1. Introduction

The volume 'Tullbergiidae' presented here is an entirely revised version, updated and translated into English, of the first edition (which appeared as Volume I of the Synopses on Palaearctic Collembola: Tullbergiinae [1994; in German language] by Bettina ZIMDARS and Wolfram DUNGER).

Accepting the proposition of DEHARVENG (2004), the 'subfamily Tullbergiinae' is again elevated to the rank as Tullbergiidae Bagnall, 1947. The diagnoses of species and genera have been completed by our own studies, mainly based on the collections of the Senckenberg Museum of Natural History Görlitz as well as on material kindly lent to us especially by the Museum of Natural History Geneva, Switzerland, the Museum of Natural History Paris, France and by several colleagues (see acknowledgements). We further took into account studies concerning the sexual status of (partly or possibly totally) parthenogenetical species of the Tullbergiidae (ZIMDARS & DUNGER 2000).

The diagnoses of the 18 palaearctic genera (from 31 genera worldwide) and 64 hol- or palaearctic species are based on original material as far as possible. Nevertheless, to a large extent this monography represents a revision of literature data. Occurrence records have been checked concerning their actuality after new descriptions.

Geographically, arctic species are included from Greenland up to north-eastern Asia as well as species from the Chinese and Himalaya regions north of 30 degrees of latitude.

Data available up to the end of 2010 were taken into consideration.

Abbreviations

a 1, 2	= setae 1, 2... of the dorsal anterior rows, counted from the 'middle line'
Abd I –VI	= abdominal tergites I–VI
Abd sternites I –VI	= abdominal sternites I–VI
Ant I–IV	= antennal segments I–IV
Ant III O	= sensory organ of Ant III
Asp	= anal spine(s)
Cl I–III	= claw(s) of leg I–III
l 1, 2	= setae of the anal lobes
l 1', 2'	= setae 1, 2... directly on the lid of the anal lobes
m 1, 2	= setae 1, 2... of the dorsal middle rows, counted from the 'middle line'
mac	= macroseta/-ae
mes	= mesoseta/-ae
mic	= microseta/-ae
ms	= microsensillum/-a
p 1, 2	= setae 1, 2... of the dorsal posterior rows, counted from the 'middle line'
PAO	= postantennal organ
pap	= papilla/-ae
pl 1, 2	= setae 1, 2... of the pleural row
pso	= pseudocellus/-i
pso type I–IV	= types of pseudocelli after WEINER & NAJT (1991)
s, sens	= sensillum/-a
Th I–III	= thoracic tergites I–III
Th sternites I–III	= thoracic sternites I–III
Tita I–III	= tibiotarsus/-i I–III
VT	= ventral tube

2. General description

Tullbergiidae Bagnall, 1947 (sensu DEHARVENG 2004)

Diagnosis

As an again upgraded family, the Tullbergiidae Bagnall, 1947, within the suborder Poduromorpha Börner, 1913, belongs to the superfamily Onychiuroidea Bagnall, 1947, which shows the plesiomorphic characters of having an elongated and segmented body and thorax I being fully developed and bearing dorsal setae. Some parts of the dorsal body show pseudocelli (special thinwalled areas of the cuticle with a surrounding ring of granules).

The Tullbergiidae differ from the other Onychiuroidea (i.e. the family Onychiuridae) by:

– having a mostly shorter and smaller body, i.e. a complete adaptation to an euedaphic life in soil,

– the sensory organ of Ant III (Ant III O) being dorsally without strong conical protecting papillae; bearing 1, 2 or 3 large sensory clubs, one or two of which are bent (in the case of two: towards each other), (1–)2 small sensory rods between the lateral clubs behind a protecting fold (sometimes 2– or 3-partitioned); furthermore bearing with one large sensory club ventrally,

– the presence of special types of pseudocelli restricted to the dorsal side, at the base of antennae, the posterior edge of the head, and at Th I–III and Abd I–V,

– the absence of parapseudocelli (present in Onychiuridae),

– more or less reduced or totally absent empodial appendages and no traces of a furca or retinaculum.
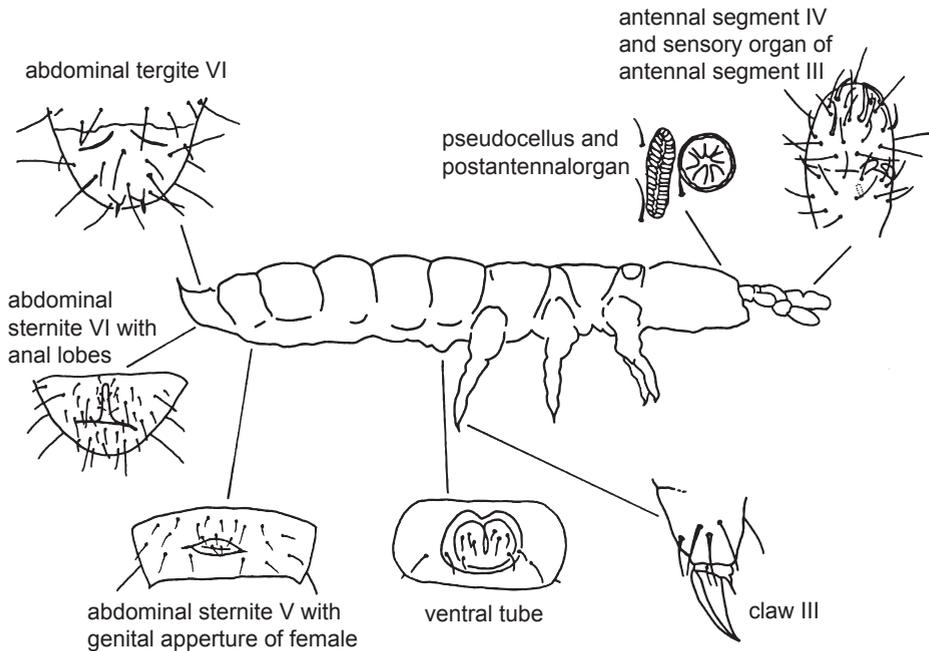
Fig. 1   Habitus of a member of Tullbergiidae with indications of important characters.

Morphological characters of Tullbergiidae (Fig. 1)

– Body extended, slender, with short legs and antennae. Small species, body length mostly between 0.4 and 1.0 mm), few species up to 4 mm (*Tullbergia arctica* Lubbock).

– Eyes never present; integument almost never pigmented (exceptions: *Metaphorura triacantha* Börner: dark blue; *Tasphorura vesiculata* Greenslade & Rusek: lively pink). Very thick cuticular areas often yellowish (e.g. anal spines).

– Integument (cuticula) mostly with fine, equally sized granulae; areas with alternating of coarse and fine granulae mostly on dorsal parts of the last abdominal segments; see Figs 23–24.

– Chaetosis of the body moderately dense, consisting of ordinary macro- and microsetae as well as sensory setae; without supplementary setae additionally to those forming the basic pattern (i.e. no plurichaetosis); see Figs 26–28.

– Sensory organ of Ant III (A III O) dorsally with 1, 2 or 3 thickened sensory clubs, (1) 2 of which are bent towards each other, between them 2 (0–4) small sensory rods, mostly protected by an integumentary fold (sometimes structured into 1–3 lobes); on the ventral side with a single thick sensory club; for details see Figs 2–4.

– Ant IV dorsally with 5 (2–8) thickened subcylindrical sensilla, one ± eversible apical vesicle, one subapical organite and one dorso-external microsensillum; for details see Figs 2–4.

– Postantennal organ (PAO) very variable: mostly elongate with 2 rows of 6–140 vesicles of highly variable shape; for details see Figs 5–15.

– Pseudocelli present in different numbers, but only dorsally: 1+1 on each half of the head; (0) 1 (2) per tergite half (Th I–III and Abd I–V). In general, four morphological types can be discerned, which can be subjected to variations during instar development; for details see Fig. 16.

– Abd VI mostly with 1+1 (rarely 2+2) smooth anal spines (denticulated only in one genus); few species with an unpaired ventral protrusion between the anal spines. On the dorsal side of Abd VI additionally up to six spine-like processes or tubercles can be present. Antero-dorsally on both sides of Abd VI frequently 1+1 crescent-shaped integumental ridges may occur; for details see Figs 17–24.

– Furca and retinaculum always absent; sometimes some ventral setae can be assigned to the furcal region.

– Tibiotarsi usually only with simple setae; claws mostly without teeth; empodial appendage normally strongly reduced or absent; for details see Figs 39, 48.

– Ventral tube with mostly 6+6 setae (exceptionally fewer); for details see Fig. 35.

Description of important characters

Antennae

The length of the antennae varies between half the length of the head diagonal and up to 10–20% longer. Antennae are always subdivided into 4 segments. The chaetosis of antennal segments I and II normally consists of 7 (I) or 11 (II) setae.

The third antennal segment (Ant III) dorso-apically bears the Ant III sensory organ ('Ant III O'), consisting of 1, 2 or 3 ± thick, subcylindrical sensory clubs (Fig. 2 sc) (sometimes also more straight and thin), which are usually bent towards each other, and

between which (0–) 2 sensory rods are present (Fig. 2 sr). In front of them there is a protecting integumentary fold (Fig. 2 if), sometimes structured as separate protecting papillae; hardly ever absent, bearing four guard saetae. Ventrally an additional, more or less thick, free-standing sensory club is present (Figs 2, 3 vsc).
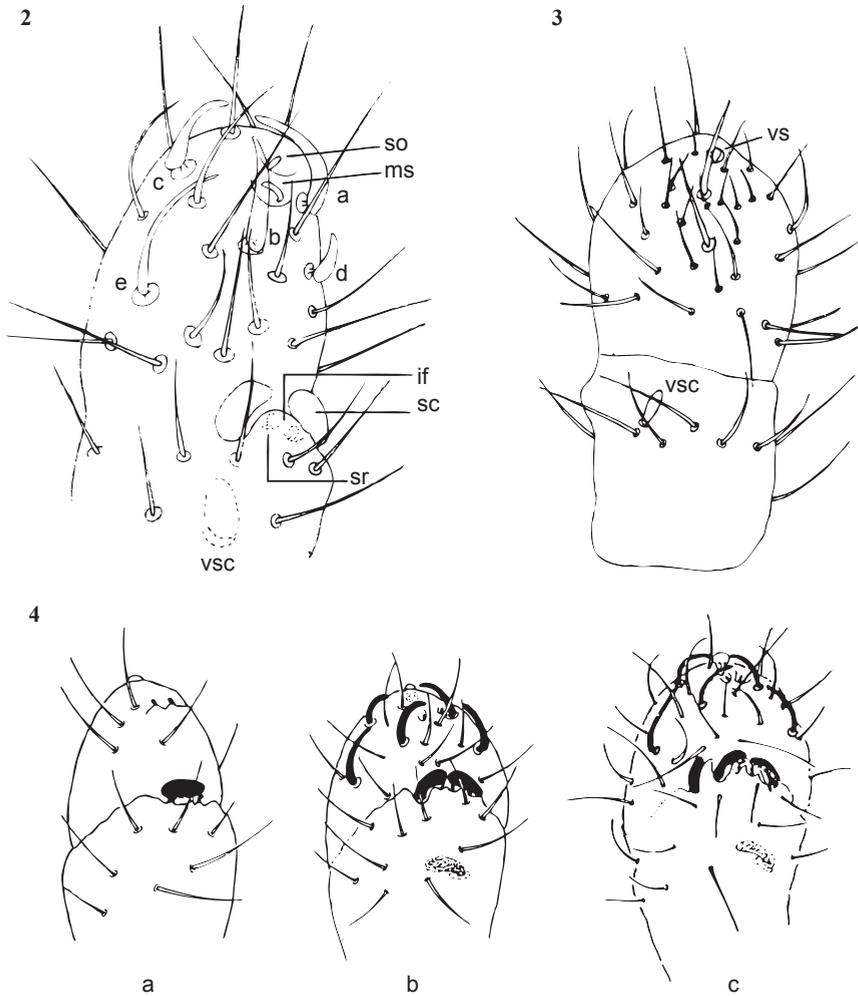
Figs 2–4 Antennal segments III and IV of Tullbergiidae.

Fig. 2 *Mesaphorura sensibilis*: dorsal view; a, b, c, d, e = large sensillae on Ant IV, sensillum c clearly showing a basal heel, so = subapical organite on Ant VI, ms = microsensillum on Ant IV, sc = thick sensory clubs on Ant III, sr = sensory rods on Ant III, if = integumentary fold on Ant III with guard setae, vsc = ventral sensory club on Ant III (after RUSEK 1974).

Fig. 3 *Mesaphorura sylvatica*: ventral view, vs = ventro-apical sensillum (papilla) on Ant IV, vsc = ventral sensory club on Ant III (after RUSEK 1971).

Fig. 4 *Fissuraphorura gisini*: development of the sensillae on Ant III and IV in the first (a), second (b), and adult stadium (c) (after LUCIÁÑEZ & SIMÓN 1992a).

The fourth antennal segment (Ant IV) on the dorsal side distally bears 2–5 (8) more or less thickened, subcylindrical (but sometimes only setaceous) sensilla, which are numbered as two rings designated as a–e (Fig. 2). Sometimes the basal parts of these sensilla are narrowed, but widened towards the distal part, thus showing a 'heel' (Fig. 2; esp. sensillum c). To meet the requirements for a consistent assessment of the number and position of setae and sensilla, a dorsal position as presented in Fig. 2 (with Ant III O situated on the left side) is suggested. Apically (mostly ventro-apically: Fig. 4) on Ant IV, one (0–2) sensillum ('subapical organite'; Fig. 2 so) is present in a depression, sometimes developed as eversible knob, papilla or apical vesicle (exceptionally two- or three-lobed). In most species, subapically, is one rod-like microsensillum (Fig. 2 ms), also inserted in a depression. The subapical organite and microsensillum are sometimes summarised as 'sensory rods' and numbered as sensilla f and g.

In some of the species (not known for all species!), the development of both sensilla on Ant IV and Ant III O gradually proceeds during the juvenile stages (Fig. 4).

Postantennal organ (PAO) (Figs 5–15)

A more or less deep depression is situated distally to the antennal basis on each side of the body, lying normally oblique to the longitudinal axis of the body. It is usually oblong, sometimes oval or even roundish (*Rotundiphorura* Rusek and *Tullbergiella* Izarra). The length of these PAO can be indicated easily by comparing them with the diagonal of the pseudocellus lying in front of the PAO. The depressions of the PAO are more or less filled by sensory vesicles, which are provided with nerves from the protocerebrum. As an exception, in the genus *Doutnacia* Rusek POMORSKI & SKARŻYŃSKI (1998) found the vesicles of the PAO not in a depression but standing free at the level of the integument (Fig. 15).

For taxonomic purposes, the PAO is assessed with its superficial figure alone. Structures which become visible by focusing on deeper layers will not be taken into account for descriptions. Disregarding of this agreement has sometimes led to misinterpretations. Besides, it should be taken into account that figures in the taxonomic literature usually show the whole PAO exactly in one optical plane, which is rarely given when a mounted specimen is studied under high magnification.

Mostly, the depression of the PAO appears filled with two rows of vesicles, which lie at an angle of about 90° to the longitudinal axis and may have a simply extended or up to kidney-shaped form ('*Mesaphorura*–type'). The number of vesicle rows can vary from only one up to several rows (in this case its shape is somewhat difficult to describe). Frequently the vesicles show a roundish centre at the basis. The shape of the vesicles can vary from the normal rod-like or roundish form to an U- or V-shaped type or can sometimes become more complicated and even intricate (Figs 9–12). The PAO – like the sensory setae of Ant III and IV – is a taxonomically important character of Tullbergiidae. Its precise description is very important. For designation of vesicle types see the legend to Tab. 3 (page 34).

