometimes, these elementary granules are square-shaped, resulting in a squared pattern (as in *Podura aquatica*);

2. Secondary granules: one or several of the primary granules are deformed and enlarged to form protuberances (Dallai, 1973; Hale & Smith, 1966). Secondary granules are found in Poduromorpha and Symphypleona but not in Entomobryomorpha (Massoud, 1969; Massoud & Thibaud, 1979);

3. Tertiary granules: the grouping of several secondary granules forms the tertiary granules characteristic of Neanurinae (Deharveng, 1983). The tubercles are a result of the tertiary granules structure deforming the cuticle. *Tetrodontophora bielanensis* also possess tertiary granules that resemble "pseudo-scales" (Massoud & Betsch, 1973). However, this structure is not homologous to the tubercles found in Neanurinae.

The integument forms hypodermic reticulation in some taxa, for example in the genera *Gulgastrura Yosii*, 1966 (Lee & Thibaud, 1987), *Willemia* (D'Haese & Weiner, 1998), *Caputanurina* Lee, 1983 (Najt & Weiner, 1992), many species of Neanurinae (Deharveng, 1983; Massoud, 1967), in Morulinae (Stach, 1951), and also in some Entomobryomorpha as in the genera *Jestella* Najt, 1977 (Najt, 1977), and *Tetracanthella* Schött, 1891 (Deharveng, 1987). These reticulations are caused by the presence of a superficial endoskeleton (Cassagnau & Lauga-Reyrel, 1984).

The integument can fold, forming digitations and bumps. Some species of Neanuridae were grouped in Uchidanurinae on this criterion alone (Cassagnau, 1980). However, digitations are found in other groups, for example in the genus *Probolaphorura* Dunger, 1976 (Onychiurinae) (Dunger, 1976).

Pseudocelli. Onychiuridae possess characteristic cuticular structures known as pseudocelli, which are unique to this group. Three main types of pseudocelli were defined (Rusek, 1984; Rusek & Weyda, 1981):

1. Simple pseudocelli are found in Tullbergiinae. The pseudocellar lid is weakly separated from the integument and weakly differentiated into one or a few flaps arranged into a rosette or tangentially. The granulation of the pseudocelli is a primary granulation or is the same as the surrounding integument (Rusek & Weyda, 1981). These pseudocelli are big in comparison to the other types of pseudocelli; In Tullbergiinae, pseudocelli were classified into four categories depending on the shape and the number of the flaps and their position (Weiner & Najt, 1991b);

2. The pseudocelli in Onychiurinae, and Tetrodontophorinae have a smooth pseudocellar lid, which is separated from the surrounding coarse secondary granulated integument by a distinct circular furrow of primary or low secondary granulation. The pseudocellar lid bears 6+6 to 20+20 ribs in two parallel rows delineated by a central superficial groove (Dallai, 1973);

3. Rusek (1984) described a third type of pseudocelli found on the trochanters of members of the genus *Onychiurus* Gervais, 1841 and named them "trochanteral pseudocelli". They are smaller than type 2 pseudocelli and lack a circular furrow. These pseudocelli are also found on other part of the body: On the subcoxae in *Allonychiurus* Yoshii, 1995 (= *Paronychiurus* Bagnall, 1948; see Weiner, 1989b); on anal valves in Onychiurinae (Christian, 1989); on the first antennal segment in *Tetrodontophora bielanensis* (see Christian, 1989); and on various body segments of *Hymenaphorura* Bagnall, 1948 both ventrally and dorsally (Pomorski, 1990; Weiner & Fjellberg, 1994). Weiner & Fjellberg (1994) proposed to name these structures parapseudocelli.

Pseudocelli are completely absent on the ventral side and legs of Tullbergiinae (Rusek, 1984) and Tetrodontophorinae.

Several hypotheses were developed to explain the role of pseudocelli. Koncek (1924) advocated a haemorragic function. Others proposed both an excretion and a defense function against predators by extruding repellent fluids (Hale & Smith, 1966; Usher & Balogun, 1966). Rusek and Weyda (1981) considered the excretion function only.

In addition to pseudocelli, tegument structures are also found in other groups; particularly the pseudopores observed in Oncopoduridae (Szeptycki, 1977), Entomobryidae, Tomoceridae, and Isotomidae (Deharveng, 1978). According to morphology and position of pseudopores, one could wonder if these structures would be homologous to the pseudocelli. A detailed study using the electron microscopy would be necessary to establish or reject that hypothesis.

Chaetotaxy. Several authors have acknowledged the utility of chaetotaxy for phylogenetic inference (Deharveng & Bedos, 1991; Luciáñez & Simón, 1993). Chaetotaxy has been successfully used in lower level phylogenies (species or genera level, e.g., Deharveng & Bedos, 1991; D'Haese, 2000; D'Haese & Weiner, 1998; Luciáñez & Simón, 1993). However, one might argue that it would be difficult to use it for higher-level phylogenies as homologies are more difficult to assess (but not impossible as it will be shown here and see D'Haese, 2002), and setae can bring a highly homoplastic signal.

Springtails possess chaetotaxic assemblages in which setae have defined positions, which are dispatched according to specific patterns (Nayrolles, 1988; Nayrolles, 1991; Nayrolles & Betsch, 1993). The chaetotaxic nomenclature proposed here is based on adjustments to the works of Yosii (1956; 1971), Cassagnau (1974) and Grow & Christiansen (1974).

Chaetotaxy of s setae. Four main types of setae are possessed by springtails: Ordinary setae, sensilla (also named setae s), scales and trichobothria (Massoud & Ellis, 1977). Neither scales and trichobothria, nor multilaterally ciliate setae are found in Poduromorpha. Sensilla of the body and of the antennae are distinguished here: The term "sensilla" is used for those of the antennae; and

"setae s" refers to sensilla of the body. In comparison to ordinary setae, setae s are smooth, blunt and have a different refractiveness under the compound microscope. They are usually subcylindrical, but can be candle flame shaped, "francisque"-shaped, etc. (Massoud & Ellis, 1977).

Within the Poduromorpha, setae s chaetotaxy is stable (with the exception of Onychiurinae and Tetrodontophorinae) compared to ordinary chaetotaxy, which is often plurichaetotic (Deharveng, 1979a). On the contrary, chaetotaxy of fourth antennal segment can present plurichaetoses or paurochaetoses of the sensilla independently in different groups.

The four families Hypogastruridae, Odontellidae, Neanuridae and Isotogastruridae possess a stable and scarce setae s chaetotaxy: 2+2 setae s (1+1 setae s in the m row, and 1+1 in the p row), and 0+0 or 1+1 microsensilla on meso- and metathorax, 1+1 setae s (in p row) on tergum of abdominal segments I to V. *Podura aquatica* has the same setae s chaetotaxy, even if setae s are indistinct from ordinary setae. Brachystomellidae are slightly different: some species have 2+2 setae s on abdominal segments. Head, prothorax, and sixth abdominal segment never bear setae s in Hypogastruridae, Odontellidae, and Neanuridae.

Setae s chaetotaxy of Onychiuridae is not well differentiated and difficult to interpret insofar that these setae are very difficult to distinguish from ordinary setae. More precisely, Onychiurinae have an abundant and not well-differentiated chaetotaxy of setae s (Deharveng, 1979a). Some species, for example in the genera *Psyllaphorura* Bagnall, 1948, *Oligaphorura* Bagnall, 1949, and *Tantulonychiurus* Pomorski, 1996 possess setae s on the head. In the two latter, there is 2+2 setae s on the head (or 3+3 in some *Psyllaphorura*, see Weiner & Najt, 2000) and on abdominal segments I to III and 1+1 on the sixth (Pomorski, 1998; Weiner, 1996). Tullbergiinae have a setae s chaetotaxy which is difficult to determine, but it seems stable compared to Onychiurinae setae s chaetotaxy and closer to Hypogastruridae one. Particularly, 1+1 setae s are clearly distinct on the fifth abdominal segment.

Head

The position of the head has been a taxonomic criterion used by some authors to establish phylogenetic relationships (e.g., Paclt, 1956; Salmon, 1964). Both authors considered Arthropleona prognathous and Symphypleona s.l. and *Podura* hypognathous. This was the major justification for placing *Podura aquatica* within the Metaxypleona, an ensemble including Actaletidae, Metaxypleona being sister group to the Symphypleona s.l. (Moen & Ellis, 1984; Salmon, 1964). However, according to my own observations, *Podura aquatica* is prognathous when alive. The head bends downward with sudden death (when put in alcohol for example). It is important to note that the hypognathous position in Symphypleona is correlated with the important development of the clypeal area. This is not the case with *Podura aquatica*. The number of clypeal setae, or pre-labral setae, is reduced to two or four in Poduromorpha whereas there are more in *Podura*

TABLE 1. Correspondences between existing systems of nomenclature for cephalic setae.

Cassagnau (1974) Najt & Rubio (1978)	Yosii (1956) Da Gama (1964)
d1	A
d2 (unpaired)	O
d3	C
d4	F
d5	G
sd3	B
sd4	E
sd5	D
Oc1	Oc p
Oc2	Oc m
Oc3	Oc a
c1	Di1
c2	De2
p1	Di2 ?
p2	De1 ?

aquatica (on average ten to 20). This character places P. aquatica close to the genus *Paraxenylla* Murphy, 1965 which has a comparable clypeal chaetotaxy. The position of *Paraxenylla* in Poduromorpha has never been challenged.

The head also possess two different kinds of sense organs: eyes and PAO.

1. Springtails have eight simple eyes on each side of the head. These ocelli always have the same position with respect to each other. These have been annoted A to H (Guthrie, 1906). In many lineages, this number is reduced to complete absence, especially in euedaphic species (Thibaud, 1976; Thibaud & Massoud, 1973).

2. The postantennal organs (PAO) are located on each side of the head in front of the ocular area, posterior to the base of the antennae. The precise function of this sense organ is unknown. It could have an olfactory function (Dallai, 1971), as well as sensitivity to temperature and humidity (Altner & Thies, 1976). It is reduced to a setae-like structure, a "peg", in Symphypleona (Dallai, 1971) and absent in some Entomobryomorpha (Entomobryidae). In Poduromorpha, the PAO is composed of a variable number of vesicles and comprises a sensory cell in which the perikaryon is located in the central nervous system (Karuhize, 1971). The shape, number, structure of vesicles and the number of rows as well as the position of the vesicles in these rows can be highly variable in the different groups. These are fundamental criteria in Onychiuridae taxonomy (Pomorski & Skarżyński, 1992; Weiner, 1996), and to a lesser extent in other groups like Pseudachorutinae (Massoud, 1967). The postantennal organ is absent in Neanurinae. Based on the connections to the nervous system, some authors considered the PAO homologous to the Tömösváry organ in Myriapoda (Denis, 1926; Willem, 1900). François (1969) proposed that the pseudoculi in Protura are homologous to the

Tömösváry organ, whereas Tuxen (1959) considered them vestiges of antennae. Recent studies tend to accept the homology of these organs among the three groups (Bitsch & Bitsch, 1998; Edgecombe et al., 2000; Haupt, 1979).

Head chaetotaxy. Homologies of cephalic setae have been established with several morphological landmarks, mainly on the basis of:

1. Relative positions of the setae to each other;
2. Relative position of the setae to the muscular insertion marks on the cuticle (Najt & Rubio, 1978);
3. Relative position of the setae to the transversal fissure separating the frontal area from the basis of the head and the fissures demarcating the ocular areas.

In Table 1, are proposed the correspondences between cephalic nomenclatures proposed by Cassagnau (1974) and Najt & Rubio (1978) for the Hypogastruridae and Tullbergiinae and the nomenclature proposed by Yosii (1956) and da Gama (1964) for the Neanurinae.

These correspondences were partially given by Cassagnau (1980). However, he considered A = sd1, O = d1, B = d2, and E = sd4. The present proposal (Table 1) is probably more accurate insofar as in Cassagnau's system the unpaired setae replace the d1 setae. Then, it assumes sd row with 6 setae (one more posterior to sd1) in the genus *Friesea* Dalla Torre, 1895 (Fig. 2C), and B setae (supposed to be d2) would be distant from the axis of d row in Neanurinae (Fig. 2E). Primary homology criterion leads to rejection of that hypothesis. The replacement of two symmetric setae by one seta in the axis (paurochaetosis by axial substitution) presents an intermediary state in species with two asymmetrical setae (Deharveng, 1983), as in some species in the genus *Anurida* for example.

Jordana et al. (1997) proposed a nomenclature for cephalic setae in Onychiurinae. However, the interpretation of the d row is erroneous in this work as d5 do exist and d0 is the unpaired expression of setae d1, (already stated by Pomorski, 1996). Setae d5 is not homologous to the unpaired setae d in *Friesea* (in this genus d2 is unpaired). In the genus *Triacanthella* Schäffer, 1897 there is also an unpaired setae d. It is probably homologous with d0 setae in Onychiurinae. However, homologies are difficult to established in *Triacanthella* because of the plurichaetoses.

Part of the diversity of cephalic chaetotaxy in Poduromorpha is presented in Figs 1B–F and 2A–E. Chaetotaxy of a first instar of *Folsomia candida* (Entomobryomorpha, Isotomidae) is provided in Fig. 1A. Row sd' in Onychiuridae is probably homologous to row oc. According to observations in *Onychiurus* first instar, sd'1 = oc1 and sd'2 = oc2 (oc2 is always a big setae compared to the other oc setae) (personal observations and Pomorski, 1996). In Onychiurinae, there are several rows of setae (rows cm, cb, cp) between rows v and p (Fig. 1D). These rows are not found in other Poduromorpha, which possess row c only (Fig. 1C). Along the same vein, Onychiurinae can have the unpaired setae a0, a'0 and a0'
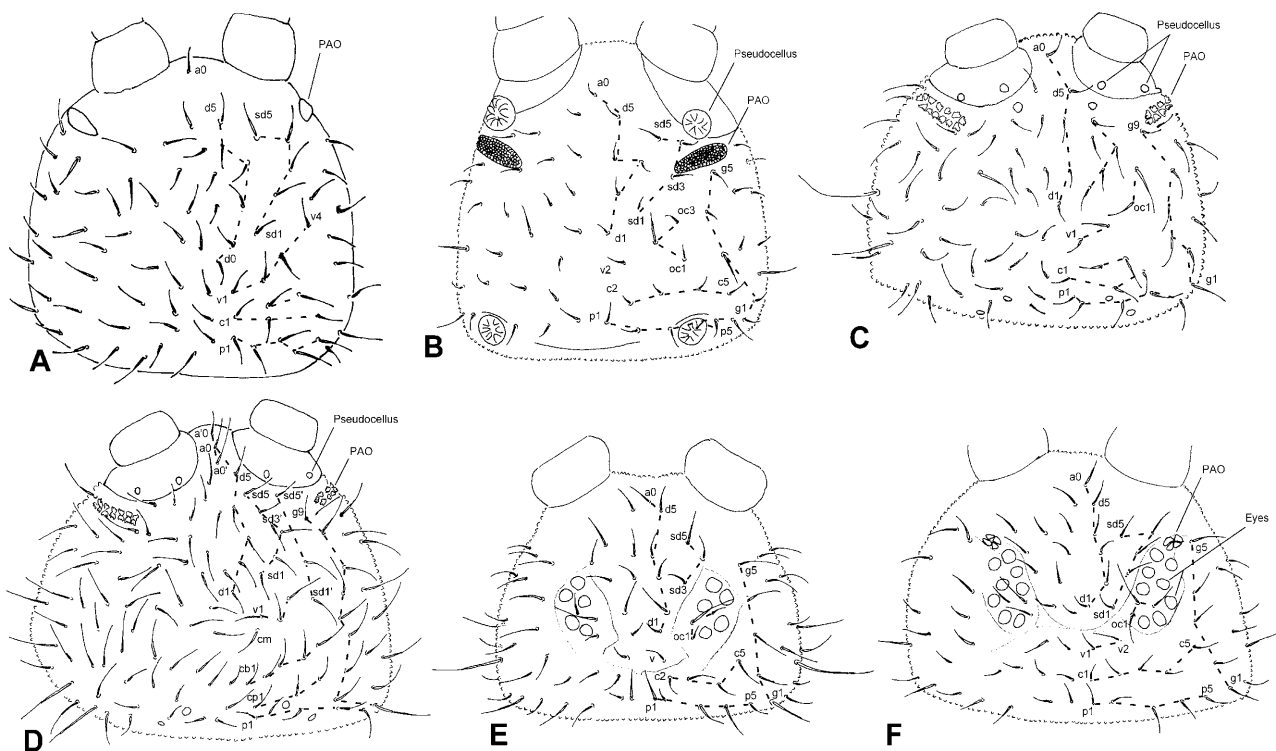
Fig. 1. Head chaetotaxy. A – *Folsomia candida* (Isotomidae), first instar; B – *Scaphaphorura arenaria* (Onychiuridae: Tullbergiinae); C – *Onychiurus ambulans* (Onychiuridae: Onychiurinae), first instar; D – *Onychiurus ambulans*, adult; E – *Hypogastrura vernalis* (Hypogastruridae); F – *Xenylla grisea* (Hypogastruridae). PAO – postantennal organ.

Fig. 2. Head chaetotaxy. A – *Microgastrura sensiliata* (Hypogastruridae); B – *Superodontella gisini* (Odontellidae); C – *Friesea truncata* (Neanuridae: Frieseinae); D – *Pseudanurida sawayana* (Neanuridae: Pseudachorutinae); E – *Monobella grassei* (Neanuridae: Neanurinae).

Fig. 3. Labium. A – *Onychiurus ambulans* (Onychiuridae: Onychiurinae); B – *Tullbergia bisetosa* (Onychiuridae: Tullbergiinae)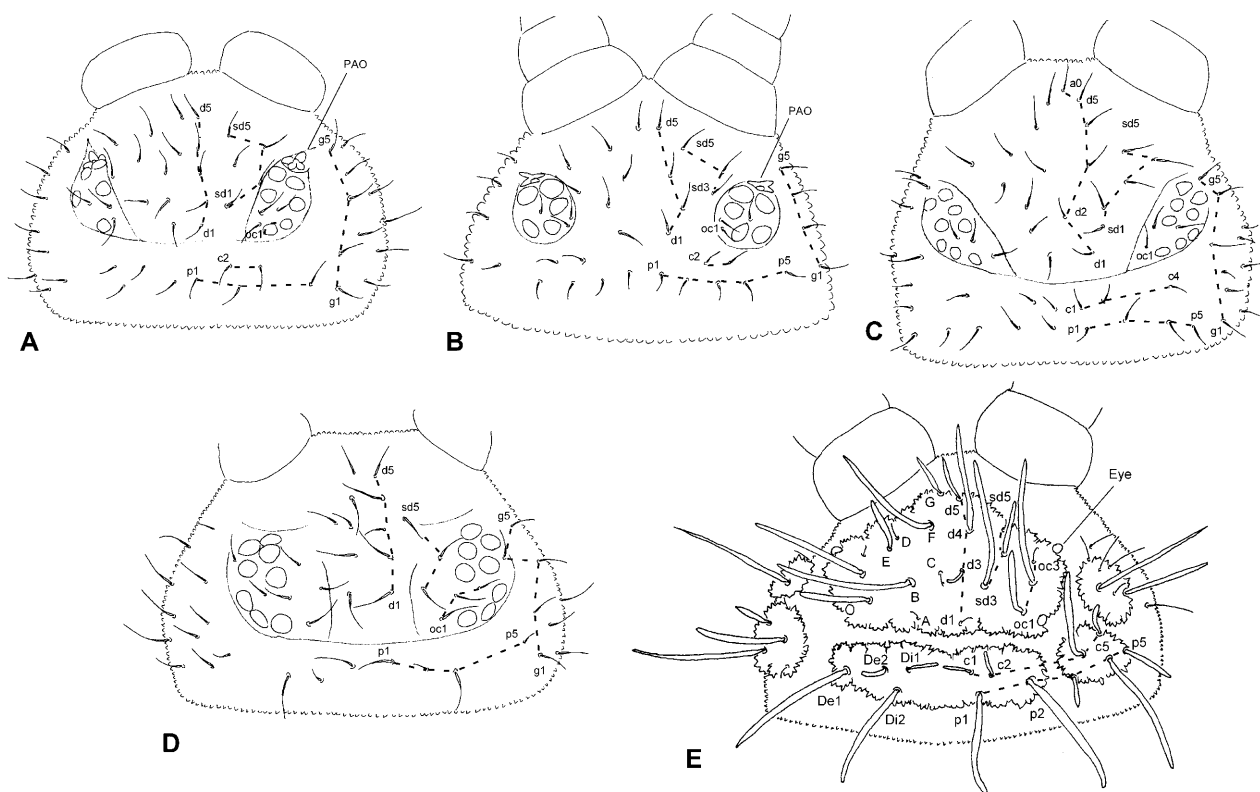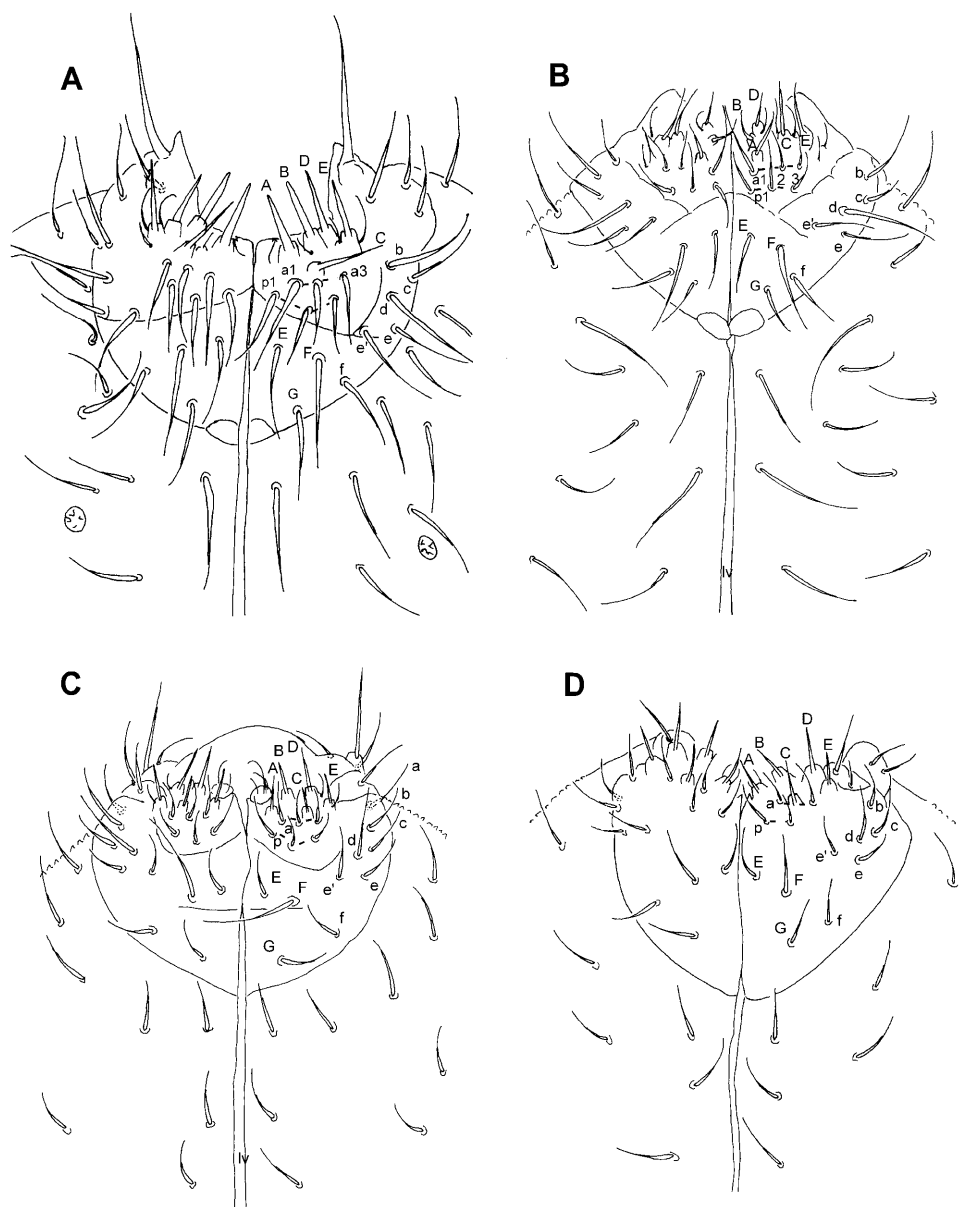; C – *Xenylla grisea* (Hypogastruridae); D – *Willemia denisi* (Hypogastruridae). lv – *linea ventralis*. Chaetotaxy of the area posterior to labium *Onychiurus* is incomplete here: there are 4 rows of setae.