The shape of the PAO is assumed to be a genus-typical character. Nevertheless it is known that during the first juvenile stadia this shape clearly deviates from the form shown in the adult stadium. For example, the first juvenile stadium of a species with a PAO of the *Mesaphorura*-type shows two rows with only 3 vesicles each, which become subdivided during the second and later stages (Fig. 5). Therefore, when regarding the PAO for species determination (as well as after some other characters), only adult individuals (with a developed sexual opening) are suitable.
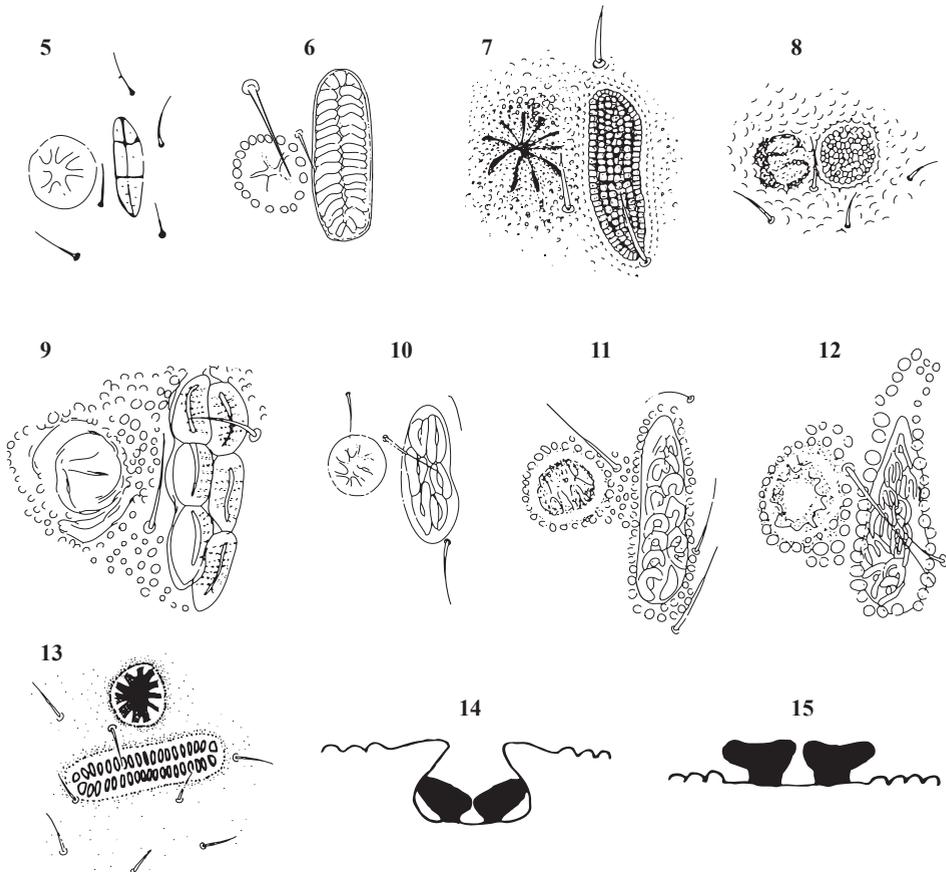
Figs 5–15   Postantennal organ types of Tullbergiidae (with pseudocellus of the antennal basis).

Fig. 5   *Mesaphorura yosii*: stadium I (after Rusek 1980).

Fig. 6   *Mesaphorura sensibilis*: PAO with approx. 35 kidney-like vesicles in 2 rows; pso type I (after RUSEK 1973).

Fig. 7   *Scaphaphorura arenaria*: PAO long elliptic with about 150 globular vesicles in 6–8 irregular rows; pso type I (after PETERSEN 1965).

Fig. 8   *Tullbergiella humilis*: PAO circular with about 60 globular vesicles; pso bipartite, irregular type II (after IZARRA 1965).

Fig. 9   *Fissuraphorura cubanica*: PAO with (coffee-)bean-shaped vesicles with a longitudinal furrow, in 2 parallel rows; pso type III (after RUSEK 1991b).

Fig. 10   *Jevania weinerae*: PAO broadly elliptic with 6 V-shaped vesicles in 2 parallel rows; pso type I (after RUSEK 1978).

Figs 11–12   *Marcuzziella tripartita*: PAO with 12–14 vesicles, in subadult specimens (**11**) horseshoe-like, in adult specimens (**12**) trident-shaped, pso type I, lids not discernible (after RUSEK 1975).

Fig. 13   *Doutnacia mols*: PAO with 37–39 bean-shaped vesicles in 2 parallel rows; pso type I (after POMORSKI & SKARŻYŃSKI 1998).

Figs 14–15   Cross sections of normally depressed PAO (*Mesaphorura*, **14**) and PAO not depressed into the integument (*Doutnacia*, **15**) (after POMORSKI & SKARŻYŃSKI 1998).

Pseudocelli

Pseudocelli (pso) are openings of defensory glands settled in the cuticula. As a reaction to any kind of irritation coming from outside, a fluid is secreted that acts towards an enemy as a deterrent or will stick his mouth parts. Pseudocelli seem to be typical for Onychiuroidea (but possibly may be wider distributed in Collembola). They become discernible as an interruption of the normal structure of the cuticula. Seen from outside, the inner part of a pseudocellus shows a relatively smooth and thin dermal surface, which is provided with stiffening structures. The outer margin of the pseudocelli can appear diffuse, rosette-like by semi-circularly arranged granulae or clearly defined by a sclerotised ring. Sometimes this boundary is only visible in form of a half ring or in another way incompletely developed. The stiffening structures ('stripes') of the dermal surface appear as an optical pattern that can be star-, stripe- or lobe-like, respectively. WEINER & NAJT (1991) distinguish 4 types of pso (Fig. 16):

Type I (star-like / stellate): Roundish pseudocelli with a more or less distinct outer border, mostly formed by 1–2 rows of granulae, and a centre with mostly 5–11 star-like arranged stripes consisting of integumentary granulae (e. g. in *Mesaphorura* or *Tullbergia*; a frequent type).

Type II (double striate): Like type I, but the stripes are arranged in two rows and leave a longitudinal axis open (e.g. in *Metaphorura*).

Type III (crescentic): The stripes or lobes, lying in numbers of 2–5 parallel and next to each other, cover the centre of the pseudocellus in a half-moon-form (especially if the middle stripes are shorter). Thus, the pseudocellus appears (half-) elliptical. The part of the margin which lies opposite to the basis of the stripes can be formed by particularly strong and fused granulae (e.g. in *Fissuraphorura* and 'Granuliphorura'-types of 'northern' *Tullbergia*).

Type IV (convergently striate): More or less oval pseudocelli with a variable border. There are mostly 1–3 stripes only, lying in one row but sometimes being bent towards one another and towards the centre (e.g. in *Paratullbergia*).

16

I	II	III	IV

|		
a	b	c
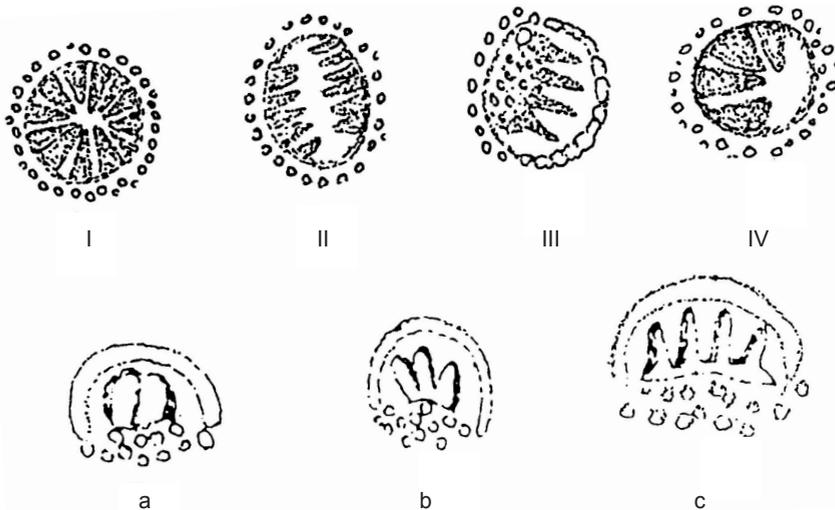
Fig. 16   Types and stadial development of pseudocelli of Tullbergiidae. Above: schemes of general types I, II, III, IV after WEINER & NAJT (1991, see text). Below: development of the pseudocelli in the first (a), second (b), and adult stadium (c) of *Fissuraphorura gisini* (after LUCIÁÑEZ & SIMÓN 1992a).

Pseudocelli are not always easily visible. Checking the number and distribution may be time-consuming and requires an exact preparation. Since juveniles show an incompletely developed pseudocellar pattern (Fig. 16, row below), only adult specimens are suitable for recognizing the types of pseudocelli. In some species, the same specimen may show different types of pseudocelli. Ventral pseudocelli are not known.

The pseudocellar formula describes the numbers of pseudocelli on the head (0–2: antennal basis/ posterior border), thorax (Th I, II, III) and abdomen (Abd I, II, III, IV, V) for one side of the body; e.g.: 11/012/22101. If the presence of pseudocelli is variable (sometimes merely pretended by a problematical visibility of some pso), the formula should be written with a comma after each part (head or segment) as follows: 1, 1/ 0–1, 1, 1–2/ 1, 1, 1, 0–1, 1.

An additional position of pso is present on the head of *Prabhergia* Salmon between the antennal basis and the posterior border (here, head's pso formula reads: 1,1,1).

The position of pseudocelli can be described in relation to the chaetotaxy pattern (Figs 25–29). These characters seem to be ontogenetically fixed (up to now there is only one known exception: the first instar of *Metaphorura denisi* have fewer pso) and intraspecifically reliable enough to be suitable for species diagnosis.

Structures of the dorsal integument

On the entire body of Tullbergiidae, the basic pattern of integumentary granulation is normally homogeneously fine, often with the exception of coarser granulation on lateral parts and especially on the last abdominal segments. Deviations from this norm can be genus- or species-specific (Fig. 23). Sometimes, the basis of the antennae has a very fine granulation (e. g. in *Tullbergia*). In some taxa, in the middle of Abd IV, a very finely granulated transversal stripe appears, dividing the tergite into two halves. This character seems to be overlooked sometimes, but should be checked more consequently.

Especially the tergite of Abd VI shows cuticular structures of high taxonomical importance (Figs 17–24). Proximally crescentic ridges can be present (Figs 17, 18), surrounding a flat pit adjoining the pseudocellus of Abd V. At least one pair of anal spines is always present, based on more or less pronounced papillae. The spines are smooth; only in the genus *Neotullbergia* Bagnall the anal spines have additional inner or outer teeth (Fig. 20). In some genera, a second pair of (outer) anal spines, also based on papillae, is present (Fig. 19). Additional cuticular tubercles, bearing only a normal seta, are sometimes developed (Fig. 18). Furthermore, supertrophicated or luxuriant granulae can show spine-like processes (processus spiniformes; *Neonaphorura* Bagnall; Fig. 21), which are sometimes (wrongly) also called 'anal spines'; up to 3+3 pairs of such spine-like processes may occur. An additional unpaired process (or roundish protuberance) can be present ventrally between the basis of the anal spines (*Marcuzziella* Rusek; Fig. 22; *Neonaphorura* Bagnall; Fig. 21).

Chaetotaxy

The dorsal chaetosis of Tullbergiidae is simple and clearly arranged as well as obviously stable to such an extent that checking the numbers and positions of setae[1] (i.e. chaetotaxy) has a prime importance in current systematics and can serve as a basis of genus and species diagnoses. A fully developed chaetotaxy can only be found in adults. The chaetosis is developed as a heterochaetosis, i.e. the basal chaetosis is differentiated into long macrosetae and shorter (mesosetae and) microsetae; in contrast to Onychiuridae which also shows plurichaetosis.

[1] Spelling 'chaeta' or 'seta'? The correct spelling is 'chaeta' (from Greek) as introduced in many compound terms, such as chaetotaxy etc., but the spelling 'seta' (from Latin) is also widely used. There is no difference in the meaning, so the more often used spelling 'seta' should be kept and in the following is used consequently.

Types of setae: There are two principal types of setae: sensory setae (sensilla[2]) and ordinary setae.

Sensory setae (as present on the tergites of the thorax and abdomen) have a blunt end and are more transparent (thinwalled) than ordinary setae; especially in Tullbergiidae they are often poorly differentiated and difficult to detect. Microsensilla are often spine-like and mostly present laterally on Th II and III in small depressions of the cuticle. Within the sensory organs of the Ant III O and Ant IV, the shape of sensory setae is conspicuously differentiated (enlarged, thickened, swollen in shape, globular to hammer-shaped).

Ordinary setae have a thicker wall and a pointed end, in contrast to the sensory setae. They vary mainly all in length (macrosetae, mesosetae, microsetae). The shortest setae ('setulae') can be found in the anal (and, if developed, in the furcal) field. Tullbergiidae mostly have smooth, erect or curved macrosetae. Their fixed position on the tergites provides important information for species identification.

Juvenile chaetotaxy. The chaetotaxy of first and second instar is different (number, development or position of setae) from adult specimens (see Figs 26–28; Th I; Abd V). These differences concern five areas (RUSEK 1980; LUCIÁÑEZ & SIMÓN 1988, 1993; POMORSKI & SKARŻYŃSKI 1997c). First instars have

– no thickened sensilla on Ant IV,

– only one thick sensory club and two sensory rods in Ant III O,

– a smaller number of vesicles in PAO,

– a smaller number of pseudocelli (known only for *Metaphorura denisi),*

– a simplified chaetotaxy of the body in general.

The study of juvenile chaetotaxy provides valuable information about the phylogenetical lines of development of the Tullbergiidae; however, at the moment, is still too poorly understood to draw deeper phylogenetical conclusions.

[2] True sensilla must be checked for having an innervation, which not usually is easily visible. CHRISTIANSEN (pers. comm. 2008) has therefore proposed to write it in single quotes ('sensory' setae). As this situation (and the difficulties connected with it) is clear to anybody studying Collembola, we use the very important characters 'sensilla' and 'sensory organs' in a morphological sense (leaving aside the innervation). Besides, there is often no clear difference between 'blunt setae' and 'sensilla'. See also 'sensillar pattern'.

Figs 17–24 Dorsal integumentary structures of Tullbergiidae.
Fig. 17   *Paratullbergia macdougalli*: Left part of Abd VI with crescentic ridges (cr.r.) and 1+1 Asp on papillae (after DUNGER 1970).
Fig. 18   *Paratullbergia callipygos*: Abd VI, lateral view with crescentic ridges (cr.r.), dorsal tubercles (tub), and 1+1 Asp on strongly differentiated papillae (after GISIN 1960).
Fig. 19   *Stenaphorura quadrispina*: Abd VI with 2+2 Asp on papillae (after LUCIÁÑEZ & SIMÓN 1992b).
Fig. 20   *Neotullbergia ramicuspis*: Asp with additional teeth (after GISIN 1960).
Fig. 21   *Neonaphorura novemspina*: Abd VI dorsal with additional spine-like processes (after ARBEA 1991).
Fig. 22   *Marcuzziella tripartita*: Abd VI ventral with a postero-medial unpaired processus between the Asp (after RUSEK 1975).
Fig. 23   *Mesaphorura hygrophila*: dorsal granulation of Th II (after RUSEK 1971).
Fig. 24   *Mesaphorura pacifica*: dorsal granulation of Abd V+VI (after RUSEK 1976).

17 cr.r.