(Fig. 1D) whereas the other Poduromorpha have one unpaired setae a0 (Figs 1B, 1E-F, and 2A-E).

Setae v are absent in Neanuridae, Brachystomellidae and *Microgastrura* Stach, 1922 (Figs 2A-E). There are 1+1 setae v in every species of the genera *Xenylla* Tullberg, 1869 (Fig. 1F), *Willemia* and *Paraxenylla*, 2+2 in the other Hypogastruridae (Fig. 1E) and Tullbergiinae (Fig. 1B) and 3+3 or more setae in Onychiurinae.

In Hypogastruridae, setae c form a complete row of 5+5 setae (*Hypogastrura*, Bourlet, 1839, *Ceratophysella* Börner, 1932, *Paraxenylla*), 4+4 setae (*Xenylla*, *Willemia*), 3+3 (*Friesea*) 2+2 (*Podura*); in Odontellidae row c comprises from 1+1 to 3+3 setae.

Buccal cone. Collembola are entognathous, with a buccal cone on the anterior part of the head that encloses

the mouthparts. This buccal cone is formed dorsally by the clypeus, which is extended by the labrum and ventrally by the labium, split into two parts by the linea ventralis. There are two main kinds of buccal cone: short, truncated (Figs 3A-D, 4A-B), and hemispherical when viewed from the side. This condition is found in most Poduromorpha: Hypogastruridae, Onychiuridae, Brachystomellidae, Frieseinae, and some Pseudachorutinae (i.e., *Anurida*); elongated, beak shaped (Figs 4C-D). The latter condition is found in Neanurinae (with simple mouthparts), some Pseudachorutinae (i.e., *Pseudanurida* Schött, 1901, *Pseudachorutes* Tullberg, 1871), and some Odontellidae.

Some species possess an intermediate state as that found in the genus *Micranurida* Börner. Elongation of the buccal cone could be correlated to the elongation of the
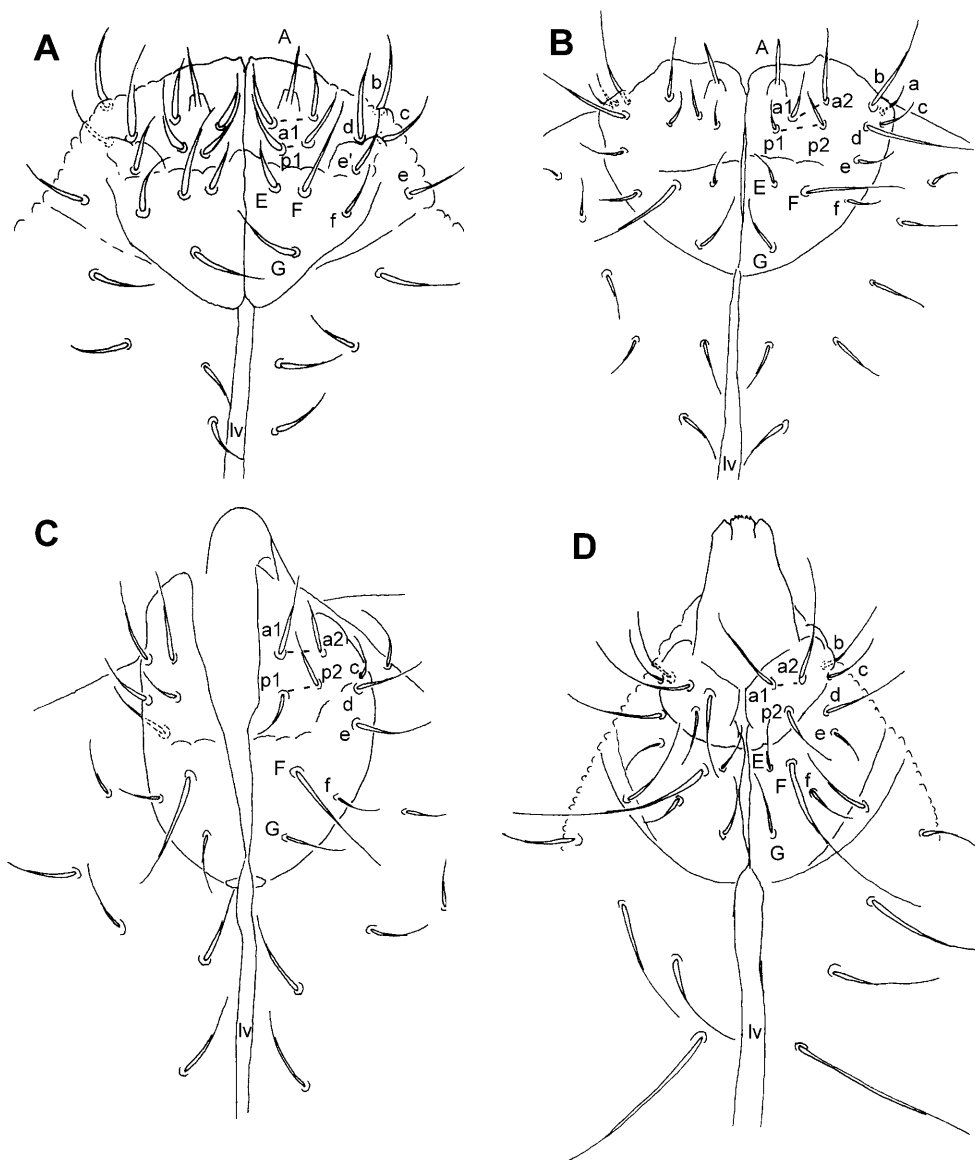
Fig. 4. Labium. A – *Brachystomella parvula* (Brachystomellidae); B – *Friesea truncata* (Neanuridae: Frieseinae); C – *Pseudachorutes palmiensis* (Neanuridae: Pseudachorutinae); D – *Neanura muscorum* (Neanuridae: Neanurinae). lv – *linea ventralis*.

maxillae, which could be linked to the feeding habits (Massoud, 1967).

Clypeal chaetotaxy is reduced to a few setae in most species. *Podura* and *Paraxenylla* have more setae and non-poduromorphan Collembola have many more. Prelabral chaetotaxy of Poduromorpha is formed by a row of four or two setae, or prelabral seate are absent (Najt & Weiner, 2002). Generally, it is composed of four setae in Entomobryomorpha (Yosii, 1976), thought three in some Isotomidae and six in Symphypleona (Betsch, 1980).

Chaetotaxy of the labrum is formed by three rows of setae (usually 5–5–4 setae) in most of the Poduromorpha and two only in Neanurinae (3 in Caputanurinae: 5–5–2). Yosii (1976) counted four rows in some species (e.g., *Anurida iriei* Yosii, 1970, *Brachystomella hawaiiensi* Yosii, 1965, and *Pseudachorutes kangchenjungae* Yosii, 1966). However, it is more likely that his two first rows (with two and three setae respectively) are homologous of

the first row (with five setae) in the three-rows system. The labrum in Entomobryomorpha and Symphypleona is rather uniform with a complete chaetotaxy of 5–5–4 setae with very few exceptions (Betsch, 1980; Chen et al., 1997; Yosii, 1967; Yosii, 1976).

Labium is formed by three distinct regions (Folsom, 1899; Massoud et al., 1975): labial palps (= setigerous lobe, Goto, 1972), mentum and submentum (the basilateral and basimedian field respectively). Labial palps possess two rows of setae inserted on papillae accompanied of guard setae (André, 1988; Fjellberg, 1999; Pomorski, 1996) three distally, and two posterior (A, C, D and F, E respectively in the nomenclature of Pomorski) (Table 2). The comprehensive nomenclature of Fjellberg (1999) is used here. Hypogastruridae and Onychiuridae possess a complete chaetotaxy with five papillae (A-E) (Figs 3A-D) as well as Entomobryomorpha and Symphypleona (Fjellberg, 1999). Brachystomellidae and Frieseinae have only

TABLE 2. Correspondences between existing systems of nomenclature for setae on papillae and guard setae on labial palps.

Massoud, 1967	L						
André, 1988	lp1	lp3	lp6	lp4	lp5	k	Г
Pomorski, 1996	A	C	F	D	E	h	B
Fjellberg, 1999	A	B	C	D	E	al	bl

one papilla (L = A) (Fig. 4A-B). In Pseudachorutinae, some species possess the papilla A while others do not (Fig. 4C). They are completely lacking in Neanurinae (Fig. 4D). Posteriorly, there are two rows with three setae (including setae A, B, C, D), these are the proximal setae sensu Fjellberg (1999). I have reclassified the setae in two rows a and p with three setae each in order to avoid confusion with the nomenclature of the papillae (Table 3). In the genus Friesea, there are four guard setae: a1-2 and p1-2 (Fig. 4B); In *Anurida, Neanura* Mac Gillivray, 1893, and *Caputanurina*, there are only three guard setae: a2 and p1-2 (Fig. 4D). In some Pseudachorutinae, Caputanurinae and Neanurinae, labial organites are found (Deharveng, 1983), between setae p1, a2 and p2.

Massoud (1967) proposed a nomenclature for mentum and submentum:

1. Mentum: setae e, d, c, b;
2. Submentum: setae E, F, G, f;

A seta e' has to be added to that nomenclature, above seta e. That seta e' is found in Onychiuridae and some Hypogastruridae (Figs. 4A-D). Homologies for mentum and submentum setae are proposed in Table 4 between nomenclatures of André (1988), Pomorski (1996) and Massoud (1967) and a proposed nomenclature based on Massoud's nomenclature.

The nomenclature of Pomorski (1996) for the setae posterior to labium is retained. Specifically, the number of setae in row i are of phylogenetic value showing a variation in number from one row to five rows: Four to five rows in Onychiurinae, *Isotogastrura* Thibaud & Najt, 1992 and *Folsomia* Willem, 1902; three in Tullbergiinae; three in Hypogastruridae; two in Neanurinae s.l.; one in the genus *Microgastrura*.

Mandibles. Springtails typically possess chewing-type mandibles. They are composed of a robust proximal component, which is pierced by a foramen allowing the insertion of mandibular muscles, and a distal part with a molar plate at the base and a toothed pars incisiva at the tip. Following the work of Stach (1949) and Gisin (1952), it was admitted that mandibles were lacking in Odontellidae (e.g., Massoud, 1967). However, they were observed in

TABLE 4. Correspondences between existing systems of nomenclature for mentum and submentum setae.

	Submentum				Mentum				
Massoud, 1967	E	F	G	f	e	–	d	c	b
André, 1988	me1	me2	sm1	sm2	me4	me3	me5	me6	me7
Pomorski, 1996	p1	p3	p2	p4	a4	a5	a3	a2	a1
Proposed nomenclature	E	F	G	f	e	e'	d	c	b

TABLE 3. Correspondences between existing systems of nomenclature for proximal setae on labial palps.

Massoud, 1967	A	B	C	D	–	–
André, 1988	lb1	Lb2	lb3	lb5	lb4	lb6
Proposed nomenclature	p1	a1	a2	p2	a3	p3

the genus *Stachia* Folsom, 1932. Deharveng (1981b) in his study on Odontellidae clearly established that mandibles are always present in this family, even if they are reduced and do not have a molar plate (sometimes one asymmetrical mandibles only is present). All the prepared specimens of Odontellidae observed for this study had at least one mandible. In the same way, it was considered that Brachystomellidae did not have mandibles. But mandibles can be found in some genera (in *Probrachystomellides* Weiner & Najt, 1991 and *Winterella* Massoud, 1967), they move under the stipes when prepared and are then difficult to see (Judith Najt, pers. com., Weiner & Najt, 1991a). However, with the data to hand, it is difficult to assess if mandibles are absent in most Brachystomellidae or present and hidden by the stipes. The same goes for some Pseudachorutinae that seem to lack the mandibles as well (Najt & Weiner, 2002).

The molar plate can be present (Entomobryomorpha, Symphypleona, Onychiuridae, Hypogastruridae) or absent (Odontellidae, Neanuridae). It is worth noting that the Hypogastruridae genus *Microgastrura* has an intermediate state, with a reduced molar plate. The pars incisiva bears either a few sub-equal teeth or is formed of a big basal tooth and smaller teeth at the tip. It is reduced to a sclerified spike in Odontellidae.

Maxillae. In the genus *Hypogastrura*, the maxillary palps (maxillary outer lobes) are simple and found on each side of the mouth with a sublobal plate including none to three sublobal setae. The number of sublobal setae is highly variable and so useful for the lower-level taxonomy of species identification (Fjellberg, 1984a). For example, in the genus *Xenylla*, 0, 1, 2 or 3 sublobal setae can be found depending on the species (Fjellberg, 1984b). Maxillary palps are found in Onychiuridae, Hypogastruridae and Poduridae, reduced in Odontellidae, highly reduced in Brachystomellidae and absent in Neanuridae.

In most Poduromorpha, the capitulum maxillaris is complete, and includes three teeth and six lamellae (Börner, 1908; Fjellberg, 1984b):

1. Lamella 1 (= median appendage, Börner, 1908) always the longest;
2. Lamella 6 (= median subsidiary appendage, Goto, 1972) in shape of small cushion, behind the basis of lamella 1 (in an axis teeth-lamella 1-lamella 6);
3. Lamella 2 and 3 ventral to lamella 6;
4. Lamellae 4 and 5 dorsal to lamella 6.

Many authors described the capitulum maxillaris in different species of Poduromorpha: *Tetrodontophora* Reuter, 1882 (Dallai, 1973), Hypogastruridae and Poduridae (Fjellberg, 1984b), *Anurida* (Folsom, 1900), *Isotogastrura* (Fjellberg, 1995), Brachystomellidae and Neanuridae (Massoud, 1967) and non-Poduromorpha:

Isotomidae (Fjellberg, 1984a), *Orchesella* Templeton (Folsom, 1899), Folsomia (Goto, 1972), and Symphypleona (Betsch, 1980). A capitulum with three teeth and six lamellae is the most widespread form. It is found in most Hypogastruridae, Poduridae, Onychiurinae and Tetrodontophorinae and in Symphypleona and Entomobryomorpha. From that groundplan, many variations are observed: capitulum maxillaris with reduced number of lamellae (e.g., Frieseinae) or lamellae completely absent (*Brachystomella* Ågren, 1903), and capitulum more or less elongated, decrease or increase in the number of teeth etc.

In almost every Collembola, cardo, stipes and fulcrum are articulated in the following order: Stipes cardo fulcrum. In Odontellidae the stipes is directly articulated to the fulcrum (Deharveng, 1981b; Gisin, 1952). The cardo and the fulcrum can be either stocky (length/width ratio low) or thin (length/width ratio high). It is important to note that the length/width ratio of the cardo is small in Onychiuridae and Hypogastruridae, higher in Brachystomellidae and Frieseinae and still higher in Neanurinae. Actually, there is a cline from a stocky cardo (Hypogastruridae) to a thin cardo (Frieseinae) and even thinner one (Neanurinae). Cardo can be straight (Frieseinae, Brachystomellidae, and Neanurinae) or twisted (Hypogastruridae). The postero-internal extension of the fulcrum (p.p.i.) can be well developed as in Hypogastruridae and Onychiuridae, or reduced as in Neanuridae and Brachystomellidae (Deharveng, 1981b).

Antennae

The antennae are subdivided into four simple segments, each with its own intrinsic muscles. In some Symphypleona, the third and fourth antennal segments can be secondarily subsegmented (Betsch, 1980; Nayrolles, 1991), thus giving more flexibility to the antennae. Secondary segmentations are also observed in some Entomobryomorpha, namely Orchesellinae (Mari Mutt, 1988) and Tomoceridae. Antennae are inserted in the anterior part of the frontal area, and are in contact with the clypeal area. However, in Symphypleona they are inserted in the middle of the frontal area and make no contact with the clypeal area (Stebaeva, 1988). The region of the head near the antennae usually presents a distinct granulation (primary granules smaller) in Onychiuridae. Antennae are slightly shorter or sub-equal to the cephalic diagonal in Poduromorpha, significantly longer in Entomobryomorpha and Symphypleona, or significantly shorter than the cephalic diagonal in Neelipleona. It is worth noting that these ratios also reflect the proportions of the other appendices: legs and to a lesser extant, the furca. This is not true for Neelipleona, which have very short antennae despite the presence of well-developed legs and furcula. The proportions and shape of the four antennal segments are also potentially informative: the four segments can have the same width (resulting in subcylindrical-shaped antennae); segments can be decreasingly wide from base to tip, resulting in a more or less pronounced conical shape (a trend seen in Neanuridae and in Odontellidae). Antennae possess many sense organs, particularly at the

tip: sense organ of the third antennal segment and above all the fourth antennal segment as a whole with many sensilla.

Generally, the first antennal segment contains seven setae: six arranged on one row and one more basally, near the external side. This conformation is observed almost uniformly in Poduromorpha (and Isotogastruridae) with few variations and with the exception of Onychiurinae, which possess one to three more setae. With ten setae, the first antennal segment chaetotaxy in the genus *Triacanthella* is very close to Onychiurinae. Primary chaetotaxy of Symphypleona is composed of seven setae as in Poduromorpha. There is only one seta on the first antennal segment in Neelipleona whereas Entomobryomorpha have a chaetotaxy with more than ten setae. The same kind of setae distribution is found on the second and third antennal segments. The second antennal segment bears from ten to 13 setae in most of Poduromorpha (including *Triacanthella*), with the exception of Onychiurinae, which have 15 to 17 setae. The third antennal segment bears from 21 to 22 setae in Onychiurinae and *Triacanthella*, and from 17 to 19 setae in the other Poduromorpha.

The sense organ of the third antennal segment is found in most Collembola. It is formed by five sensilla: two internal sensilla, two guard sensilla (one dorsal, one ventral), and one small ventral sensillum. These sensilla are accompanied by guard setae. Guard sensilla bend in the same direction in Hypogastruridae, and one against another in Tullbergiinae. It has to be said that tribes of Tullbergiinae have been defined according to the number of guard sensilla (Luciáñez & Simón, 1993). However, according to their phylogenetic analyses, the three tribes were found to be paraphyletic. In Onychiurinae, Tetrodontophorinae and Isotogastruridae, the integumental papillae protect the sensilla of the third antennae sensory organ. In Tullbergiinae, the same structure is found but is not as developed as in Onychiurinae and Tetrodontophorinae.

A typical fourth antennal segment of Poduromorpha bears many sensilla, a subapical vesicle, a subapical organite and a dorso-external microsensillum. These sensillary structures can be developed or sometimes absent. The microsensillum can be located in the distal third portion of the fourth antennal segment, in the basal third portion or it can be absent. Another way to describe the position of the microsensillum is to consider its proximity to the subapical organite. Different nomenclatural systems for the sensilla of the fourth antennal segment have been proposed for different groups: Neanurinae (Deharveng, 1981a), Tullbergiinae (Rusek, 1976), the genus *Ceratophysella* (Yosii, 1962) and the genus *Anurida* (Babenko, 1997; Fjellberg, 1985a – both confused sensilla f with c, g with d, c with e and e with f), the genus *Willemia* (Arbea & Jordana, 1986; Fjellberg, 1994; Potapov, 1994) and for *Xenylla jocquei* André, 1988 (André, 1988). To date, no comprehensive system of nomenclature, which would indicate homologies, has been proposed. Table 5 summarizes the possible homologies for

sensilla .... ●
ordinary seta ....②
seta i .... +
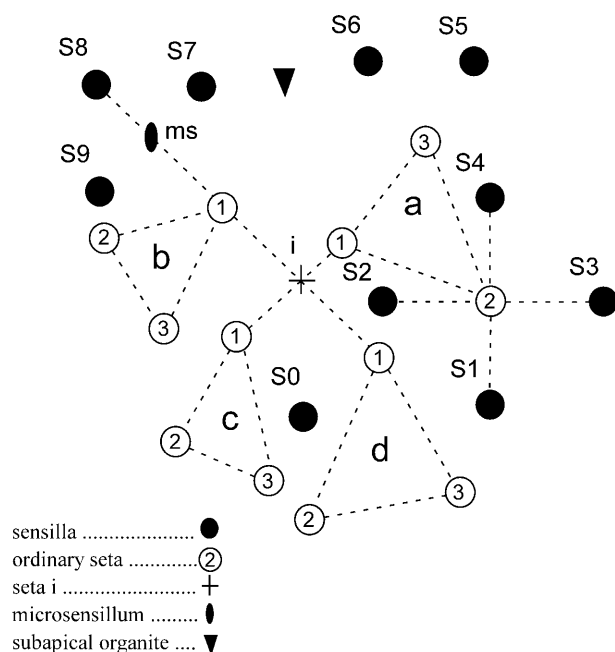microsensillum .... ●
subapical organite .... ▼

Fig. 5. Two-dimensional hypothetical scheme of a left fourth antennal segment of a Poduromorpha.

sensilla of the fourth antennal segment between the different groups and a proposition for a unified system.

Seta x (Yosii, 1962) was named i by Deharveng (1981a), m by Fjellberg (1985a) and ad3 by André (1988). Microsensillum f (Rusek, 1976) was named Se by Deharveng (1981a), s by Fjellberg (1985a), and wa4 by André (1988).

Homologies for sensillary structures of fourth antennal segment were established using the connections principle (Geoffroy Saint-Hilaire, 1818) with 4 main landmarks:

1. subapical organite;
2. dorso-external microsensillum ms;
3. seta i (acute seta, thinner and shorter than the other ordinary setae);
4. position of ordinary setae (in 4 triangles a, b, c, and d made of 3 setae a1, a2, a3, b1, b2, b3, c1, c2, c3, d1, d2 and d3 (Deharveng, 1981a); named daζ, dp3ζ, d4ζ,

ad4ζ, al2ζ, alζ, ad2ζ, -, ad1ζ, d2ζ, d1ζ, dp1ζ respectively in the nomenclature of André (1988).

Some examples of position are given here: sensillumS7 (= b = e3 = wa3) always located between the subapical organite (= wa1) and the microsensillum (= ms = wa4); dorso-external microsensillum located between S7 and S8; seta i located between the microsensillum or sensilla S7 and S2; a2 located at the intersection of segments [S1-S4] and [S2-S3]; S8, microsensillum, b1 and i in alignment, i at the intersection of segments [a1-c1] and [b1-d1] with a1-c1 < b1-d1 and i closer to a1 than c1; S2 located between a1 and d1. See Fig. 5 for a theoretical scheme of fourth antennal segment. Compared to this basic scheme, the microsensillum is located under the subapical organite in Tullbergiinae and is generally located at the base of fourth antennal segment in Onychiurinae. The unified nomenclature proposed here for the Poduromorpha with the exception of Onychiurinae and Tetrodontophorinae is based on the nomenclature proposed by Deharveng (1981a) for Neanurinae only. Sensilla S0 (= D) and S9 (= e1 = se1 = wa5) were added to sensilla S1 to S8 proposed by Deharveng. There are ten sensilla as a maximum, besides any plurichaetosis (Fig. 5):

1. Dorso-external sensilla: S7, S8, and S9;
2. Dorso-internal sensilla: S0, S1, S2, S3, S4, S5, and S6.

A very stable chaetotaxic scheme is observed in all the Neanurinae (Fig. 6A), with 8 sensilla S1, S2, S3, S4, S5, S6, S7, and S8; the microsensillum is absent (Deharveng, 1981a). Caputanurinae show a very close structure with six sensilla S1, S2, S3, S4, S7, and S8 but without S5 and S6 (Fig. 6B). The same chaetotaxy is found in the genera *Friesea* (Fig. 6C), *Pseudachorutes* (Fig. 6D), *Stachorutes* Dallai, 1973, *Pratanurida* Rusek, 1973, *Pseudachorutella* Stach, 1949, *Cassagnaudina* Massoud, 1967, *Gastranurida* Bagnall, 1949, *Micranurida*, and *Rusekella* Deharveng, 1982 (in the latter two genera S2 is lacking). This six-sensilla scheme is observed in most of the species of the genus *Anurida*. However, some species of that genus possess a secondary plurichaetosis of the sensilla (one to four sensilla) that is located between sensilla S7

Table 5. Correspondences between existing systems of nomenclature for sensilla of fourth antennal segment and proposition for a unified system.