18 cr.r. tub
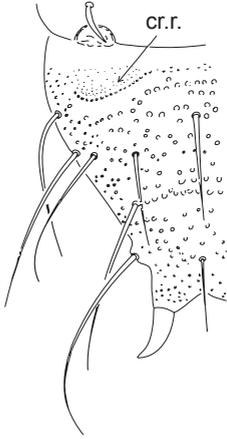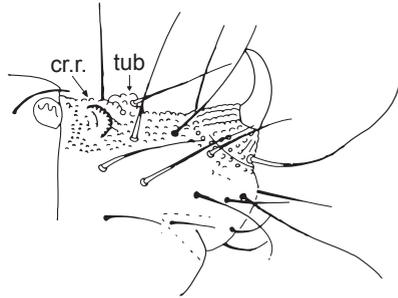
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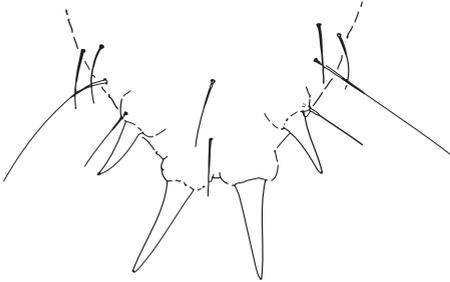
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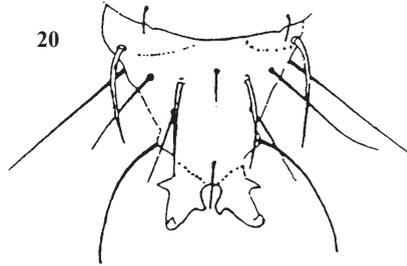
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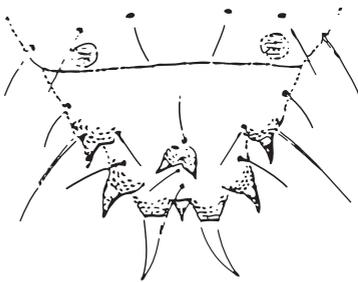
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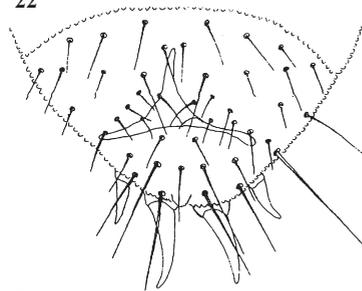
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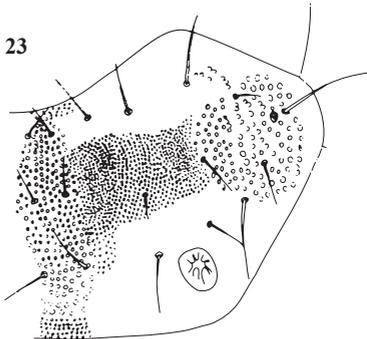
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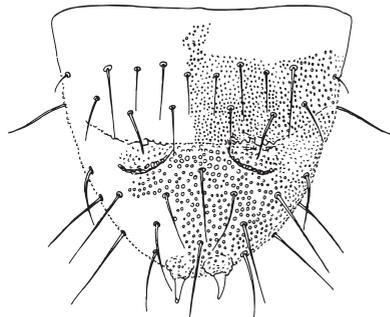
Dorsal chaetotaxy. If all setae of the basic pattern are present, the tergites bear three rows of 5 (6–7) setae on each side. The rows are named anterior (*a*), median (*m*) and posterior (*p*). Within the rows, the setae are numbered from the midline outwards (e.g. *p*1, *p*2, *p*3....*p*6), taking in account all setae which are to be expected from the positions of the basic pattern. In fact, in nearly all cases some setae are absent, especially in the *m*-row (Figs 25–28). Problems in assigning the position of individual setae may arise from a 'natural shifting of positions', resulting in a more anterior or posterior position within the row or an aberrant distance from the midline. Such 'shifting' may also result from a wrong preparation technique, especially when the cover slip has been pressed against the specimen. Macrosetae or basal setae, when developed as sensilla, will lead to further complications. Such variabilities have sometimes led to misinterpretations.

A complete pattern of dorsal chaetotaxy should include not only the 'mid-dorsal' or true tergite setae but also the pleural setae, being named as a 'fourth row' (*pl*-row) (see Tab. 1 and Fig. 25). An example of dorsal chaetotaxy of a plesiomorphic species with nearly complete sets of setae is given in Tab. 1.

Tab. 1   Dorsal chaetotaxy of *Tasphorura vesiculata* Greenslade & Rusek (numbers of setae of complete rows) (After GREENSLADE & RUSEK 1996)

row	Thorax			Abdomen				
	I	II	III	I	II	III	IV	V
a	-	10	10	10	10	10	10	8
m	-	10	10	4**	4	4	8*	4**
p	8	10	10	10	10	10	10	6***
pl	2	3	3	2	5	5	10	2

* *m*3 missing, ** *m*4+5 present, *** *p*2,3,5 present

**Sensillar pattern.** Fig. 29 shows the basic pattern of sensilla of the dorsal side for the family Tullbergiidae. Setae on the thorax or abdomen are interpreted as sensilla if they are not evenly pointed towards the tip and/or are thinwalled. The microsensilla on Th II and III are positioned in depressions, thus being easily overlooked. When counting setae for a complete chaetotaxy, the sensilla are counted as if being normal setae.

Chaetotaxy of the head. Fig. 30 shows the dorsal chaetotaxy of the head. For species diagnosis, presence or absence of unpaired setae (here: *a*0) in the middle line and the relative length of *p*1+2 are of importance. Within the ventral chaetosis of the head (Fig. 31), especially the number of setae along the linea ventralis (here: 3+3) is of interest.

Ventral chaetotaxy of thorax and abdomen. On Th I, II and III there are mostly 0, 1, 1 (seldom more) setae on both sides of the linea ventralis. This character has mostly been ignored in older descriptions and therefore is only known for few species.

The chaetotaxy of the ventral tube (Fig. 35) is not very variable (mostly 4+2 setae on each side). Here, some authors register only the 2 pairs inserted directly at the ventral tube, others also include the two setae directly neighbouring it. In some species/genera a 'furcal field' appears in the position of the absent furca (Fig. 34). Of higher importance is the study of male and female genital plates (Fig. 36, 37). Even in this region, sensilla or spine-like setae may occur. Special attention needs to be drawn to the chaetotaxy of the *l*-setae on the anal lobes (Fig. 38), especially the presence of *l*' setae inserted directly at the lid of the anal lobe (*l*2', *l*3').
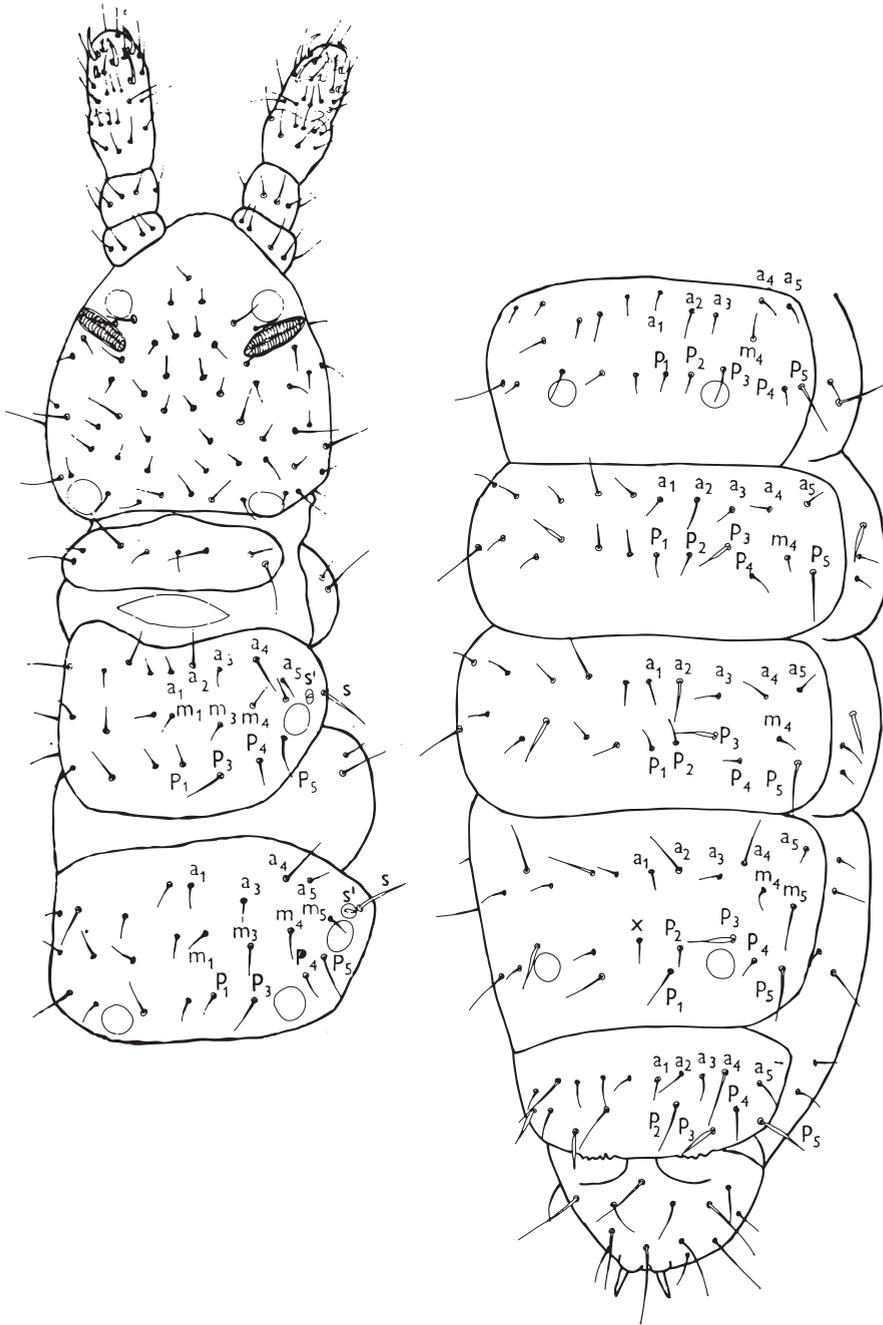
Fig. 25 Dorsal chaetotaxy of Tullbergiidae.
Mesaphorura sensibilis: dorsal chaetotaxy (after RUSEK 1973).
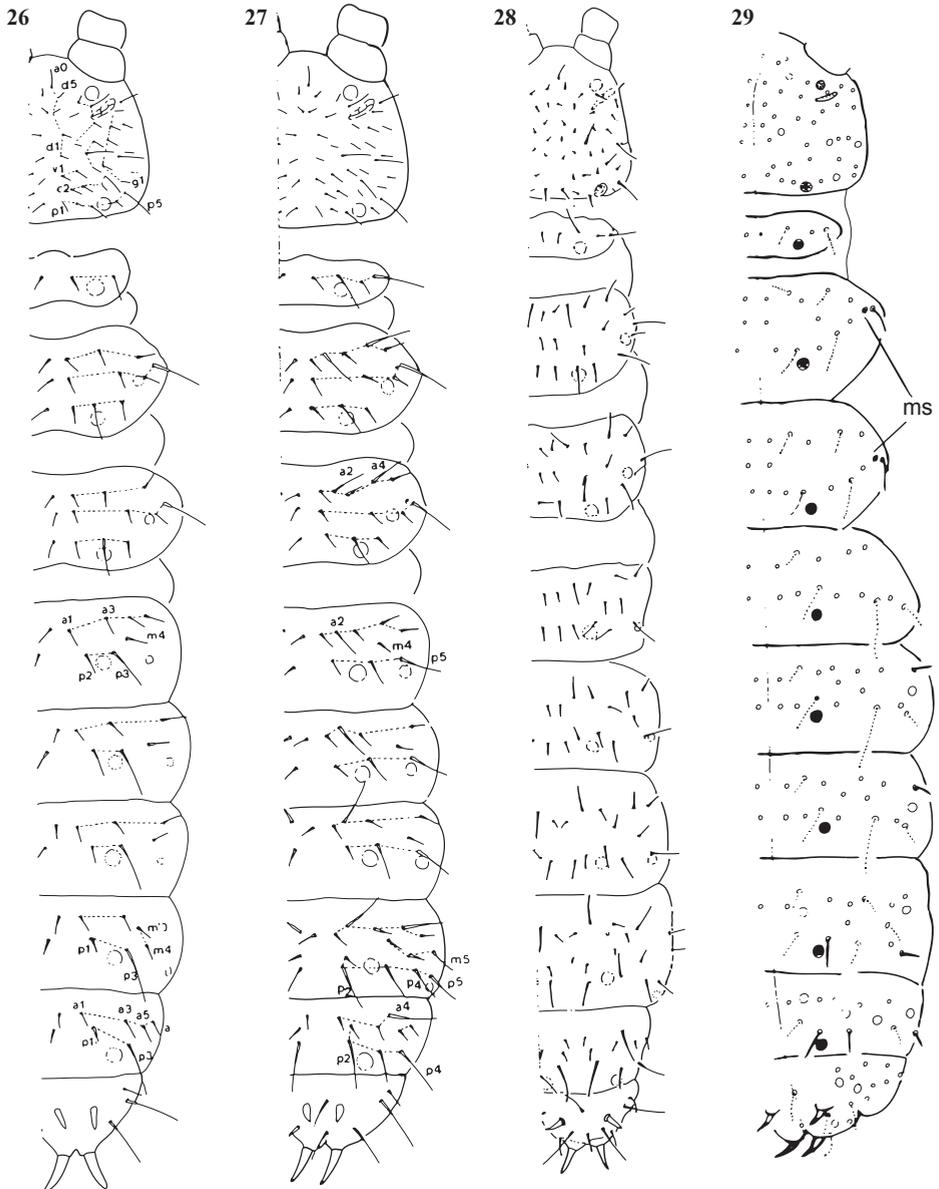
Dorsal chaetotaxy of Tullbergiidae.

Figs 26–28 Stadial dorsal chaetotaxy of *Fissuraphorura gisini*: first (**26**), second (**27**) and adult
stadium (**28**) (after LUCIÁÑEZ & SIMÓN 1992b).