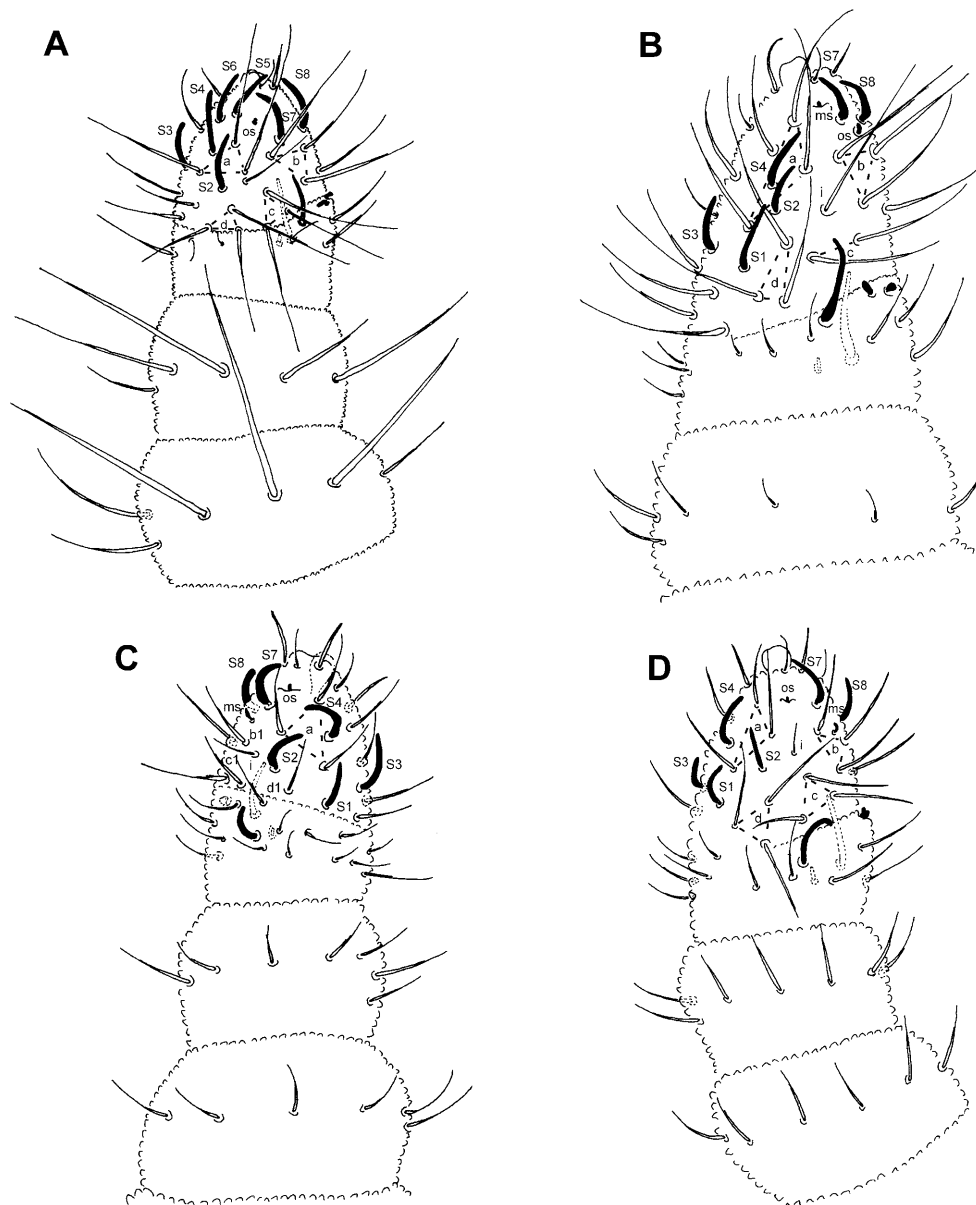| Deharveng, 1981b	Fjellberg, 1985a; Babenko, 1997	Yosii, 1962	André, 1988	Arbea & Jordana, 1986	Potapov,1994	Rusek, 1976	Unified system
Neanurinae	*Anurida*	*Ceratophysella*	*Xenylla jocquei*	*Willemia*	*Willemia*	Tullbergiinae	Poduromorpha
–	–	D	–	–	–	–	S0
S1	F	E	–	si1	i1	e	S1
S2	E	C	–	sd	d	–	S2
S3	D	G	wp2	–	–	–	S3
S4	C	F	wp1	si2	i2	c	S4
S5	–	–	–	–	–	–	S5
S6	–	–	–	–	–	–	S6
S7	B	B	wp3	se3	e3	b	S7
S8	A	A	wa2	se2	e2	a	S8
–	–	–	wa5	se1	e1	d	S9

Fig. 6. Antenna. A – *Neanura muscorum* (Neanuridae: Neanurinae); B – *Caputanurina turbator* (Neanuridae: Caputanurinae); C – *Friesea truncata* (Neanuridae: Frieseinae); D – *Pseudachorutes parvulus* (Neanuridae: Pseudachorutinae).

and S8 and sensilla S2 and S4 (for example in *A. kolymensis* Tshelnokov, 1988, *A. parapapillosa* Tshelnokov, 1988, *A. caprariensis* Dallai, 1969, *A. thalassophila* (Bagnall, 1939)).

Morulinae possess a chaetotaxy of sensilla which are not or only slightly distinct from ordinary setae (Deharveng, 1981a).

Important variations are observed in Odontellidae with plurichaetoses, mostly on the dorso-external side, or reductions. *Xenyllodes* Axelson, 1903 (Fig. 7A) and *Superodontella* Stach, 1949 possess sensilla S7, S8, and S9, the latter being relatively basal. Four other sensilla are found: S1, S2, S3, and S4 with slightly different positions in comparison to the other groups: S1 is slightly higher and more external, S3 has a more internal position and S4 is located a more interno-basally on the segment [a2-S3] and S2 positioned higher up under the subapical organit.

Compared to other families, it appears that sensilla S1, S2, and S4 rotated around the ordinary seta a2 clock-wise in a left-antennae, and S3 was pushed internally by S4 coming. Migration of these sensilla is perhaps correlated with the shortening of the basis of the fourth antennal segment (which causes the conical shape of the antennae). Another hypothesis would be that S3 (S4 in the previous hypothesis) does not really move and S4 (S3 in the previous hypothesis) migrates further, on the internal side. Both hypotheses require a rotation around ordinary seta a2.

Brachystomella parvula Schäffer, 1896 possess six sensilla S1, S3, S4, S7, S8, and S9; S2 seems to be absent.

The genera *Ceratophysella* (Fig. 7B) and *Schaefferia* Absolon, 1900 (Hypogastruridae) have sensilla S0, S1, S2, S3, S4, S7, and S8. Some species show variations, namely reductions (particularly the absence of S0) and
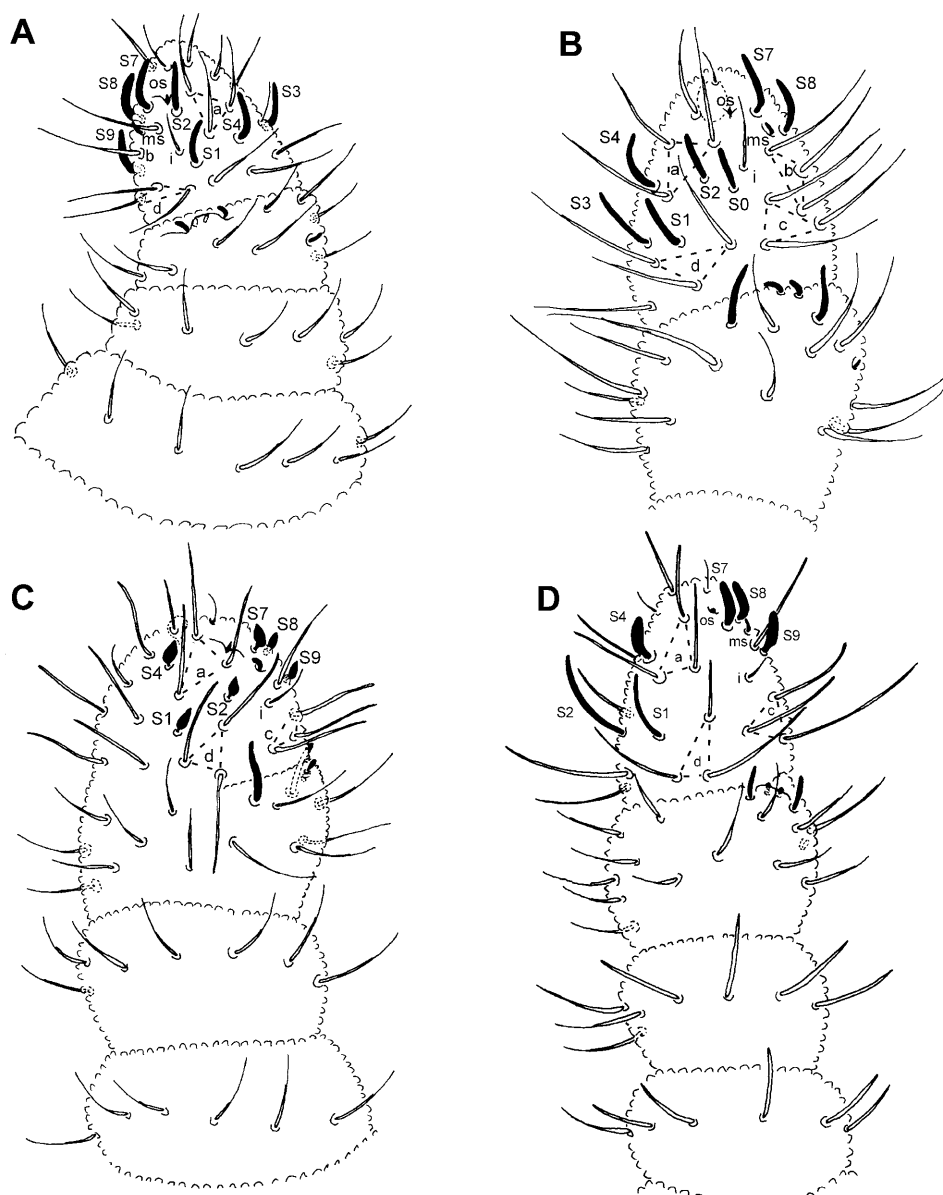
395

Fig. 7. Antenna. A – *Xenyllodes armatus* (Odontellidae); B – *Ceratophysella gibbosa* (Hypogastruridae); C – *Willemia denisi* (Hypogastruridae); D – *Xenylla grisea* (Hypogastruridae).

plurichaetoses of the dorso-internal side of antennae. Sensilla S1, S2, S3, S4, S7, S8, and S9 are present in *Hypogastrura vernalis* (Carl, 1901). The other species of the genus *Hypogastrura* have the same scheme or slight variations from this scheme, with reductions in the number of sensilla or secondary plurichaetoses. The genera *Mucrella* Fjellberg, 1985, *Pseudacherontides* Djanashvili, 1971, and *Acherontiella* Absolon, 1913 possess the same scheme (presence of sensilla S7, S8, and S9) with a reduction of dorso-internal setae. The genus *Willemia* (Fig. 7C) possesses sensilla S1, S2, S4, S7, S8, and S9, with secondary losses in some species (D'Haese, 1998, 2000; D'Haese & Weiner, 1998). In the genus *Xenylla* (Fig. 7D) sensilla S4, S7, S8, and S9 are very thick, and sensilla S1 and S3 are very thin. The latter two are absent in some species, or more difficult to distinguish from ordinary setae. The same chaetotaxic scheme is

found in the genus *Paraxenylla*, with sensilla S1 and S3 absent or indistinct from ordinary setae. In *Microgastrura sensiliata* Jordana, 1981 (Fig. 8A), sensilla S1, S2, S3, S4, S7, and S8 are present. Sensillum S3 has a more internal position in comparison to the other Hypogastruridae and S4 is located lower down on the axis [a2-S3]. In the other species of the genus, three dorso-external sensilla are found, including S9; its absence in *M. sensiliata* is probably a secondary loss.