Fig. 29 Sensillar pattern of the dorsal side of *Stenaphorura quadrispina*: black circles
= pseudocelli, large open circles = macrochaetae, small points = microchaetae,
ms = microsensillae on Th II and III, black setae = sensillae of diver-
gent length, stippled setae = blunt macro- or microchaeteae (after DEHARVENG
1979).
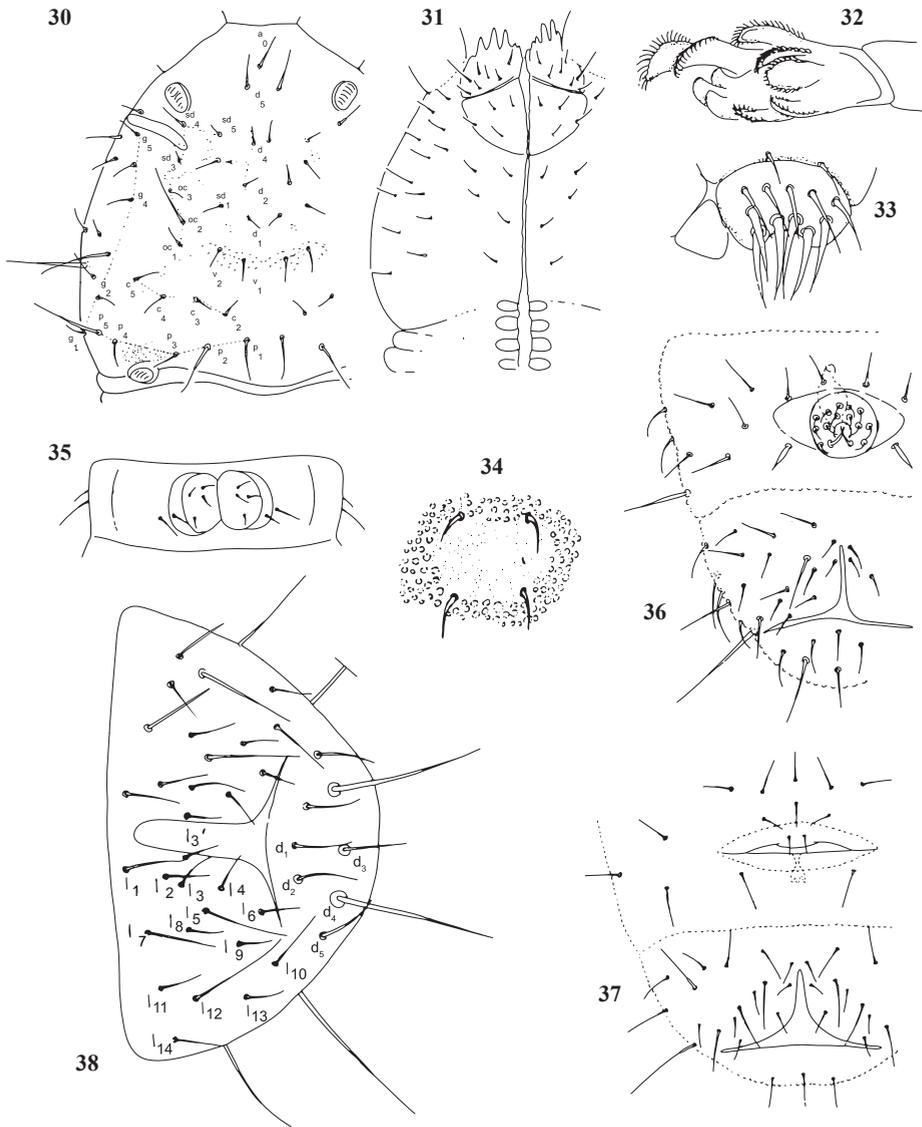
Figs 30–38 Detailed characteristics of dorsal and ventral chaetotaxy and morphology of Tullbergiidae.

Fig. 30 *Dinaphorura americana*: dorsal chaetotaxy of the head (NAJT & RUBIO 1978).

Figs 31–33 *Karlstejnia norvegica*: ventral cheatotxy of the head (**31**), maxilla, proximal view (**32**), and labrum (**33**) (after FJELLBERG 1974).

Fig. 34 *Metaphorura affinis*: furcal field (after FJELLBERG 1998).

Fig. 35 *Mesaphorura hygrophila*: chaetotaxy of the VT (after RUSEK 1971).

Fig. 36 *Fissuraphorura cubanica* (male): Abd sternites V and VI (after RUSEK 1991b).

Fig. 37 *Jevania weinerae* (female): Abd sternites V and VI (after RUSEK 1978).

Fig. 38 *Mesaphorura krausbaueri*: Abd sternite VI with l2' absent (after RUSEK 1971).

Chaetotaxy and morphology of the legs. An example of a relatively basal chaetotaxy of the legs is shown in Tab. 2. Especially the presence of spatulate (clavate) hairs (Fig. 48) on the tibiotarsi is of interest. In the most complete case, the chaetotaxy of the tibiotarsi in Tullbergiidae (as in *Mesaphorura clavata*) comprises two whorls of setae (A, B) with 7 setae each and one internal M-seta (Fig. 39). Derived from this type, stepwise reductions of setae lead to a central *Tullbergia*- type, including nordic species of *Tullbergia* and *Stenaphorura*, from which three divergent lines separated (1) by a reduction of the M-seta to the *gisini / duplex* type (with allocation of the genera *Stenaphorura* and *Tullbergia* remaining unclear) and the *Metaphorura affinis* type; (2) by a reduction of seta B_1 to the *multivesicula*- type (with 4 species); (3) by a reduction of the setae B_{2+7} to the *Mesaphorura* type (with 8 species; also including *Paratullbergia, Neotullbergia, Scaphaphorura, Wankeliella* and *Karlstejnia*). These lines may be seen as evolutionary sequences, but do not yet allow clear phylogenetical conclusions (FJELLBERG 1991, 1998).

Tab. 2   Chaetotaxy of the legs of *Mesaphorura florae.* (after SIMÓN et al. 1994)

	first leg	second leg	third leg
Coxa	3	7–8	6–7
Trochanter	6	6	5
Femur	9	9	9
Tibiotarsus	11	11	11
Praetarsus	2	2	2

The claws bear neither inner nor outer teeth. An exceptional shape of the claws is developed in the genus *Scaphaphorura* (Figs 40, 41). Usually the empodial appendage ('empodium') is not longer than about 25 % of the inner crest of the claw and, in such cases, is of seta-like shape. Frequently the empodium is present only in form of a papilla or is completely reduced.

Mouthparts of Tullbergiidae have been most extensively studied by FJELLBERG (1974, 1991, 1998, 1999). The mouth region shows (Fig. 43), in anterior view, dorsally a prelabrum with 4 setae and a labrum with 6–11 setae, medially the oral fields with the maxillary outer lobe and palp, and ventrally the labium. The labium (Fig. 42) bears at the apical part five teethstump-like labial papillae (A–E), five apical guard setae (0–6; $g_{1–7}$; g_3 absent) and (4–) 6 proximal setae; it bears the hyaline plate with normally three hypostomal setae (H, h', h"). The basal part of the labium bears 4–9 hypostomal setae. The mandibles and maxillae (Fig. 44, 45) are variable as well. These examples indicate that the mouthparts show very specific characters. Unfortunately, they have not been studied in detail very often, since such examinations are difficult and time-consuming and therefore are presently not often used for species characterisation.

Basic questions in taxonomy of Tullbergiidae

Since the descriptions of *Tullbergia antarctica* given by LUBBOCK (1876)*, Stenaphorura japygiformis* by ABSOLON (1900) and *Mesaphorura krausbaueri* by BÖRNER (1901), the taxonomy of Tullbergiidae has developed up to now by the addition of newly described species, some of which were based on very delicate morphological and chaetotactic characters. Furthermore, it must be noted that nearly half of these species were based on spanandric or totally parthenogenetic entities. The situation partially resembles the development in taxonomy of Onychiuridae.
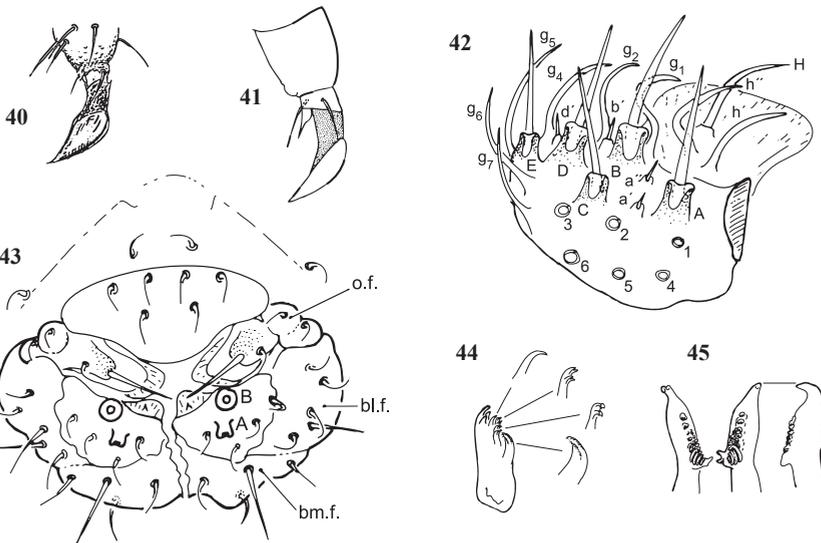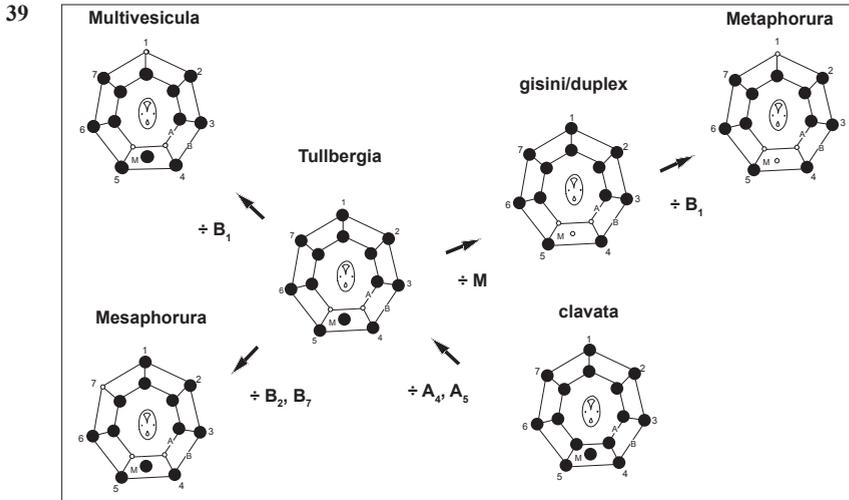
Fig. 39 Typological arrangement of tibiotarsal chaetotaxy in Tullbergiidae (at the basis of the right mesotibiotarsus) (after FJELLBERG 1991).

Figs 40–41 *Scaphaphorura arenaria*: claw III (Fig. 40 after PETERSEN 1965, Fig. 41 after MASSOUD & THIBAUD 1985).

Figs 42–45 Mouthparts of Tullbergiidae.

Fig. 42 *Paratullbergia callipygos*: apical part of labium with 5 papillae (A–E), 6 apical guard setae (g1, g2 g4–g7), 6 proximal setae (insertion-rings 1–6, further basal setae, hypostomal setae and presence of accessory papillae (after FJELLBERG 1998).

Fig. 43 *Pongeiella falca*: mouth region, anterior view, A, B = labial papillae, o.f. = oral field, bl.f. = basal field, bm.f. = basomedian field of labium (after FJELLBERG 1998).

Fig. 44 *Pongeiella falca*: maxilla (after FJELLBERG 1998).

Fig. 45 *Pongeiella falca*: mandibles (after FJELLBERG 1998).

Therefore, the question arises whether these morphospecies (completely or partly agamospecies or spanandric species, respectively) may represent real biological species. To obtain a better understanding, ZIMDARS & DUNGER (2000) studied clonal lines of four *Mesaphorura* species for up to 15 generations in cultures under constant and variable conditions, but found no variability that would affect the taxonomically important characters (e.g. chaetotaxy). Secondly, field studies investigating possible divergent ecological preferences of *Mesaphorura* morphospecies within a natural continuum of ecological factors found no deviation of variability in ecological preferences in these morphospecies. Finally it was studied whether these species could be characterized by selected chemical parameters, using isoenzyme electrophoresis and RAPD-PCR techniques. As far as these methods gave significant results, the agamospecies under study behaved like true species according to taxonomic rules.

Based on these studies, the question of ecologists, whether the very time-consuming identification of Tullbergiidae down to species level will lead to genetically good species that represent taxonomic units of equal importance, sensible and meaningful enough to discuss ecological questions, can clearly be answered positively. However, as a general recent problem, the time factor remains: ecological information raised earlier than 1985 is to be questioned regarding validity since most of the taxonomical and ecological diversity of species in Tullbergiidae became apparent to scientific knowledge later than that.

Phylogenetical lines and intra-familiary classification of Tullbergiidae

Tullbergiids are to a high degree basically adapted for living in small soil cavities by reduction of body length, extremities and setae, as well as by loss of the furca and eyes. As possibly suitable characters for constructing cladistic lines, apart from chaetotaxy, the development of sensory organs (PAO, Ant III O, Ant IV) have been frequently used, but up to now with limited success. The best results came from studies on the successive reduction of dorsal and ventral chaetotaxy following the hypothesis that cladistic lines developed from a 'fully equipped' status to several levels of chaetotactic reduction. First attempts to construct cladistic lines, albeit not fully satisfyingly, were made by LUCIÁÑEZ & SIMÓN (1992b, 1993). As in general for soil arthropod groups, practical phylogenetic analyses are needed, listing all possible plesiomorphic character states of a stem species pattern with relevance for the analysis (as shown in modern studies on Oribatids: WEIGMANN 2009).

Caused by this lack of knowledge, taxonomical results are mostly – and especially for Tullbergiidae – given for easy compilation and quick determination without consequences for phylogenetic systematics. This leads to the taxonomical problem of unjustified rejections of introduced genera, primarily concerning the genus *Austraphorura* Bagnall, 1947, which was synonymised by NAJT & RUBIO (1978) with *Dinaphorura* Bagnall, 1935. The recent taxonomy of Tullbergiidae, as proposed by the Fauna Europaea (2004 and later years), is mainly based on BELLINGER, CHRISTIANSEN & JANSSENS (1996–2008). Here, two genera were rejected: *Chaetaphorura* Rusek, 1976 and *Granuliphorura* Rusek, 1976. The 12 species of *Chaetaphorura* are with priority referred to *Tullbergia*; the only species of *Granuliphorura* is also referred to *Tullbergia*. These new combinations are reflected, but not annotated in this book.

Some constructions of higher taxa within the family Tullbergiidae remain questionable. This primarily concerns many cases of new descriptions of genera (and their rejection), for the allocation of species to other genera as well as the construction of suprageneric taxa (tribus/subfamilies). Evaluations of the basal phylogenetic systematics (KUKALOVA-PECK 2008) are mostly missing in these cases. However, these questions cannot be discussed here.

LUCIÁÑEZ & SIMÓN (1992b, 1993) have proposed to construct 3 tribus (elevated to subfamily rank by JANSSENS 2007) within the Tullbergiidae:

– Austraphorurinae: Ant III O with only one sensory club; Th II+III without $m2+3$ and $p2$. Type genus: *Austraphorura* Bagnall, 1947

– Mesaphorurinae[3]: Ant III O with 2 sensory clubs; Th II+III without $m2$ and $p2$; with or without $m3$. Type genus: *Mesaphorura* Börner, 1901.

– Tullbergiinae: Ant III O with 3 sensory clubs; Th II+III without $m2$, with or without $m3$ and $p2$. Type genus: *Tullbergia* Lubbock, 1876.

This classification is mainly based on the presence of one to three sensory clubs in the Ant III O. WEINER & THIBAUD (1991) have doubted the number of sensory clubs to be of high significance, referring to the development of these organs in the juvenile stages. BELLINGER, CHRISTIANSEN & JANSSENS (1996–2008) came up with a 'Solomonic judgement' by excluding eight genera from the proposed subfamilies: *Multivesicula* Rusek, *Pongeiella* Rusek, *Psammophorura* Thibaud & Weiner, *Rotundiphorura* Rusek, *Sensilatullbergia* Thibaud & Ndiaye, *Spicatella* Thibaud, *Tasphorura* Greenslade & Rusek and *Weinera* Thibaud.

These exclusions clearly show that there is presently no satisfying subfamilar classification of the Tullbergiidae.

Ecology and Biology

General adaptations

Tullbergiids are basically preadapted to euedaphic environments by their minute body length, short legs and reduction of the furca (RUSEK 1978), but they are not restricted to these microhabitats. Special adaptations to cave dwelling are not known.

Reproduction

About half of the Tullbergiidae are parthenogenetic or spanandric (PETERSEN 1980). PETERSEN (2002) considered parthenogenesis to be a possible adaptation for survival in stable but resource-scarce environments (as can be found in deeper soil horizons). To avoid an oversimplification, he refers to conclusions drawn by NIKLASSON et al. (2000). These authors studied a population of *Mesaphorura macrochaeta* along a 50 m long transect from the open sea shore inland to a more stable, plant-covered habitat. They found that the population was parthenogenetic at the sea shore and bisexual beneath the plant cover.

According to results gained by RAPD, the genetic variability was highest – contrary to the expectations – in the parthenogenetic population while the bisexual population was more resistant to drought and high temperatures. Such profound studies of larger sets of populations are still scarce, albeit necessary, and bear a higher probability of clearing up questions of sexual behaviour.