Sensilla chaetotaxy of the fourth antennal segment of Tullbergiinae (Fig. 8B) is difficult to compare with sensilla chaetotaxy of Hypogastruridae, Odontellidae, Brachystomellidae, and Neanuridae. Five well-differentiated sensilla are found in Tullbergiinae: two dorso-externals and three dorso-internals. These could be homologous with sensilla S8 and S9 on one side and sensilla S1, S2, and S4 on the other side. It is worth noting that the micro-
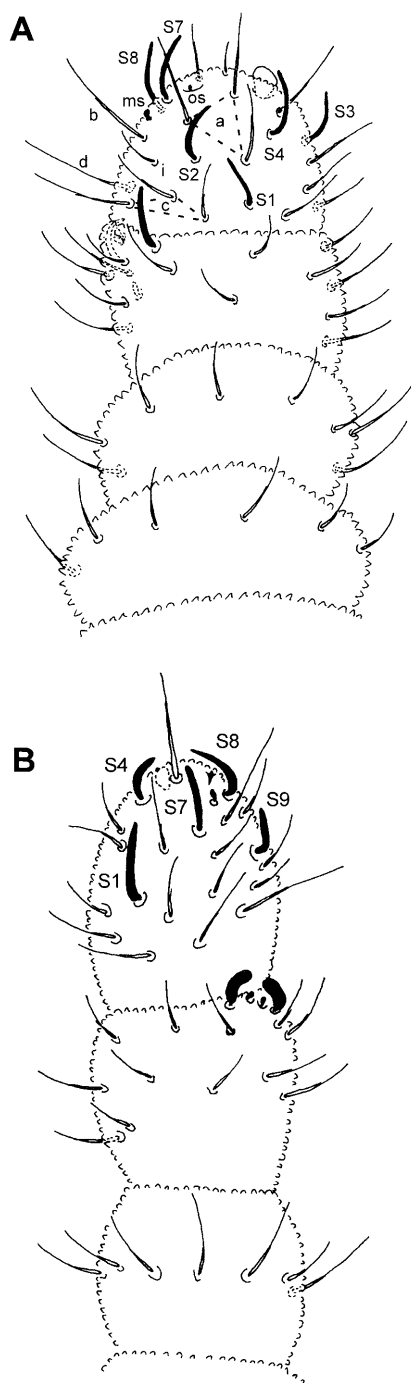
Fig. 8. Antenna. A – *Microgastrura sensiliata* (Hypogastruridae); B – *Mesaphorura macrocheta* (Onychiuridae: Tullbergiinae).

rura Weiner & Najt, 2000), however it was not possible to establish homologies.

Podura aquatica possesses a fourth antennal segment chaetotaxy very similar to Hypogastruridae, but the sensilla are not distinct from the ordinary setae.

Frequently, secondary losses or plurichaetoses of sensilla are observed independently in different groups.

Thorax

The prothorax is well developed in Poduromorpha and bears setae. It is well differentiated except in *Caputanurina* where it merges with the head (this is a diagnostic character of the genus); this merger is less complete in the other Caputanurinae. In Isotogastruridae, the prothorax is well developed but does not bear setae. The number of rows of setae and number of setae within these rows vary according to the different groups: 1 row of setae in Tullbergiinae, Hypogastruridae, Odontellidae, Brachystomellidae, and Neanuridae, 2 rows in Onychiurinae, more than 2 rows in *Tetrodontophora bielanensis*.

An organ present on the prothorax of Collembola's embryos may help hatching (Jura, 1967; Philiptschenko, 1912; Tamarelle, 1971, 1981; Thiegs, 1942; Wheeler, 1893). The organ has been found in the embryos of all Collembola studied thus far (Jura & Krzysztofowicz, 1978). This organ can persist in the first instar. According to Deharveng (1983), this dorsal organite of the prothorax would be characteristic of the first instar of Neanurinae, but was observed in Caputanurinae (*Caputanurina turbator* Najt & Weiner, 1992) and Brachystomellidae (Najt & Weiner, 1992). According to my own observations, this structure is present in the first instar of *Onychiurus ambulans*, *Mesaphorura macrocheta*, *Xenylla grisea*, *Neanura muscorum*, and *Folsomia candida* (Entomobryomorpha, Isotomidae). Actually, this organite is widely present in Entomobryomorpha (Judith Najt, pers. com.). It is probably present in Collembola as a whole. The prothorax is highly reduced and does not bear setae in Entomobryomorpha, Symphypleona, and Neelipleona. In the first instar of *Folsomia candida*, the second thoracic segment bears one more row of setae than the third thoracic segment. More generally, the mesothorax bears additional rows of setae on the anterior part compared to the metathorax in the genera *Tetracanthella*, *Isotomiella* Bagnall, 1939, and probably in every Entomobryomorpha. The mesothorax and metathorax have an almost identical chaetotaxy in Poduromorpha. Additional rows of setae on the mesothorax may have originated ontogenetically from the prothorax. Some authors believe that the prothorax tergum is fused with the mesothorax (e.g., Denis, 1949).

The number of rows of setae on the meso-, and metathorax is variable among the different families. In Poduromorpha, two to five rows are observed, and more than five in Entomobryomorpha. Microsensilla on the metathorax are present in Onychiurinae (with few exceptions like *Micraphorura pieninensis* Weiner, 1988), Tetrodontophorinae, Tullbergiinae, and Odontellidae. Microsensilla are absent in Hypogastruridae, Brachystomellidae, and Neanuridae. Thoracic sternites can bear setae. However, that character is probably not very informative for

sensillum is located under the subapical organite, which has migrated to the external side of the antennae (the microsensillum is located between S7 and S8 in Hypogastruridae, Odontellidae, Brachystomellidae, and Neanuridae). It was not possible to identify seta i, as it is either absent or indistinct from the other ordinary setae. In Onychiurinae and Tetrodontophorinae the sensilla are indistinguishable when viewed under a compound microscope. In some species, the sensilla are visible (as in *Psyllapho-*

dorsal side

anterior side

- ordinary setae • - claw
- tenant hair ◉
- seta absent on tIII (•) - unguiculus ◊

Fig. 9. Complete scheme of tibiotarsal chaetotaxy in Poduro-morpha, right leg (after Deharveng, 1983).

Poduromorpha as a whole since those setae can be present or absent in the same genus.

Legs

Yosii (1962), Lawrence (1977), Deharveng (1983), and Nayrolles (1988) studied the chaetotaxy of tibiotarsi. In the present work, I will use the nomenclature proposed by Deharveng, which was based on the work of Lawrence (1977) (see Fig. 9 for a theoretical scheme of tibiotarsal chaetotaxy). This nomenclature has already been used to describe the tibiotarsi in Tullbergiinae (Fjellberg, 1991a), and in the genus *Willemia* (Fjellberg, 1991b).

Onychiurinae and Tetrodontophorinae have a complete tibiotarsal chaetotaxy, with the presence of the rows A, B, C, and T as well as seta Y, which is absent in the other groups (Figs 10 & 11). This chaetotaxic scheme can be concealed by a secondary plurichaetosis (*Tetrodonto-phora*). Comparatively, other Poduromorpha have a less abundant chaetotaxy with row C and seta Y lacking. Hypogastruridae, Neanuridae, and Poduridae (*Podura aquatica*) are typical of this model, with generally 19 setae on tibiotarsi I and II, and 18 setae on tibiotarsi III split up into rows T, A, and B. Seta B7 is lacking on tibi-otarsi III, except in *Podura aquatica* which possesses 19 setae on every tibiotarsi. Secondary losses are frequently observed in different groups, for example setae T2, and T3 are lacking in *Willemia denisi*, species of that genus have 17, 17, 16 setae at least (see Fig. 11). Rows A, and B can be relatively complete in Tullbergiinae (Fig. 10) and row T is always absent. Unguiculus (empodial appendage) is generally present in Onychiuridae, Odon-tellidae, and Hypogastruridae, but is often absent, particu-larly in the genera *Podura*, *Xenylla*, and *Paraxenylla* (Figs 11B, 11F & 11G). It is always absent in Neanuridae, and Brachystomellidae (Massoud, 1967), see Fig. 12. Generally, in Neanuridae and Brachystomellidae, rows T, A, and B are relatively complete and seta M is

present, with the exception of Frieseinae in which M is always absent (Fig. 12) but in *Friesea* species of the south hemisphere (Deharveng & Bedos, 1991; Greenslade & Deharveng, 1997).

Leg chaetotaxy is fixed (no addition of setae during the development) from the first instar onward in Tullbergii-nae, Odontellidae, Hypogastruridae, Brachystomellidae, and Neanuridae. During postembryonic development, setae are added on the legs in Onychiurinae (observations based on cultures of many species: *Onychiurus*, *Kalapho-rura* Absolon, 1901, *Protaphorura* Absolon, 1901 etc.). Setae are also added during the development in non-poduromorphan Collembola: in Symphypleona (Nayrolles, 1988), and more generally in Entomobryo-morpha as a whole (cf. Fig. 13 for Isotomidae – personal observations).

Tibiotarsi have a decreasing antero-posterior gradient of the number of setae in Neanuridae, Hypogastruridae, and Onychiuridae (except *for Protaphorura*): seta B7 is absent on the third pair of tibiotarsi. It is the opposite in Isotomidae and Symphypleona. The tibiotarsi and femora also present a decreasing antero-posterior gradient of the number of setae in almost all Poduromorpha. The same applies for trochanters, with the exception of Onychi-urinae with a postero-anterior gradient. In every Poduro-morpha, the first and second subcoxae have a decreasing postero-anterior gradient of the number of setae. Coxae have a number of setae: leg I < leg II = leg III in every Poduromorpha except in Onychiuridae and *Podura aquatica* in which leg I < leg II < leg III.

In Poduromorpha and Isotomidae, the number of setae per row is seven (Deharveng, 1983). Eight setae per row are observed in Symphypleona (Nayrolles, 1998), and six in Neelipleona. The number of rows is fixed according to the different groups: four (rows T, A, B, and C) or less in Poduromorpha and Isotomidae (Deharveng, 1983), and five (rows I to V) in Symphypleona in first instar (Nay-rolles, 1998).

The pretarsus terminates by a claw with three lamellae (these can also bear teeth) and an empodial tubercle, which bears the unguiculus. The unguiculus is formed by four lamellae in Symphypleona and Entomobryidae (Christiansen, 1965), three in Isotomidae and Tomo-ceridae and only one in Hypogastruridae.

The relative proportions of the different parts of the body are variable between the different groups of Collem-bola: Poduromorpha are relatively stocky, whereas Ento-mobryomorpha and Symphypleona possess elongate or very elongate appendages relatively to the body. This could be related to the habitat: generally edaphic in the former, more epigeic in the latter two. The legs are short compared to the length of the body in Poduromorpha, whereas they are long in Entomobryomorpha, Neeli-pleona, and Symphypleona. The ratio of tibiotarsus to claw reflects this: the ratio is near one in Poduromorpha, much higher in the others.