As one reason for the absence of males, an infection by *Wolbachia* has been described. These Proteobacteria are assumed to kill selectively male embryos in many arthropod species. Within Tullbergiidae, up to now only *Mesaphorura macrochaeta* has been tested positively for contamination with *Wolbachia* (TIMMERMANS et al. 2004). A comparison using rDNA markers showed that the *Wolbachia* strain harboured by *M. macrochaeta* belongs to the group that was also found in *Folsomia candida* (the 'laboratory collembola'). Observations by TIMMERMANS & ELLERS (2009) suggested that reproduction in *F. candida* is a threshold

[3]After the revision of *Stenaphorura* Absolon by RUSEK (2010) (with the conclusion that *Stenaphorura* Absolon has 3 sensory clubs in the Ant III O), the proposed 'subfamily Stenaphorurinae' should better be named 'subfamily Mesaphorurinae' with the 'type genus' *Mesaphorura* sensu RUSEK (1973).

effect requiring a critical *Wolbachia* density. Complete loss of *Wolbachia* infection was associated with full egg hatching failure. Nevertheless, such results cannot give an ecological explanation for the observation of NIKLASSON et al. (2000) that within a distance of only 50 m the populations of *M. macrochaeta* are parthenogenetic at the seashore and bisexual at plant cover. To maintain the attention to such ecological situations, a careful investigation of the presence or absence of males in Tullbergiid associations is valuable.

Embryonic development

Females lay eggs mostly in batches of up to 50 and more. These batches are laid into small cavities without special protection. The developmental time span depends on temperature, moisture and other factors including pH (HUTSON 1978). Optimal conditions were found ranging between pH 4 and 6, with 25–52 eggs per batch and an optimal hatching percentage (about 95%) with an embryonic developmental time of 24 days.

Ecological preferences

Ecological preferences are mostly deduced from the characteristics of the habitats in which animals were found. In this way only very general descriptions of preferred habitats will result: in wet/medium/dry soils with sandy/loamy texture; or in open soils, under grasses or (deciduous/ conifer) woodlands. Somewhat more exact are often descriptions of the soil depth from where the specimens have been sampled. However, information about vertical distribution of species can be controversial. For example, HÅGVAR (1984) found *Mesaphorura macrochaeta* in Norwegian soils in depths beneath 4 cm. In recultivated soils of Eastern Germany, DUNGER (1986) found this species also in depths of 35–40 cm. Long-term studies on the Tullbergiidae complex in open-dry sandy soil plots in a young coniferous plantation (near Bautzen, Eastern Germany) showed very different preferences of the 4 occurring Tullbergiid species (DUNGER 1984). The vertical distribution was checked at two stands of a sandy arid grassland with a soil covered by ('a') different xerophytes with only up to 50% ground cover and ('b') leaf-rosettes of *Hieracium pilosella* with nearly 100% ground cover. Regardless of ground cover, *M. yosii* showed its highest population density in 0–5 cm depth; *M. norvegica* had highest densities in 5–10 cm depth at the stands 'a' and 'b'; but *M. critica* and *hylophila* had their highest densities in 0–5 cm depth only at stand 'b' under the protection of *Hieracium pilosella,* whereas these species lived at the more open stand 'a' only in 5–10 cm depth. Generally, information about ecological preferences only being derived from the situation of a single locality (e.g. the locus typicus of a species) should not be generalized without scrutiny.

Colonisation behaviour of Tullbergiid species

The invasion of species in freshly heaped spoil dumps from brown coal open casts was studied by DUNGER et al. (2004) in Eastern Germany. They showed ecological potentials and preferences of 17 Tullbergiid species found at areas of altogether 250 m^2 over 50 years of primary succession (in direction to fresh deciduous woodlands) compared with a nearly native bottomland forest ('w').

The results reflect 8 types of colonisation behaviour:

Fugitive primary colonisers: *Mesaphorura florae, M. yosii* (freshly heaped, vegetation-free soils, 0–2 years)

Constant colonisers: *Mesaphorura macrochaeta* (eudominant over the entire time except for years 0–2; in 'w' subdominant)

Post-pioneer colonisers: *Paratullbergia macdougalli* (between the 4th and 10th year)

Pioneer woodland colonisers: *Mesaphorura hylophila, Metaphorura affinis* ([4th–] 20th–35th year)

Euryoecious woodland colonisers: *Stenaphorura quadrispina, Paratullbergia callipygos* (4th–50th year +'w')

Pre-woodland colonisers: *Mesaphorura tenuisensillata,* [*Neonaphorura dungeri, M. critica*] (30th–50th year + 'w')

Stenoecious woodland colonisers: *Mesaphorura krausbaueri, Stenaphorura denisi* (only 'w'; subdominant)

Sporadical colonisers: *Karlstejnia annae, Mesaphorura sylvatica, Neotullbergia ramicuspis.*

The colonisation of the dumps for over 50 years was clearly dominated by *Mesaphorura macrochaeta*, showing the same colonisation type as in agricultural soils of this region (DUNGER et al. 2008).

Tullbergiids in the interstitial fauna of fine sand sediments

Not earlier than 1985, populations in fine sands of supralitoral and inland 'dry' sands as well as in 'humid' interstitial sands were studied by using special techniques. A considerable part of the sand-faunal Collembola are Tullbergiidae because they are 'preadapted' to the fine pore architecture between the sand grains. Some of the species were already known from the European fauna (*Mesaphorura critica* Ellis, 1976; *M. italica* (Rusek, 1971), *M. macrochaeta* (Rusek, 1976), *Metaphorura affinis* Börner, 1902, *Scaphaphorura arenaria* (Petersen, 1965)) (THIBAUD & CHRISTIAN 1989). Others were found only by the recent study of sands: *Doutnacia mols* Fjellberg, 1998, *Mesaphorura petterdassi* (Fjellberg, 1988), *M. schembrii* (Thibaud & Christian, 1989), *Najtiaphorura sandrinae* (Weiner & Thibaud, 1991), *N. olivieri* (Weiner & Thibaud, 1991), *Psammophorura gedanica* (Thibaud & Weiner, 1994) and *Pongeiella luciaelvirae* (Thibaud & Peja, 1996). For *Scaphaphorura cubana* Thibaud, 1994 and *M. subitalica* Thibaud, 1996, a transatlantic distribution between the Canary Islands and Northern Morocco has been indicated (by water or air transport) (THIBAUD 2006).

Arctic fauna

The arctic distribution of Tullbergiidae has recently been shown by BABENKO & FJELLBERG (2006). There are 23 species listed as inhabitants of the Arctic region north to the natural timber line. Most of these species were discovered in the Norwegian and the Alaskan (and Greenland) regions. Only few species of Tullbergiidae were found in these regions: *Mesaphorura macrochaeta* Rusek, 1976 in East Siberia and North-eastern Asia; *M. tenuisensillata* Rusek, *Multivesicula dolomitica* Rusek, 1982 and *Wankeliella intermedia* Potapov & Stebaeva, 1997 were found in western and central Siberia. All these species are not exclusively specialised to the Arctic regions but are widely distributed.

Extreme factors affecting habitat preferences

As a predominating factor of ecological influence, the pH-value has been described as distinguishing between acidophilic species (*Mesaphorura yosii, M. tenuisensillata),* acido-intolerant species (*Mesaphorura italica, M. jarmilae, M. hylophila, M. krausbaueri, Metaphorura affinis, Stenaphorura denisi, Wankeliella pongei*) and indifferent, widely distributed and dominant species (*Mesaphorura macrochaeta*) (PONGE 2000). But already in 1990, HÅGVAR argued that competition is a key factor in such situations (PETERSEN 2000).

Natural successions of Tullbergiid species along xerothermic rendzinas studied by RUSEK (1979b) showed different preferences of species along a hygric and thermic catena. Studies made by DUNGER (1986, 1991) in Thuringia showed that *Mesaphorura yosii, M. macrochaeta* and *M. hylophila* inhabit the extreme basic and xerothermic plots, dominating in different ways. Roughly the same species could be found inhabiting another slope being heavily polluted by immissions of Na, F and P with pH-values below 9 (FRITZLAR et al. 1986). These examples indicate that competitive power can obscure normal preferences (Fig. 46). Such situations should be kept in mind when interpreting ecological information given in the taxonomy part of this volume.
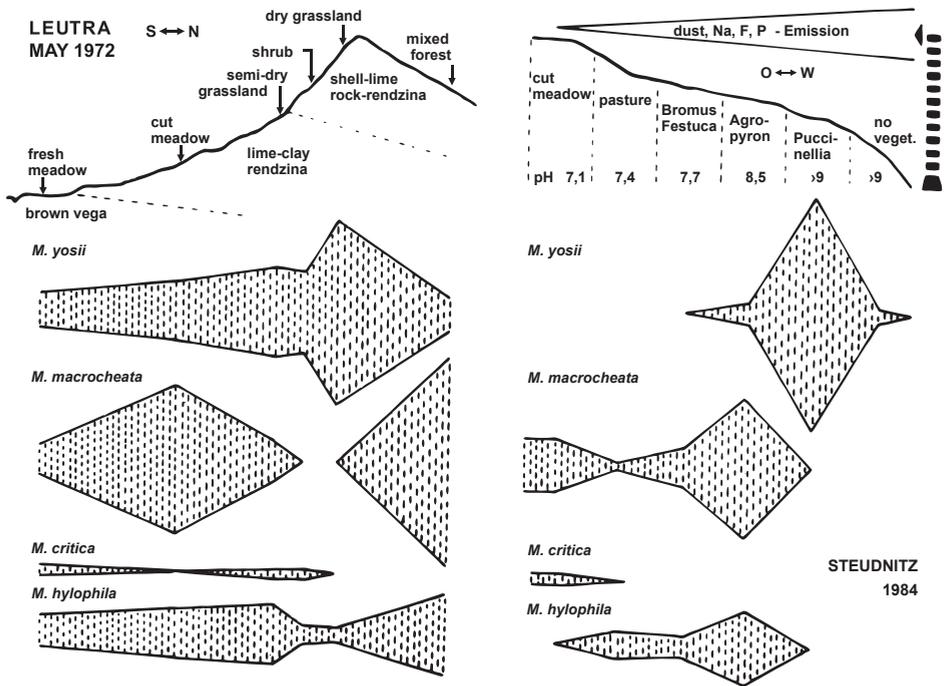
Fig. 46   Relative abundance of *Mesaphorura* species along gradients (after DUNGER 1986). Left: along a xerothermic slope (Leutra, Thuringia, Germany, 1972). Right: along a pollution gradient. (Steudnitz, Thuringia, Germany, 1980–1983)

History

The genus *Tullbergia* was erected for the first time by LUBBOCK (1876) for *Tullbergia antarctica*. Later followed the descriptions by ABSOLON (1900) for *Stenaphorura japygiformis* from a cave of Moravia and BÖRNER (1901c) for *Mesaphorura krausbaueri,* which he found in 3 specimens 'under flower pots near Bremen'. As early as 1902 BÖRNER revised all descriptions of the then 10 known species as belonging to a homogeneous genus *Tullbergia*. Not earlier than 1935, BAGNALL studied this group more intensely and elevated the Tullbergiinae to the status of a subfamily, later even to the level of a family Tullbergiidae (BAGNALL 1947). During this time, contributions to the knowledge of Tullbergiids were given in particular by WOMERSLEY (1930) for the English and by SALMON (1943) for the Australian area. STACH (1954) summarised about 50 known species of Tullbergiinae. From these, GISIN (1960) accepted only 15 species for Europe and – following the example of BÖRNER (1902) – combined all these species into one genus *Tullbergia* (using 5 subgenera). *Tullbergia krausbaueri* (Börner, 1901), considered to be easily discernible, attained a high importance for soil biology because it was emphasised by GISIN (1955) as being an indicator for good vineyard soils and by GILAROV (1965) even as a general indicator for fertile soils.

The publications by PETERSEN (1965) and especially by RUSEK (1971) opened a new era of knowledge about Tullbergiidae. Up to now, worldwide, 31 supraspecific taxa have been described and are actually accepted, partly as genera, partly as subgenera (which actually are also to be accepted as valid genera). Nevertheless, CHRISTIANSEN & BELLINGER (1998) decided to lump together all 23 (24) nearctic species of Tullbergiidae into the genus *Tullbergia,* accepting the subgenera *Metaphorura, Neonaphorura* and *Stenaphorura*. For the fauna of Norway, FJELLBERG (1980), in addition to *Tullbergia,* only accepted the genera *Karlstejnia* and *Wankeliella;* for the Fauna Scandinavica (FJELLBERG 1998) he already described 13 genera.

The present synopsis takes into account 64 Palaearctic species from 18 genera; for the Nearctic region a further 14 (16) species are to be added according to CHRISTIANSEN & BELLINGER (1998). A critical worldwide revision seems to be necessary.

3. Key to the genera of Tullbergiidae Bagnall, 1947 of the world

The geographical distribution is indicated as: [PA] present in the Palaearctic; [HA] Holarctic; [NA] Nearctic; [T] Tropics; [S] Subantarctic region; [WW] worldwide.

1   Body salmon pink in life; white in alcohol; Ant IV with an extremely large apical papilla (Fig. 47) [S]   ***Tasphorura*** Greenslade & Rusek, 1996
            type species: *Tasphorura vesiculata* Greenslade & Rusek, 1996; Tasmania

=   Body with dark blue pigment [PA]   *Metaphorura triacantha* (Börner, 1901); Sicily

–   Body white (without pigment); Ant IV without an extremely large apical papilla   **2**

2   Tita with 2 groups of long clavate setae at the distal end (Fig. 48); Ant III O with 6 dorsal sensory elements (1 pair of outer clubs, 1 pair of inner rods, between these 1 pair of medium-sized sensilla) [S]   ***Clavaphorura*** Salmon, 1943
            type species: *Clavaphorura septemseta* Salmon, 1943; New Zealand

–   Tita without clavate setae (seldom: few weakly developed ones); Ant III O dorsal with max. 5 sensory elements   **3**

3   Ant III O dorsal with only one large, bent sensory club (in adults!)   **4**

–   Ant III O dorsal with 2–3 large sensory clubs (in adults!; see Fig. 4 b, c)   **7**

4   Claws large with a handle-like basal and a shovel-like distal part (Fig. 40, 41); PAO with many (150–180) globular vesicles in irregular rows [PA]
            Scaphaphorura (Petersen, 1965)
            type species: *Tullbergia (Scaphaphorura) arenaria* (Petersen, 1965); Denmark

–   Claws normal; PAO mostly with fewer vesicles   **5**

5   PAO with 6 V-shaped vesicles in 2 rows (Fig. 49) [PA]   ***Jevania*** Rusek, 1978
            type species: *Jevania fageticola* Rusek, 1978; Czechia

–   PAO with more or differently shaped vesicles   **6**

6   Ant IV with one apical papilla and two subapical sensory rods (Fig. 50); PAO with 17–28 simple vesicles (Fig. 51) [PA]
            Najtiaphorura Weiner & Thibaud, 1991
            type species: *Najtiaphorura sandrinae* Weiner & Thibaud, 1991; France

–   Ant IV without an apical papilla; with only one subapical microsensillum and a very thick sensillum b (Fig. 52); PAO with up to 37 longish to oval vesicles (Fig. 53) [PA]   ***Doutnacia*** Rusek, 1974
            type species: *Doutnacia xerophila* Rusek, 1974; Czechia