Abdomen

Entomobryomorpha and Poduromorpha possess an elongate and well-segmented body. On the contrary, the
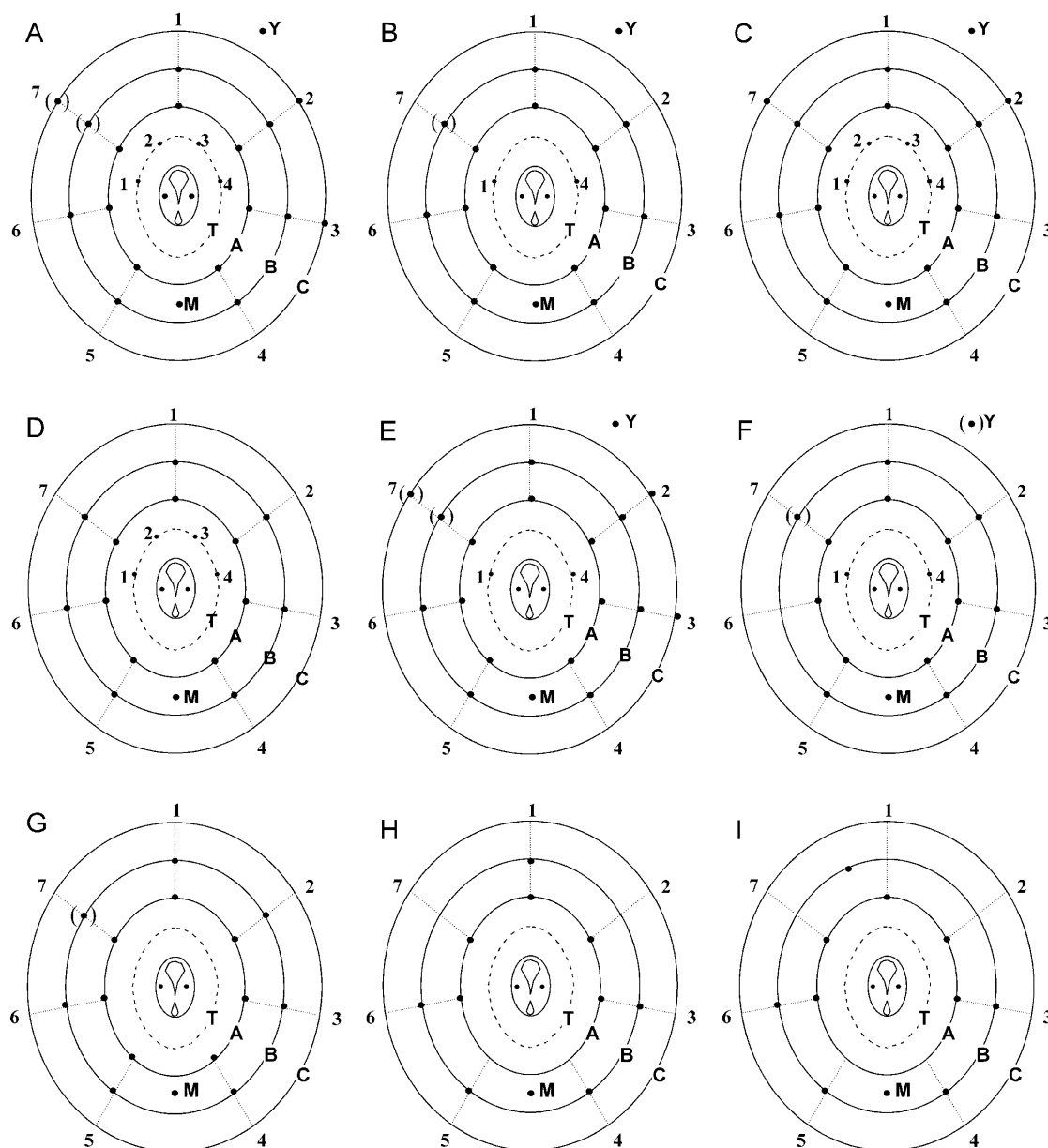
Fig. 10. Tibiotarsal chaetotaxy. A – *Kalaphorura paradoxa* (Onychiuridae: Onychiurinae); B – *Micraphorura absoloni* (Onychiuridae: Onychiurinae); C – *Protaphorura armata* (Onychiuridae: Onychiurinae), first and second tibiotarsi; D – *Protaphorura armata* (Onychiuridae: Onychiurinae) first instar; E – *Onychiurus ambulans* (Onychiuridae: Onychiurinae); F – *Onychiurus ambulans* first instar; G – *Tullbergia bisetosa* (Onychiuridae: Tullbergiinae); H – *Mesaphorura macrocheta* (Onychiuridae: Tullbergiinae); I – *Scaphaphorura arenaria* (Onychiuridae: Tullbergiinae). Notice the presence of row C and seta Y in Onychiurinae and the absence of seta Y, row C, and row T in Tullbergiinae.

Symphypleona and Neelipleona are globular. The Symphypleona have a characteristic globular shape formed by the enlargement and fusion of the posterior thoracic and anterior abdominal segments forming the large abdomen, and the last abdominal segments are distinct, forming the small abdomen (e.g., Betsch, 1980). On the other hand, the globular body of Neelipleona is one whole structure and is mainly the result of the enlargement of the thoracic segments (Massoud, 1971a).

Poduromorpha have well-developed and sub-equal abdominal segments. Entomobryomorpha present fusions of some of the segments: fusion of fourth and fifth abdominal segments or fusion of the fourth, fifth, and sixth abdominal segments. The fourth abdominal segment is normally developed in Poduromorpha, Isotomidae and Tomoceridae, and longer in other Entomobryomorpha, Symphypleona, and Neelipleona (Massoud, 1971a).

Dorsal chaetotaxy is described here with the classic system with three rows of setae: anterior (a), middle (m), and posterior (p) proposed by Yosii (1956), and developed for Hypogastruridae by Cassagnau (1974) and Grow & Christiansen (1974), and applied to Poduromorpha as a whole. Fjellberg (1985b) established the correspondences between the classic rows a, m, and p system and the system of Di, De, Dl, and L that Cassagnau (1980) and Deharveng (1979b; 1983) developed for Neanurinae.
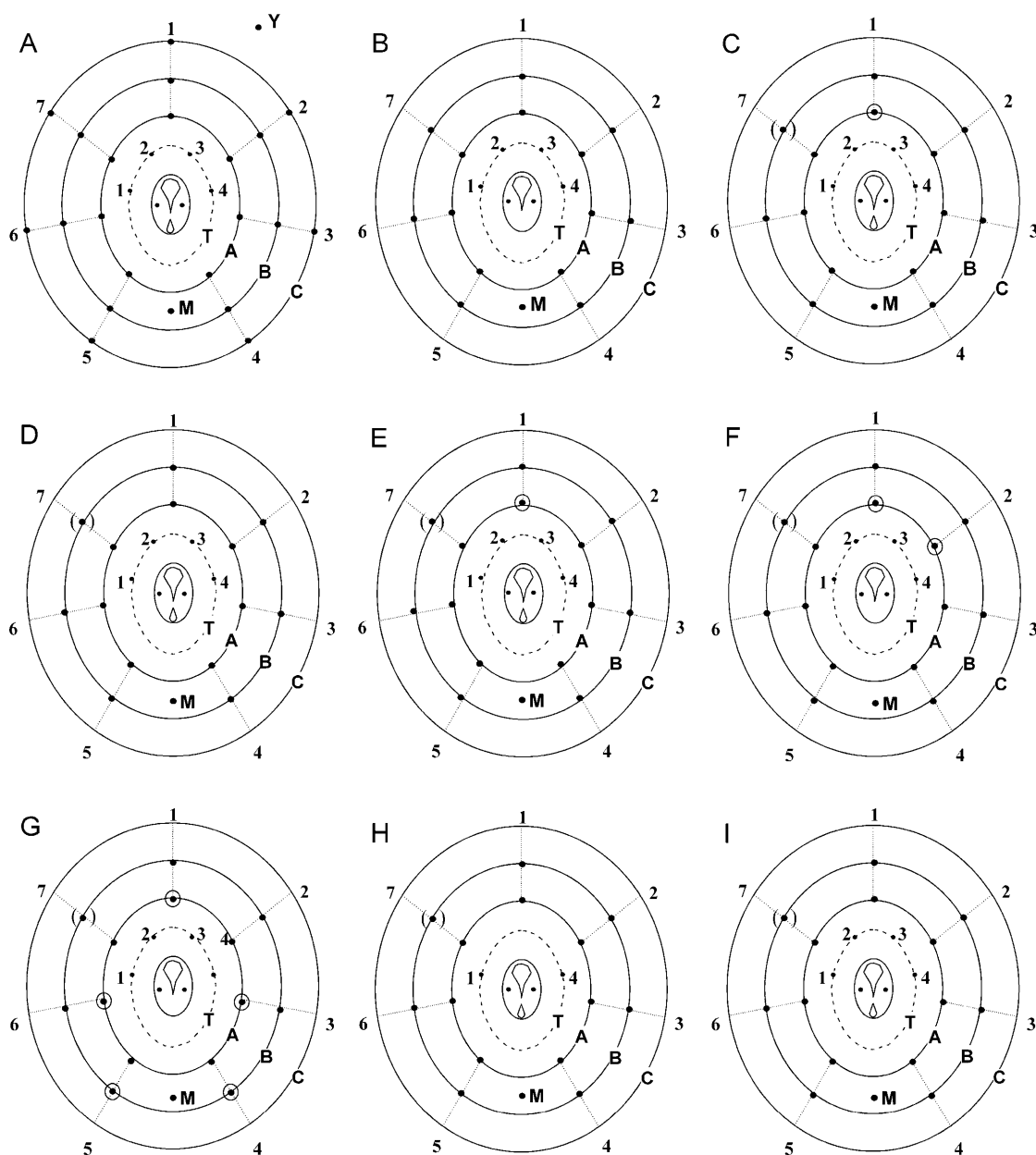
Fig. 11. Tibotarsal chaetotaxy. A – *Lophognathella choreutes* (Onychiuridae: Tetrodontophorinae); B – *Podura aquatica* (Poduridae); C – *Triacanthella perfecta* (Hypogastruridae); D – *Ceratophysella gibbosa* (Hypogastruridae); E – *Hypogastrura vernalis* (Hypogastruridae); F – *Xenylla tullbergi* (Hypogastruridae); G – *Paraxenylla affiniformis* (Hypogastruridae); H – *Willemia denisi* (Hypogastruridae); I – *Microgastrura sensiliata* (Hypogastruridae). Notice the presence of row C, and seta Y in Tetrodontophorinae, their absence in Hypogastruridae and Poduridae.

On the ventral side, the unpaired setae chaetotaxy is of interest. They are present in Onychiuridae but seem to be absent in Hypogastruridae, Odontellidae, Brachystomellidae, and Neanuridae. The number of ventral setae rows is more important in every segment in Onychiurinae, and Tetrodontophorinae compared to the other Poduromorpha. One or two unpaired setae are found on the sixth abdominal segment in *Triacanthella*, every Tullbergiinae, and most of Onychiurinae. Ventrally, between the anus and the anal spines, there are a maximum of three unpaired setae (the most distal seta can be transformed to an unpaired anal spine). There are no unpaired setae on sixth abdominal segment in Neanurinae. On the other

hand, there are three unpaired setae between the anal spines and anus and two unpaired setae on the tergum in Tullbergiinae. Anal spines can be present or absent. However, this character is highly homoplastic in Poduromorpha since both character states can be found in the same genus (e.g., in the genus *Willemia*, D'Haese, 2000).

Anal valves. Within Poduromorpha, two types of anal valves can be found:

1. The three valves are sub-equal, and non-overlapping; the supra-anal valve has a convex edge (Fig. 14A). These kinds of anal valves are found in Onychiurinae,
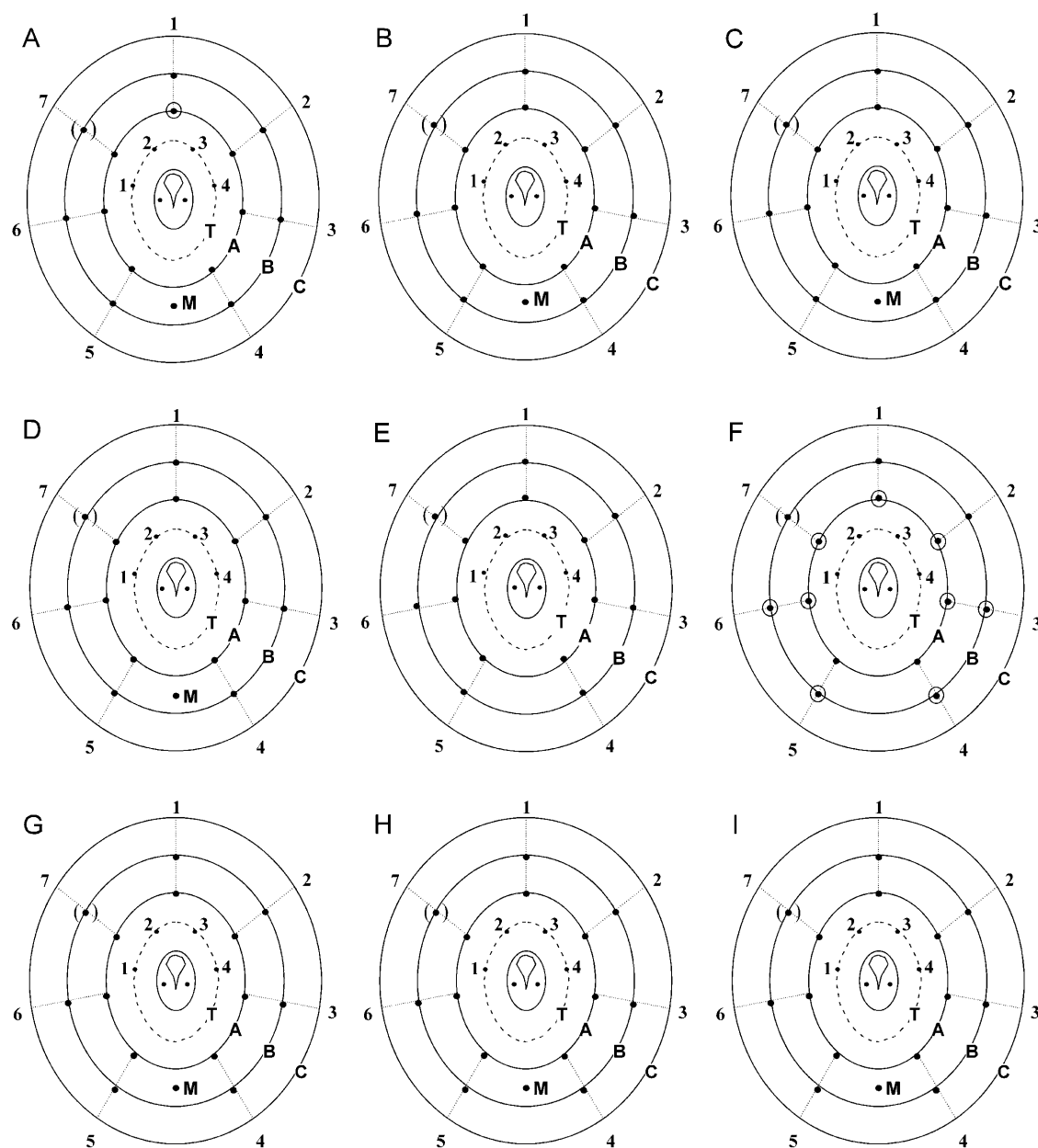
Fig. 12. Tibotarsal chaetotaxy. A – *Brachystomella parvula* (Brachystomellidae); B – *Anurida granaria* (Neanuridae: Pseudacho-rutinae); C – *Pseudachorutes palmiensis* (Neanuridae: Pseudachorutinae); D – *Pseudanurida sawayana* (Neanuridae: Pseudachoruti-nae); E – *Friesea truncata* (Neanuridae: Frieseinae); F – *Friesea jeanneli* (Neanuridae: Frieseinae); G – *Caputanurina turbator* (Neanuridae: Caputanurinae); H – *Caledonimeria mirabilis* (Neanuridae: Uchidanurinae); I – *Neanura muscorum* (Neanuridae: Neanurinae). Notice the absence of row C, seta Y, and empodial appendage in every Brachystomellidae and Neanuridae and the absence of seta M in Frieseinae.