7   Asp with secondary lateral spines ('branched', Fig. 54); PAO with up to 70 rod-like or bilobate vesicles [PA]   ***Neotullbergia*** Bagnall, 1935

type species: *Tullbergia tricuspis* Börner, 1902; Italy

–   Asp smooth   **8**

8   Abd VI with a ventro-medial protuberance (Fig. 55; not always visible from above!)   **9**

–   Abd VI without a ventro-medial protuberance   **13**

9   Abd VI with one pair of Asp   **10**

–   Abd VI with two pairs of Asp   **12**

10   Abd VI with spiniform processes in dorso-external position, pso of different types   **11**

–   Abd VI without spiniform processes, doubly striated pso (type II), pso formula 11/0–1, 1, 1/11111 [HA]   ***Metaphorura*** Bagnall, 1936

type species: *Tullbergia affinis* Börner, 1902; Germany

11   Abd VI with crescentic ridges (Fig. 17, 18), doubly striated pso (type II), pso-formula 11/122/22221 [T/S]   ***Delamarephorura*** Weiner & Najt, 1999

type species: *Mesaphorura salti* Delamare Deboutteville, 1953; Tanzania

–   Abd VI without crescentic ridges, with 3+3 additional, short dorsal spines (Fig. 57); pseudocelli elliptical with ridges perpendicular to the long axis (type III), pso formula 11/0–1, 1,1/11111 [S/T]   ***Dinaphorura*** Bagnall, 1935

type species: *Tullbergia spinosissima* Wahlgren, 1906; Argentina

12   Pseudocelli roundish, doubly striated (type II), PAO with tripartite vesicles (Fig. 58) [PA]   ***Marcuzziella*** Rusek, 1975

type species: *Marcuzziella tripartita* Rusek, 1975; Italy

–   Pseudocelli elliptical, with ridges perpendicular to the long axis (type III), PAO elliptical with 10–17 vesicles, sometimes secondarily divided (Fig. 59) [HA]   ***Neonaphorura*** Bagnall, 1935

type species: *Tullbergia duboscqi* Denis, 1932; France

13   Ant III O with three sensory clubs, two of them bent towards one another (Fig. 60); Abd VI without crescentic ridges   **14**

–   Ant III O with two sensory clubs, bent towards one another (Fig. 61); Abd VI with or without crescentic ridges   **19**

14   Abd VI with 1+1 dorso-lateral spines in front of the posterior pair of anal
         spines (Fig. 62)   **15**

–   Abd VI without dorso-lateral spines   **17**

15   Abd I–III with 2+2 pso each; PAO with 6–8 long-oval vesicles in 2 rows [PA]
                                        Fissuraphorura gisini (Selga, 1963); Spain

–   Abd I–III with 1+1 pso each; PAO with 25–90 vesicles in 2 rows   **16**

16   PAO with ca. 60 simple rod-like vesicles in two rows perpendicular to the longer axis [T]
                                                        Anaphorura Izarra, 1972
                        type species: *Tullbergia (Anaphorura) lavadoi* Izarra, 1972; Argentina

–   PAO with 38–100 globular vesicles in 2–3 rows (Fig. 63) [PA]
                                                        Stenaphorura Absolon, 1900
                        type species: *Stenaphorura japygiformis* Absolon, 1900; Moravia

17   Th I–III with 0,0,1 pseudocelli; pso formula 11/001/01011; pso of type I; PAO elongated;
         Asp very short, 1/3 the length of claw III [S]   ***Tillieria*** Weiner & Najt, 1991
                        type species: *Tillieria insularis* Weiner & Najt, 1991; New Caledonia

=   Th I–III with 0,1,1 pseudocelli; pso formula 11/011/11111; pso of type I
                                        'Southern group' of ***Tullbergia*** Lubbock, 1876
                        reference species: *Tullbergia antarctica* Lubbock, 1876; Antarctic

–   Th I–III with 1,1–2,1–2 pseudocelli   **18**

18   PAO with 40–50 rod-like vesicles in 2 rows (*T. pomorskii* Smolis with 60–90 vesicles
         in 4 rows); Ant III O with a well visible protecting fold [HA]
                                        'Nordic group' of ***Tullbergia*** Lubbock, 1876
                        reference species: *Tullbergia arctica* Wahlgren, 1900; Holarctic

–   PAO with 6–8 coffee-bean-like vesicles in 2 rows (Fig. 9) [HA]
                                                        Fissuraphorura Rusek, 1991
                        type species: *Fissuraphorura cubanica* Rusek, 1991; Cuba

19   Ant III O without small sensory rods between the two sensory clubs; PAO
         with 6–10 quadrangular vesicles (Fig. 64) [T]   ***Prabhergia*** Salmon, 1965
                        type species: *Prabhergia nayarii* Salmon, 1965; South India

–   Ant III O with two sensory clubs and (1–) 2 small sensory rods (Fig. 61)   **20**

20   Anterior border of Abd VI with crescentic ridges (Fig. 65)   **21**

–   Anterior border of Abd VI without crescentic ridges   **25**

21   PAO with 6 vesicles (Fig. 66)   **22**

–   PAO with more than 18 vesicles   **23**

22   PAO with 6 elongate vesicles arranged in two inaccurately separated rows (Fig. 67) [PA]
                                                              Karlstejnia Rusek, 1974
                            type species: *Karlstejnia annae* Rusek, 1974; Bohemia

–   PAO with 6 V-shaped vesicles in two rows (Fig. 68) [PA]   ***Wankeliella*** Rusek, 1975
                            type species: *Wankeliella peterseni* Rusek, 1975; Jutland

23   PAO broad, with 60–110 simple vesicles lying in 4–7 irregular longitudinal rows
        (Fig. 69) [HA]   ***Multivesicula*** Rusek, 1982
                            type species: *Multivesicula columbica* Rusek, 1982; Canada

–   PAO elongated, with 18–68 vesicles lying in 2 (–3) rows (Fig. 6)   **24**

24   Pseudocelli only of type I (star-like; Fig. 16 I); Asp small, shorter than claws;
        body length 0.4–2.0) mm [WW]   ***Mesaphorura*** Börner, 1901
                            type species: *Mesaphorura krausbaueri* Börner, 1901; Germany

–   Pseudocelli of type IV (convergently striate, Fig. 16 IV), especially at the antennal base;
        Asp stronger, longer than claws; body length 0.7–1.2 mm [HA]
                                                     Paratullbergia Womersley, 1930
                            type species: *Paratullbergia concolor* Womersley, 1930; England

25   PAO irregular, vesicles not in rows   **26**

–   PAO more or less regular with vesicles lying in rows   **27**

26   Abd I–III with 0,0,1 pseudocelli; PAO aberrant (Fig. 70); dorsal sensory clubs of Ant III O
        exceptionally large [T]   ***Sensilatullbergia*** Thibaud & Ndiaye, 2006
                            type species: *Sensilatullbergia senegalensis* Thibaud & Ndiaye, 2006; Senegal

–   Abd I–III with 2,2,2 pseudocelli; dorsal sensory clubs of Ant III O of normal length [NA]
                                                     Rotundiphorura Rusek, 1991
                            type species: *Rotundiphorura habanica* Rusek, 1991; Cuba

27   PAO with 12–18 vesicles; pso formula 11/122/22221; PAO with 12–18 rod-like vesicles [T]
                                                     Spicatella Thibaud, 2002
                            type species: *Spicatella bedosae* Thibaud, 2002; Vietnam

–   PAO with more than 18 vesicles   **28**

28   Vesicles of the PAO more or less rod-like   **29**

–   Vesicles of the PAO more or less ovoid   **30**

29   Th I–III with 0,1,1 pso; pso type I or IV; sensilla on Ant IV normal, not hammer-shaped; pseudocelli of two types: on head and Abd V type I (Fig. 71a) and on Th II–Abd IV type IV (Fig. 71b) [PA]

Psammophorura Thibaud & Weiner 1994

type species: *Psammophorura gedanica* Thibaud & Weiner, 1994; Poland

–   Th I–III with 1,2,2 pso   **31**

30   Pseudocellar formula 11/122/11121; PAO with 17–40 rod-like vesicles; Ant III O with an only indistinct protecting fold [T]   ***Weinera*** Thibaud, 1993

type species: *Weinera ghislaineae* Thibaud, 1993; Martinique

–   Pseudocellar formula 11/122/22221

Stenaphorura sensu Thibaud, 2002 [non Absolon, 1900!]

type species: *Stenaphorura marionae* Thibaud, 2002; Vietnam

(invalid genus name; see remarks to *Stenaphorura* Rusek, 2010)

31   Pseudocellar formula 11/122/22221; PAO 2.7 times the length of nearest pseudocellus; with 35–36 vesicles [S]   ***Boudinotia*** Weiner & Najt, 1991

type species: *Boudinotia prima* Weiner & Najt; New Caledonia

–   Th I–III with 0,1,1 pso   **32**

32   Abd I–III with 0,1,1 pseudocelli; sensilla on Ant IV hammer-shaped (Fig. 72); pseudocelli of type III with incomplete ring border [HA]   ***Pongeiella*** Rusek, 1991

type species: *Tullbergia falca* Christiansen & Bellinger, 1980; Ontario

–   Abd I–III with 1,0,0 pseudocelli; PAO elongated with about 60 vesicles in 2 rows [T]

Tullbergiella Izarra, 1965

type species: *Tullbergia (Tullbergiella) humilis* Izarra, 1965; Bahia Blanca

   Not included in this key is the recently used generic name *Spinaphorura* Arbea, 1987, mentioned by the author in his unpublished thesis '*Spinaphorura clavata*'. This name is referred to in the catalogue of JORDANA, ARBEA & ARIÑO (1990: 129) as '= *Neonaphorura* sp.'. Therefore, *Spinaphorura* Arbea is an invalid name.

   Only provisionally included are the taxa of the 'southern group' of *Tullbergia* with *Tullbergia antarctica* Lubbock, 1876. A comprehensive revision is necessary to detect a clear separation of the 'northern and southern groups' from the traditional taxon *Tullbergia* Lubbock, 1876.
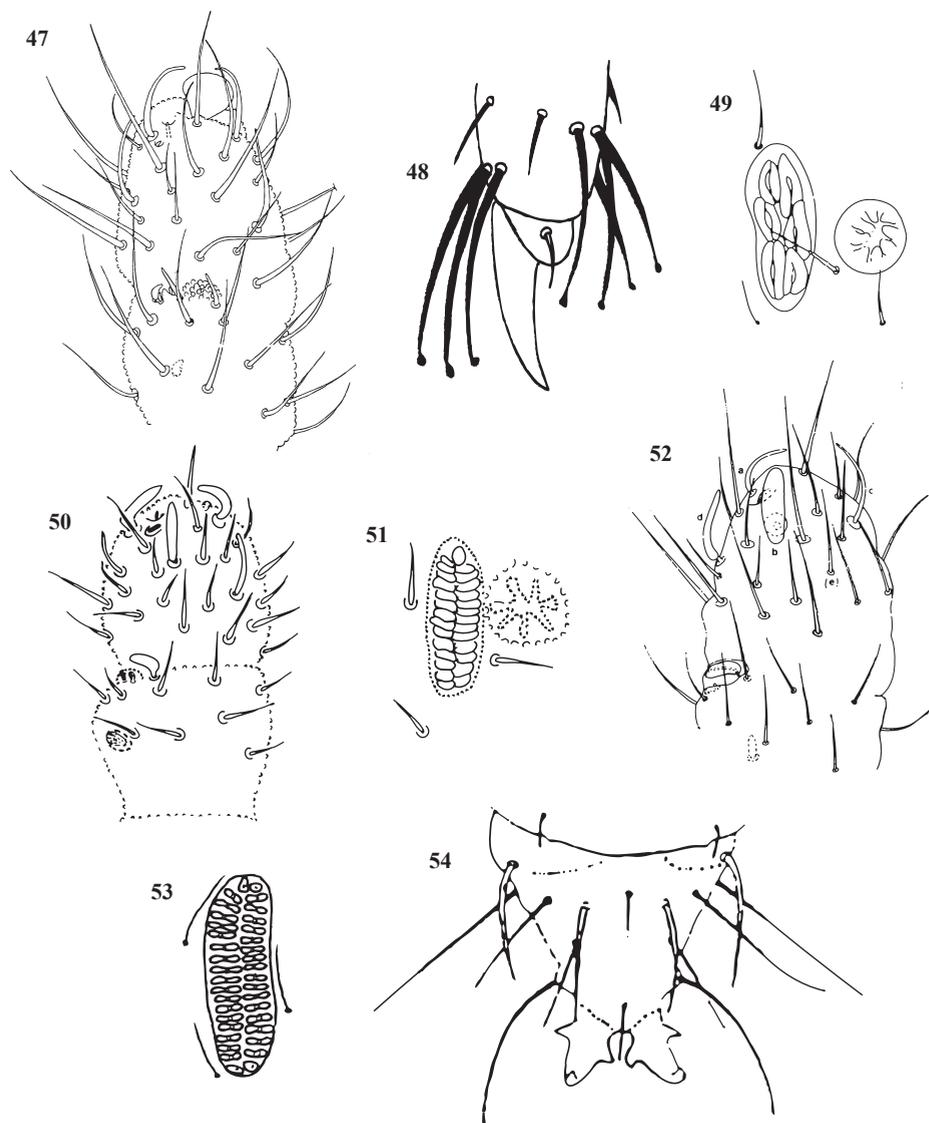
Fig. 47 *Tasphorura vesiculata*: Ant III+IV (after GREENSLADE & RUSEK 1996).
Fig. 48 *Clavaphorura septemseta*: clavate setae (after SALOMON 1943).
Fig. 49 *Jevania weinerae*: PAO and pso (after RUSEK 1978).
Figs 50–51 *Najtiaphorura sandrinae*: Ant III+IV (**50**) and PAO (**51**) with pso (after WEINER & THIBAUD 1991).
Figs 52–53 *Doutnacia xerophila*: Ant III+IV (**52**) and PAO (**53**) (after RUSEK 1974).
Fig. 54 *Neotullbergia ramicuspis*: Abd VI (after GISIN 1960).
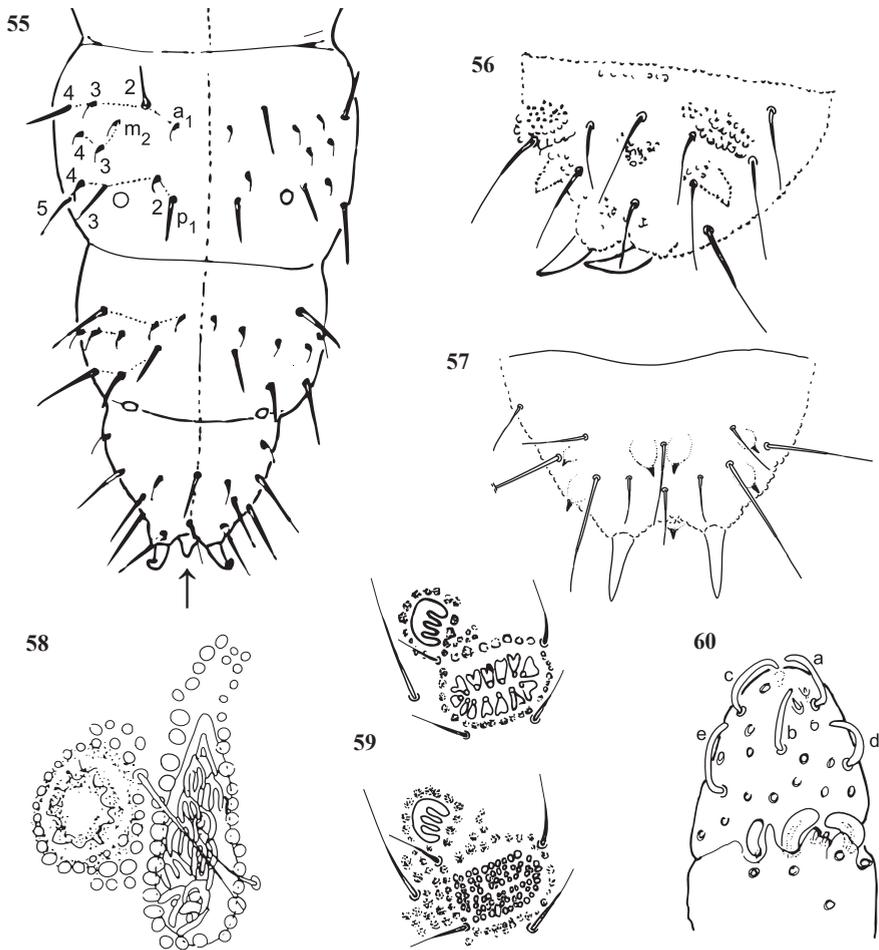
Fig. 55   *Metaphorura affinis*: Abd IV–VI; ↑ = ventromedial protuberance (after FJELLBERG 2007).
Fig. 56   *Delamarephorura salti*: Abd VI (after WEINER & NAJT 1999).
Fig. 57   *Dinaphorura kerguelensis*: Abd VI (after DEHARVENG 1981).
Fig. 58   *Marcuzziella tripartita*: Pso and PAO (after RUSEK 1975).
Fig. 59   *Neonaphorura loksai*: Pso and different optical levels of PAO (after TRASER & THIBAUD 1999).
Fig. 60   *Tullbergia simplex*: Ant III+IV (after FJELLBERG 1998).
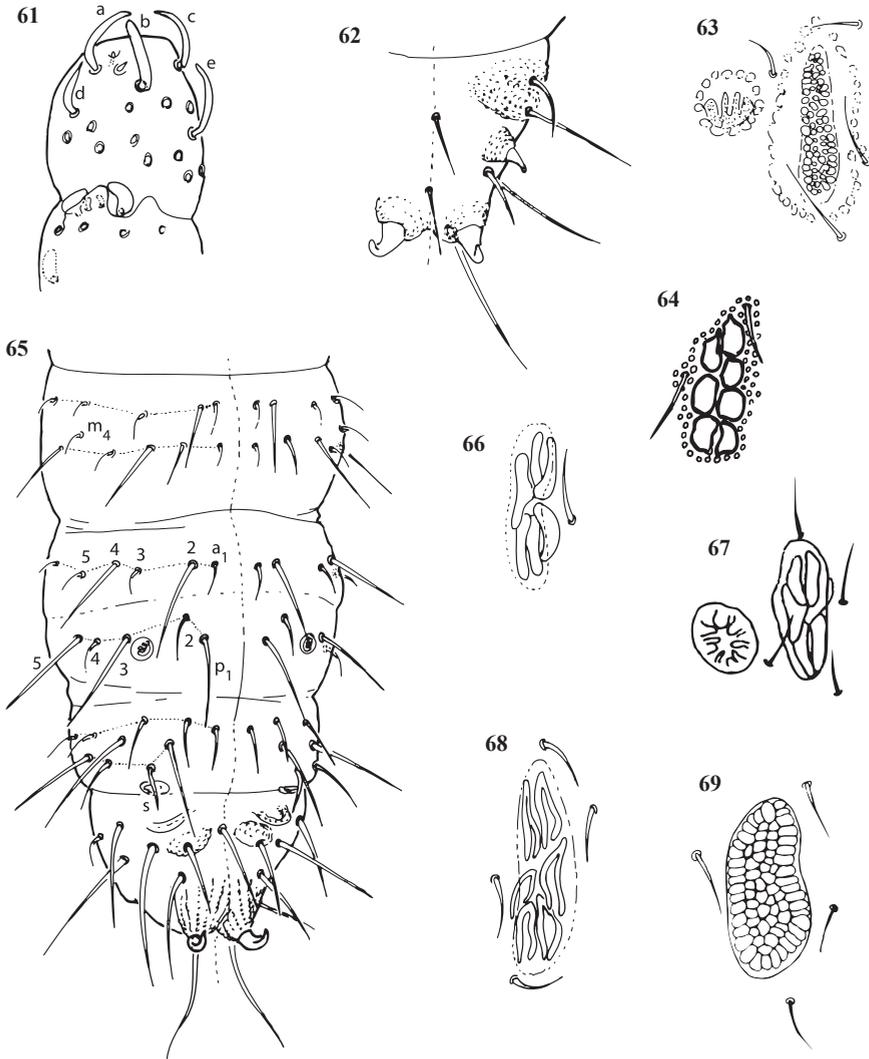
Fig. 61   *Mesaphorura spp*.: Ant III+IV (after FJELLBERG 1998).
Fig. 62   *Stenaphorura quadrispina*: Abd VI (after FJELLBERG 1998).
Fig. 63   *Stenaphorura quadrispina*: Pso and PAO (after FJELLBERG 1998).
Fig. 64   *Prabhergia nayarii*: PAO (after SALMON 1965).
Fig. 65   *Paratullbergia callipygos*: Abd III–VI (after FJELLBERG 1998).
Fig. 66   *Karlstejnia norvegica*: PAO (after FJELLBERG 1998).
Fig. 67   *Karlstejnia montana*: Pso and PAO (after WEINER 1983).
Fig. 68   *Wankeliella medialis*: PAO (after FJELLBERG 1998).
Fig. 69   *Multivesicula giljarovi*: PAO (after RUSEK 1982a).