Tetrodontophorinae, Neelipleona, Symphypleona, and Entomobryomorpha;

2. The paired valves partially overlap the supra-anal valve; the supra-anal valve has an almost straight edge (Fig. 14B). These kinds of anal valves are present in Hypogastruridae, Brachystomellidae, Odontellidae, Neanuridae, and Tullbergiinae. However, in the latter family, the supra-anal valve has a slightly convex edge but is recovered by the two other valves.

Three distinct nomenclatures were proposed to name the setae of paired anal valves: one established for the genus *Willemia* (see Hüther, 1962), one for the sub-family Tullbergiinae (see Rusek, 1976), and the last one for the genus *Onychiurus* (Yoshii, 1996). Anal valve chaetotaxy in Poduromorpha is quite homogeneous and therefore it is easy to propose homologies between the 3 nomenclatures, and generalized it to all Poduromorpha (see Table 6). Generally 1+1 setae z are present (there can be more in some Onychiurinae) or can be absent. In the same way, 3+3 setae hr are generally found, but some taxa have less. Lawrence (1978) proposed a nomenclature for the setae of the anal valves for Symphypleona (see also Yosii, 1969). It should be possible to establish
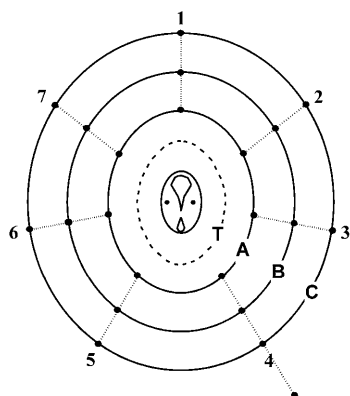
Fig. 13. Tibotarsal chaetotaxy of an Isotomidae (*Folsomia candida*) first instar.

homologies for the chaetotaxy of the anal valves of the four order of Collembola (Poduromorpha, Entomobryomorpha, Symphypleona, and Neelipleona). However, these comparisons are beyond the scope of the present work. Strong plurichaetoses can conceal the described chaetotaxic scheme (*Tetrodontophora, Triacanthella...*), making it difficult or impossible to establish homologies. This is also applicable to the chaetotaxy of the whole body.

Ventral tube. The ventral tube, or collophore, is formed by a pair of vesicles primitively derived from a pair of primitive appendages (the collophore is probably homologous to the coxae). The ventral tube is located on the sternum of the first abdominal segment, at the posterior end of the linea ventralis. It plays an important role in
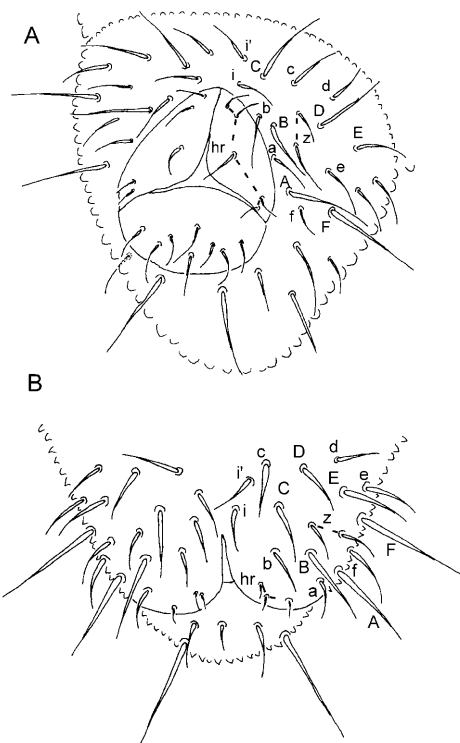
Fig. 14. Anal valves. A – *Kalaphorura paradoxa* (Onychiuridae: Onychiurinae); B – *Friesea truncata* (Neanuridae: Frieseinae).

TABLE 6. Correspondence between existing systems of nomenclature for setae of the anal valves.

Hüther, 1962	Rusek, 1976	Yoshii, 1996
A	l10	b-2
a	l9	b-1
B	l5	b-0
b	l3	b-1
C	l2	–
c	l1	–
D	l7	–
d	l11	–
E	l12	–
e	l14	–
F	–	–
f	l13	–
hr	l3'	a-1
hr	l4	a-0
hr	l6	a-1
z	l8	–
i	l3'	b-2
i'	l2'	–

maintenance of water and ion balance. Urine is discharged from the labial nephridia (ventral side of the head) into the linea ventralis and carried to the ventral tube by capillary action (Eisenbeis, 1974; Rusek, 1987; Verhoef et al., 1979; Verhoef et al., 1983). Fluid and salt are then exchanged at the apical part of the organ (water is reabsorbed). The coronal section of the collophore is oval in Poduromorpha and circular in Symphypleona and Entomobryomorpha (Massoud, 1967). In other words, the ventral tube is a short oval-shaped structure in Poduromorpha, whereas it is a rather elongate cylinder in Symphypleona, Neelipleona, and Entomobryomorpha. Symphypleona have apical eversible vesicles on the ventral tube that can be smooth or covered with hemispherical papillae (Betsch, 1980).

In Hypogastruridae, Odontellidae, and Neanuridae, three kinds of ventral tube chaetotaxy are found (Deharveng, 1983):

1. 3+3 setae: td1, td2, and tp1 in most Brachystomellidae and Odontellidae;
2. 4+4 setae: td1, td2, td3 (sometimes td4 also), and tp1 in Neanurinae, Caputanurinae, and *Caledonimeria mirabilis* Delamare Deboutteville & Massoud, 1962;
3. 4+4 setae: td1, td2, tp1, and tp2 in Hypogastruridae, some Pseudachorutinae, Frieseinae, and Morulinae.

Tullbergiinae have the same ventral tube chaetotaxy as Hypogastruridae. Frequently in Onychiurinae plurichaetoses are observed: row td comprising more than 4+4 setae, and row tp more than 2+2 setae. Distal setae td are homologous with "subapical setae" described by Pomorski (1996) in Onychiurinae, and proximal setae tp are homologous with "additional setae".

Tenaculum and furcula. The tenaculum is located on the third abdominal sternum. It is formed of a corpus and

two rami bearing a variable number of teeth on the outer side. The tenaculum holds the furcula against the abdomen. In Poduromorpha, the corpus is rudimentary, and does not bear setae unlike Symphypleona and Entomobryomorpha, which possess a well-developed corpus with setae.

Reductions of furcula and retinaculum are largely correlated.

Furcula is the jumping organ characteristic of Collembola. It can either be well developed as in the more epigeic species, reduced or completely absent (trend in the more edaphic species). From an evolutionary point of view, the furcula is probably the result of the partial merging of a pair of primitive appendages located on the sternum of the fourth abdominal segment. The fusion of the proximal region formed the manubrium; the distal portions remain free, forming the dentes, with each one ending with a mucro. The degree of development of the furcula, the number of setae on the manubrium and on the dentes, as well as the shape of the mucro are variable characters among the species and are widely used in taxonomy.

REMARKS ON FIRST INSTAR

Postembryonic development in Arthropleona always involves the addition of setae, never their loss (Deharveng, 1983; Thibaud, 1970). Therefore, the first instars are fundamental to understand structures that can be difficult to interpret in adults (Collazo, 2000), like, for example, in case of plurichaetosis (Szeptycki, 1972).

The first instar in the genus *Onychiurus* has relatively few setae, and its simple chaetotaxy appears to be very similar to the chaetotaxy of adult Hypogastruridae. A large number of setae appear when molting during postembryonic development. Pomorski (1996) described first instars of many species of Onychiurinae. Observations made on other species of the same sub-family for this study are in complete agreement with Pomorski's results.

Contrary to Onychiurinae, the first instar of *Neanura muscorum* has relatively complete chaetotaxy, which is almost identical with an adult one (labium, head, body, and all segments of the leg). However, some setae are not present in first instar, e.g. i' on the anal valves. The only present sensilla on the antennae are S5 and S6. Furthermore, in addition to present microsensillum, sensilla are always absent in first instar in the other Poduromorpha. Similar conclusions on chaetotaxy of the first instar were reached for *Neanura tatricola* Massoud, 1967 (Gruia, 1974) and *Thaumanura ruffoi* Dallai, 1969 (Dallai & Martinozzi, 1980). This may be applicable to the entire sub-family Neanurinae. The first instar of *Caputanurina turbator* (the Caputanurinae are phylogenetically close to Neanurinae, D'Haese, 2003) was described (Najt & Weiner, 1992). This group shows relatively complete chaetotaxy, but not as complete as in Neanurinae. For example, sensilla are absent on the fourth antennal segment in the first instar.

Thibaud has described the first instar of some species of Hypogastruridae, particularly in the genera *Ceratophysella*, *Schaefferia*, *Mesogastrura* Bonet, 1930, *Mesachorutes* Absolon, 1900, and *Typhlogastrura* Bonet, 1930 (Thibaud, 1967; Thibaud, 1969; Thibaud, 1970). Weiner (1989a) described the first instar of *Ceratophysella mosquensis* (Becker, 1910). These studies and observations made for the present work indicate that the first instar chaetotaxy of a Hypogastruridae is more complete than in Onychiurinae and less so in Neanuridae. In Hypogastruridae, the trochanters, femurs, and tibiotarsi of first instar present the same chaetotaxy as the adults. On the contrary, the proximal segments show an incomplete chaetotaxy. The same results were found for Tullbergiinae confirming observations on *Mesaphorura* and *Fissuraphorura* Rusek, 1991 (Luciáñez & Simón, 1988; Luciáñez & Simón, 1992; Rusek, 1980).

If one confronts the observations on the first instars to the phylogeny of Poduromorpha (D'Haese, 2002, 2003), some interesting conclusions can be drawn. From Onychiurinae to Neanurinae, the chaetotaxy is increasingly complete (compared to the adult) in the first instar. Tullbergiinae, Hypogastruridae and non-neanurinae Neanuridae are intermediate: the first instar chaetotaxy is more complete than that in Onychiurinae but less complete than in Neanurinae. However, the adults have chaetotaxic schemes increasingly paurochaetotic beginning with the Onychiurinae through Tullbergiinae and then Hypogastruridae to Neanurinae. There appears to be a trend in Poduromorpha, which drives the adult descendants to maintain a chaetotaxy similar to the juvenile instars of its ancestor without change of the growing rate and size. In other words, phenomenon of paedomorphosis by neoteny could have been among the driving forces at the origin of diversification within Poduromorpha.

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