Tab. 3   Characteristics of the genera of Tullbergiidae of the world.

Genus	Ant III O			Ant IV sensory			Postantennal Organ				Pseudocelli		Abdomen VI			Length	Males	Geography
	sc	sr	pf	as	ss	sa	rl	vf	m	vn	type	formula	cr.r	dmsp	Asp	mm		
Anaphorura	3	2	p2	1	5	-?	3	r	2	60 (25–80)	IV/in	1,1 / 1,1,1 / 1 / 1,1,1,1	-	2	2	1.2	-	T
Boudinotia	2	2	f0	1	5	2	2,7	r-ov	2	35–36	I/co	1,1 / 1,2,2 / 2,2,2,2,1	-	-	2	0.8	-	S
Clavaphorura	4	2	f–p3	1 (-2?)	2	0?	?	r	2	35–36	I	1,1 / 1,2,2 / 1,1,1,2,1	-?	-	2	1.2	?	S
Delamare-phorura	2	2	p3	1	5	2	2–3	r-q	2	14–15	I–II	1,1 / 1,2,2 / 2,2,2,2,1	+	2	2+1	1.0–1.4	+	T
Dinaphorura	3	2	fp	1	5–8	2	2	r-ob	2	12–30	III	1,1 / 0–1,1,1 / 1,1,1,1,1	-	3–8	2+1	0.7–1.8	+	T/S
Doutnacia	1	2	fs	1	4	2	2.3	os	2	37–39	I/co	1,1 / 0,1,1 / 0–1,1,1,1,1	-/+	-	2	0.25–0.5	+	PA
Fissur-aphorura	3	2	p3	1	5	2	2.5	d	2	6–8	III/in	1,1 / 1,2,2 / 2,2,2,2,1	-	0–2	2	0.7–1.1	+	HA
Jevania	1	2	fs	1	4	2	2	d	2	6	I/co	1,1 / 0,2,2 / 1,1,1,1,1	+	-	2	0.5	-	PA
Karlstejnia	2	1–2	fp	0–1	4	1–2	1.5	d	ir	6	I	1,1 / 0,2,2 / 1,1,1,1,1	+	-	2	0.4–0.6	+	PA
Marcuzziella	2	2	p2	1	5	2	2.0–2.5	d	ir	12–14	II/co	1,1 / 1,2,2 / 2,2,2,2,2	-	2	2+1	0.9	-	PA
Mesaphorura	2	2	fb	(0)–1	(3–)5	2	1.2–2.4	r	2	18–55	I/co	1,1 / 0–1,0–1,1–2 / 0–1,0–1,0–1,0–1	+	-	2	0.4–1.0	(+)	WW
Metaphorura	2	2	p3	1	5–8	2	2.8–3.8	d	2	18–28	II/co	1,1 / 0–1,1–2,1–2 / 0–2,1–2,1–2,1	-	-	2+1	0.7–1.5	?	HA
Multivesicula	2	2	fp	1	4	2	2	r-g	4–7	60–110	I/co	1,1 / 0,1,1–2 / 0–1,1,0–1,1,1	+	-	2	0.4–0.6	-	HA
Najtiaphorura	1	2	fs	1	5	2	2	r	2	17–30	I/co	1,1 / 0,0–2,1–2 / 0–1,0–1,0–1,0–1,1	+	-	2	0.5	+	PA
Neonaphorura	3–2	2	p3	1–(2)	5–8	2	1.5–2	d	2	10–26	III;IV/ co	1,1 / 1,1–2,1–2 / 1–2,1–2,1–2,1–2,1	-	4–8	2+1	0.7–1.4	+	HA

Genus																	
Neotullbergia *	2	2	p2	1	4–5	2	3.8–4.4	r2	2	50–60	IV/co	1,1 / 0,1,1 / 1,0,0,1,1	+	2	2	0.6–1.1	+	PA
Neotullbergia **	3	2	p2	1	5	2	5–5.5	r2	2(4)	50–60	III/in	1,1 / 1,1,1 / 1,1,1,1,1	-	2	2	0.7–1.3	+	PA
Paratullbergia	2	2	fb–p2	0–1	4–5	2	2	r2	2(4)	35–68 (70–100)	I;IV/co	1,0–1 / 0,0–1,0–1 / 1,0–1,0–1,1,1	+	0–2	2	0.6–1.2	+	HA
Pongeiella	2	2	fs	(3–)4	3	2	2.3	os	2	23–30	III/in	1,1 / 0,1,1 / 1,1,1,1,1	-	-	2r	0.5–0.6	-	HA
Prabhergia	2	0	fs	?	(3–)5–6	0?	1.5	qu	2	(6–)7–8 (–10)	I/bp	1,1,1 / 0,1,1 / 1,1,1,1,0	+	-	2	0.4	?	T
Psammophorura	2	2	p3	1	5	2	2	r	2(–3)	30–40	I;IV	1,1 / 0,1,1 / 1,1,1,1,1	-	-	2	0.5–0.6	+	PA
Rotundiphorura	2	2	fb	1	5	2	1.1	g	ir	>50	I/co	1,1 / 1,2,2 / 2,2,2,2,1	-	-	2	0.5	-	NA
Scaphaphorura	1	2	f(0–p)	1	1(–3)	1	2.3	g	5–8 (ir)	60–180	I/in	1,1 / 0,0–1,1 / 0,1,0,1,1	-	-	2	0.4–0.5	+	PA
Sensilatullbergia	2	2	fo	1	5	1	1.5	d	ir	10+x	I (?)	1,1 / 0,1,1 / 0,0,1,2,1	-	-	2	0.4–0.6	+	T
Spicatella	2	2	p3	1	5	2	2	d	2	12–18	III (?)	1,1 / 1,2,2 / 2,2,2,2,1	-	-	2	0.4–0.55	+	T
Stenaphorura	3	2	f2–3	1	5	2	3–5.6	r–g	2–4	38–100	III/IV	1,1–2 / 1,1–2,1–2 / 1,1,1,1–2,1	-	2	2	0.8–1.5	+	PA
Tasphorura	3	2	-	1	5	1+1	5	r	2	90	I co	1,1 / 1,1,1 / 1,1,1,2,1	-	-	2	1.5	+	S
Tillieria	3	2	f0	1	5	2	4.5	d	2	48–64	I/co	1,1 / 0,0,1 / 0,1,0,1,1	-	-	2	1.1–1.7	+	S
Tullbergia (HA)	3	2	fs	1	5–6	?	2.5	ov	2	40–50	III/co	1,1 / 1,2,2 / 1,1,1,2,1	-	-	2	0.6–4.0	+	HA
Tullbergia (T, AA)	3	?	f0	1	5–6	?	?	r–g	2–5	40–120	I/co	1,1 / 0,1,1 / 1,1,1,1,1	-	-	2	1.0–1.6	+	TS
Tullbergiella	2	2	f0	1	3	0	1.1	g	ir	60	I/co	1,1 / 0,1,1 / 1,0,0,1,1	-	-	2	0.5–0.7	-	T
Wankeliella	2	2	fb	1	4	2	2.5–3	d	ir	6	II/co	1,1 / 0,2,2 / 0–1,1,1,1,1	-	-	2r	0.5–0.7	-	PA
Weinera	2	2	fs–f0?	1	6	2	2.5	r–ov	2–3	17–40	II/co	1,1 / 1,2,2 / 1,1,1,2,1	-	-	2r	0.3–0.4	+	T

Abbreviations: see page 34.

* *Neotullbergia ramicuspis* and *N. crassicuspis*; ** *Neotullbergia staudacheri* and *N. tricuspis*

Abbreviations (Tab. 3, page 32–33)

A III O

dorsal sensory organ of third antennal segment, **sc:** number of (mostly thickened) sensory clubs, **sr:** number of sensory rods, **pf:** types of the protecting fold: not developed **(f0)**, small or shallow **(fs)**, papillae-like **(fp)** or broad **(fb),** or there are two to three distinct papillae **(p2, p3)**.

Ant IV sensory

sensilla of the dorsal side of the 4th antennal segment, **as:** number of (ventro-) apical vesicles, **ss:** number of tickened long sensilla (a–e), **sa:** number of subapical sensory rods (subapical organite + microsensillum).

Postantennal organ

rl: relative length compared to the pseudocellus of the antennal basis; **vf:** form (type) of the vesicles: rod-like **(r)**, rod-like with two heads **(r2)**, globular **(g)**, quadrangular **(qu)**, ovoid **(ov)**, longish oval with centric stem **(os)**, oblique to the long axis **(ob)** or divergently formed **(d)**; **rn:** number of rows; irregular **(ir)**; **vn:** number of vesicles.

Pseudocelli

type/border: type I (star-like/stellate), **II** (double striate), **III** (crescentic), **IV (**convergently striate) (Fig. 16) **border:** distinct border by a ± clearly visible complete ring or rosette **(co),** or incompletely ringed **(in),** in rare cases bipartite **(bp), formula:** numbers on one side of the head/ thorax I…III/ abdomen I…V; variations are given as '1–2' between the commas.

Abdomen VI

characters of the tergite of Abdomen VI, **cr.r:** presence (+)/absence (-) of proximal crescentic ridges (Fig. 17, 18), **dmsp:** number of medial (dorsal/lateral) tubercles with spines or strong setae, **Asp:** number of anal spines present (+) or absent (-); weakly developed (+/-); branched (br); a ventral protuberance between Asp present (+1); sometimes present (+0–1).

Length

maximum body length (without antennae) in mm.

Males

have been seen (+) or not (-).

Geography

general distribution: **(PA)** Palaearctic; **(HA)** Holarctic; **NA** Nearctic; **(T)** Tropics; (**AA**) Antarctic; (**WW**) worldwide.
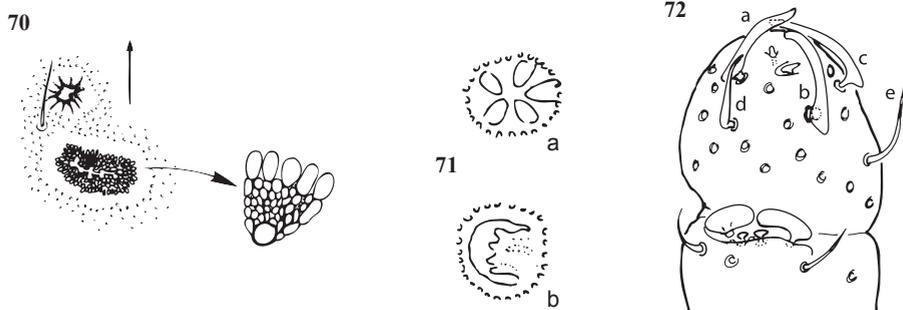

Fig. 70 *Sensilatullbergia senegalensis*: Pso and PAO (after THIBAUD & NDIAYE 2006).

Fig. 71 *Psammophorura gedanica*: Pso type I (a) and type II (b) (after THIBAUD & WEINER 1994).

Fig. 72 *Pongeiella falca*: Ant III+IV (after FJELLBERG 1998).

4. Keys and diagnoses on the Palaearctic taxa of Tullbergiidae (with keys to the holarctic species)

Genus *Doutnacia* Rusek, 1974 (64)

Key to the species of the world

1	Abd I with 1+1 pseudocelli	*xerophila* Rusek, 1974
–	Abd I without pseudocelli (Fig. 77)	*mols* Fjellberg, 1998

Diagnosis of the genus

Body slender, *Mesaphorura*-like; length 0.40–0.45 mm; without pigment. Granulation of the integument fine, uniform, somewhat coarser on Abd VI. Ant IV (Fig. 73, 74) dorsally with a very thick sensillum b; sensilla a, c and e setaceous; sensillum d can be slightly thickened; further a small apical bulb as well as a subapical organite and a microsensillum are present (POMORSKI & SKARŻYŃSKI 1998). Ant III O with only one large, bent sensory bulb and two small sensory clubs (standing close together) behind a low protecting fold. Ventrally with a large, erect sensory bulb. PAO long-oval, 2.0–2.5 times as long as the next pso (Fig. 75, 76); with 37–39 vesicles in two rows. The vesicles are narrow, somewhat constricted in the middle (bean-shaped), inserting from a circular stalk. Exceptionally, the vesicles are not located in a depression but standing open at the level of the integument (Fig. 75, 76). Pseudocelli with rosette-like edges and a star-like centre (type I); pseudocellar formula: 11/011/0–1, 1, 1, 1, 1. Dorsal pso on Th II–III in a lateral position (between *m*5 and *p*5); on Abd I (II)–IV in a dorsal position (between *p*2+4); on Abd V behind *p*1. Mouth parts (after FJELLBERG 1998): Labrum with 11 setae, 4 prelabral setae; labium with 5 papillae (A–E) and 6 proximal setae; basolabial fields with 4+5 setae.

Dorsal chaetotaxy (Fig. 77): Th I: 0/ 8/ 0; Th II: 10/ 8/ 8; Th III: 8/ 8/ 8; Abd I: 8/ 2/ 10; Abd II: 10/ 2/ 10; Abd III: 10/ 2/ 10; Abd IV: 10/ 0 (4)/ 10; Abd V: 8/ 0/ 6 (8). Mac well differentiated. Abd IV with setae *m*4+5, *p*1–*p*1 more widely separated than *p*2–*p*2. Abd V with 2+2 short *a*-setae between the long *a*3; sensillum *p*3 spine-like. Other dorsal sensilla on tergites setaceous. Crescentic ridges on Abd VI present or absent. Two Asp shorter than claws, on weakly developed papillae.

Ventral chaetotaxy: Tita with a *Mesaphorura*-type of chaetotaxy. Claws as in *Mesaphorura*, without teeth; empodium rudimentary. VT with 5+5 setae (2+2 distal, 2+2 posterobasal, 1+1 lateral). Anal lobes without setae *l*2 and *l*2'. Both sexes are known .

Distribution: From Scandinavia to Central Europe.

Genus description: RUSEK (1974: 64), POMORSKI & SKARŻYŃSKI (1998), FJELLBERG (1998).

Type species: *Doutnacia xerophila* Rusek, 1974 (65).

Remarks: MASSOUD & THIBAUD 1985 (42) described as a nov. spec. *Doutnacia coineaui* from La Grande Motte, south of Montpellier, France; in costal sand dunes, up to 20–40 cm depth. This species probably belongs to another genus due to having some divergent characters: formula of pseudocelli 11/011/10011; pso on Abd II+III missing; presence of 1+1 candle-like lateral sensilla on Th II+III and Abd III+IV; 2+2 such sensilla on Abd V. Both the absence of an apical papilla (organite) on Ant IV and the type of PAO (lying in the bottom of a deep depression) further separate '*Doutnacia coineaui*' from the genus *Doutnacia.* The species is very briefly and incompletely described; a re-examination of the type specimens by Schulz & Dunger in 2009 did not reveal new information. Therefore we consider '*Doutnacia coineaui*' to represent a mere species inquirenda.

Diagnoses of the species

Doutnacia mols Fjellberg, 1998 (146)
Syn.: *Doutnacia ammophila* Pomorski & Skarżýnski, 1998 (247)

Body length 0.4–0.5 mm; habitus slender, *Mesaphorura*-like; without pigment. Ant IV (Fig. 74) with 4 sensilla: sensillum b not elongated, thick; sensillum d slightly thickened, sensilla a, c and e setaceous. A small apical bulb present. Ant III O dorsal with one large, thickened, bent sensory bulb and two small rods behind a low protecting fold; one large ventro-lateral sensory bulb. PAO (Fig. 76) narrow (length/width ratio 4–5:1), not subjacent to the integument, with 35–39 bean-shaped vesicles in two parallel rows. Vesicles simple, sometimes with a shallow deepening in the middle, not compactly arranged. Pseudocelli circular, star-like (type I); pseudocellar formula: 11/ 011/ 01111. Mouth parts: Labrum with 11 setae; 4 prelabral setae. Labium with 5 papillae (A–E) and 6 proximal setae. Basolabial fields with 4+5 setae. Four apical guard setae ($g1$, $g2$, $g4$, $g7$). Mandibles and maxilla unmodified.

Dorsal chaetotaxy (Fig. 77) as typical for the genus; but on Abd IV 5+5 setae in the *a*-row. Macrosetae well differentiated. Th III–Abd I without seta $a2$. On Abd IV setae $m4+5$ present, $p1$–$p1$ slightly more widely separated than $p2$–$p2$. Abd V with 2+2 short *a*-setae between the long $a4$; sensillum $p3$ spine-like. Other dorsal sensilla on tergites setaceous. Pso on Abd V protruding (Fig. 78). Abd VI without clear crescentic ridges. The two Asp curved, shorter than claws.

Ventral chaetotaxy: Claws simple, without teeth, empodial appendage rudimentary. Tita with 11, 11, 11 setae. VT with 6+6 setae. Abd sternite IV without trace of furca. Anal lobes without setae $l2$ and $l2$'. Males known only for '*Doutnacia ammophila*'-records from Bulgaria.

Locus typicus: Hills above the Mols laboratory in Denmark; abundant among roots of *Corynephora arborescens* in a dry, sandy, south-facing slope with scattered vegetation.

Occurrence: The records of '*Doutnacia ammophila*' (junior synonym) by POMORSKI & SKARŻÝNSKI (1998) enlarge the knowledge of distribution: Bulgaria, Arkutino near Sozopol, on roots of plants on sand dune, and dry meadow, south slope, Winiary near Busko-Zdrój, Poland. Further Hungary (Bükk Mts., Kiskunság; DÁNYI & TRASER 2008).

Taxonomy: FJELLBERG (1998), POMORSKI & SKARŻÝNSKI (1998).

Doutnacia xerophila Rusek, 1974 (65)

Body length 0.46 mm; without pigment. Granulation of the integument regularly fine; on Abd VI coarser. Ant shorter than the head. Ant IV (Fig. 73) with 4 thickened sensilla (a–d), sensillum e setaceous; b very thick, c thin and longest. Ant III O dorsally with one large, bent sensory club, two small sensory rods and a protecting papilla; ventrally with a straight, unbent sensory club. PAO long oval with 37 simple, not depressed vesicles arranged in two rows, which are somewhat contracted in the middle and placed on a circular stalk (Fig. 75). Pseudocelli with rosette-like edges and a star-like centre (type I). Pseudocellar formula: 11/011/11111. Ps.oc. on Th II+III between $m5$ and $p5$.

Dorsal chaetotaxy: Mac and mic well differentiated. Th II without setae $m2$ and $p2$, Th III without $a2$. Lateral sensilla on Th II+III longer than mac, microsensilla s' present. Abd I with $a2$ absent and $m3$ present; Abd II with $m4$ present. Abd V (Fig. 79) with $p3$ present as a thickened, spindle-like sensillum. Abd VI with clear crescentic ridges (in specimens from Central Europe; in Nordic specimens 'ridges are most weakly indicated by a special arrangement of skin granulation' [FJELLBERG 1998]). Further on Abd VI two Asp (shorter than claw) on low papillae.
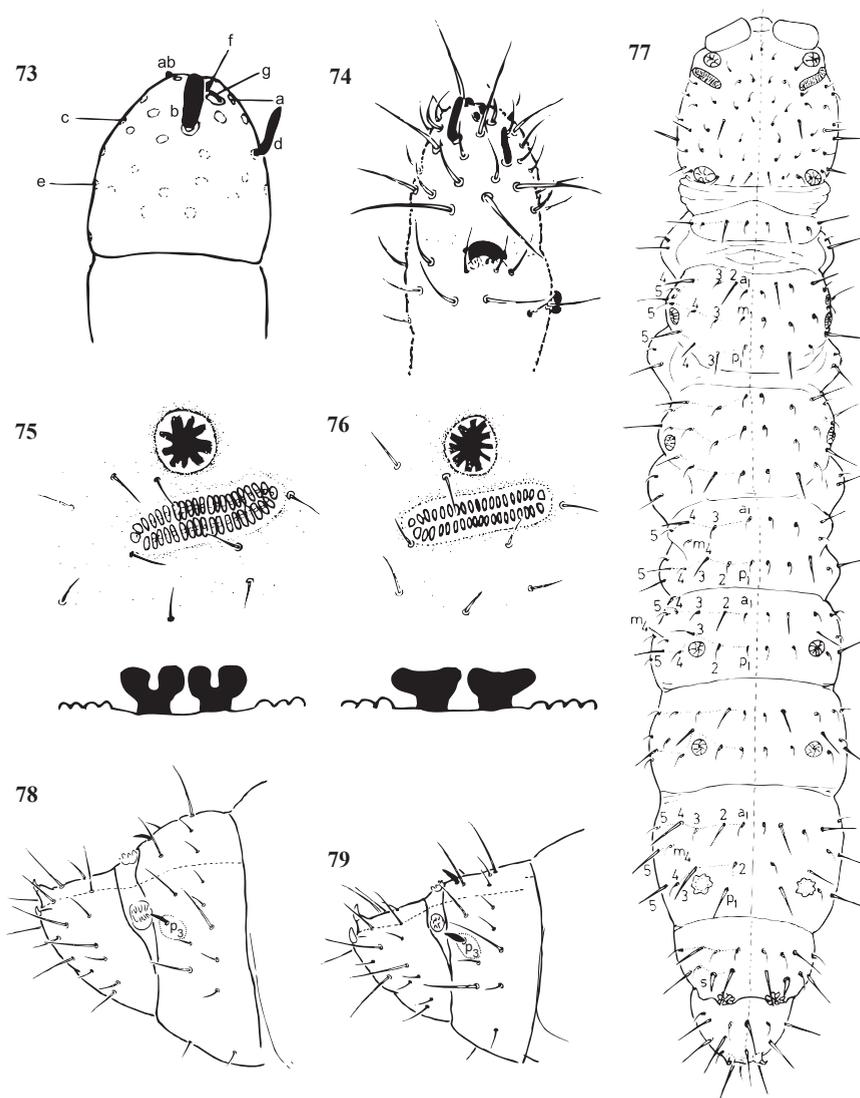
Fig. 73 *Doutnacia xerophila*: Ant IV, scheme, dorsal view; ab = apical bulb, a–e = sensillae.
Fig. 74 *Doutnacia mols*: Ant III+IV, right antenna, dorsolateral view.
Fig. 75 *Doutnacia xerophila*: (on top) Pso and PAO, (below) cross section of PAO with surrounding skin.
Fig. 76 *Doutnacia mols*: (on top) Pso and PAO, (below) cross section of PAO with surrounding skin.
Fig. 77 *Doutnacia mols*: dorsal chaetotaxy.
Fig. 78 *Doutnacia mols*: chaetotaxy of Abd V+VI.
Fig. 79 *Doutnacia xerophila*: chaetotaxy of Abd V+VI.

(Figs 73–76, 78, 79 after POMORSKI & SKARŻYŃSKI 1998, Fig. 77 after FJELLBERG 1998).

Ventral chaetotaxy: Claws without teeth; 10 μm; empodial appendage small, without inner lamella. VT with 5+5 setae, further 1+1 setae aside. No trace of furca. Female genital plate with 1+1 mic, lateral with 1+1 somewhat thicker setae. Male genital plate with 13 setae. Anal lobes with setae *l*2 *and l*2'; setae l3,5,8–10 in one row.

Locus typicus: near Doutnác, Bohemian karst; sw Praha, Czechia; grass-steppe (Festucetum).

Occurrence: a few records from Denmark and Sweden; in dry beach meadows (FJELLBERG 1998), Italy (macchia mediterranea), Serbia (sands with *Pinus nigra*), Latvia (JUCEVIČA 2003), Hungary (DÁNYI & TRASER 2008); thermophilous in the Slovak Karst (RASCHMANOVÁ et al. 2008), *Festuca* meadows in the Upper Rhine valley near Heidelberg (RUSSELL 2008), forest steppes of the Middle Volga basin (SHVEENKOVA 2010).

Ecology: prefers xerothermic and woody steppes (RUSEK 1979b).

Genus *Fissuraphorura Rusek*, 1991 (145)

Key to the holarctic species

1   Abd VI with one pair of small dorsal spines in front of the normal 1+1 Asp
                                                                    gisini (Selga, 1963)
–   Abd VI without dorsal spines, with the normal 1+1 Asp
                                                                    duplex (Gama, 1962)

Diagnosis of the genus

Body slender, *Mesaphorura*-like*;* length 0.7–1.0 mm; without pigment. Ant IV (Figs 4, 80–81) with 5 unequally thickened sensilla (a–e), two subapical sensilla (f, g) and one apical papilla. Ant III O in juveniles (Fig. 4) with only l–2, in adults with 3 large sensory clubs, two of them bent towards one another, 2 sensory rods between the clubs and 3 protecting papillae (the inner one less developed). The ventral sensory club of Ant III O laterally curved. PAO (Figs 9, 82) oblong-oval, about 2.5 times as long as the adjacent pseudocellus; with 6–8 vesicles in two rows, all coffee-bean-shaped and with a longitudinal furrow, but with variable microstructure. If this furrow is very deep, the vesicles may appear U-shaped and, on deeper layers, show about 6 rod-like structures (Fig. 9 after *F. cubanica* Rusek); in European species each vesicle seems to be largely subdivided into about 6 crosswise lying rods (therefore with 35–50 vesicles after original descriptions for *F. duplex* and *F. gisini*). Pseudocellar formula: 11/122/22221. A distinct boundary of the pseudocelli will appear only along ca. half to three quarters of their margin; their centre showing 1 (juveniles) to 6 (adults) stripes (type III, Fig. 16).

Dorsal chaetotaxy (Figs 26–28): Head with 2+2 *v*-setae. On Th II+III *p*2 absent, *a*2 present. Abd IV without transversal groove. On Abd V sensillum *p*3 basally thickened. Abd VI without crescentic ridges, with 2 Asp on distinct papillae; in some species (*F. gisini*) the *a*1-setae are present as spines.

Ventral chaetotaxy: Claws without teeth, Empodium weakly developed or completely absent. VT with 6+6 or 7+7 setae (4+4 distal and 2+2 or 3+3 posterobasal). Both sexes are known; males see Fig. 36.

Juvenile stages, esp. development of chaetotaxy (of *F. gisini)*, are described by LUCIÁÑEZ & SIMÓN (1992a) (Figs 26–28).

Occurrence: Iberian Peninsula, Cuba, Indonesia, India.

Genus description: RUSEK (1991b: 145); LUCIÁÑEZ & SIMÓN (1992b: 108).

Type species: *Fissuraphorura cubanica* Rusek, 1991.