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CONTRIBUTION TO THE KNOWLEDGE OF THE CEPHALIC SENSILLA AND WATER-UPTAKE SYSTEM OF ADULTS AND NYMPHS OF *VERNONIELLA BERGI* (KELLOGG 1906) (INSECTA; PHTHIRAPTERA: ISCHNOCERA).

ARMANDO C. CICCHINO and ALBERTO H. ABRAHAMOVICH*[1]

* División Entomología, Facultad de Ciencias Naturales y Museo. Paseo del Bosque s/n, 1900, La Plata, Buenos Aires, Argentina.

1 Fellow of CONICET (Argentina)

Short Title: External sensilla and Water-Uptake system of *V. bergi* (insecta).

Key words: Mechanoreceptors, Chemoreceptors, Water-Uptake system, *Vernoniella bergi*.

ABSTRACT: The external morphology of the different kinds of sensilla found on the surface of the head of *Vernoniella bergi* (Kellogg 1906), as well as the different devices of the water-uptake system, are studied by means of combined techniques of SEM and light microscopy. This study was carried out in a comparative form, analyzing the qualitative and quantitative variations among the three nymphal instars, male and female imagoes. For a reason of convenience, the louse head has been divided into: head capsule, antennae and mouthparts, and their sensilla studied separately. The water-uptake system was treated independently, and its mechanism investigated in living lice reared in Petri-dishes. The principal results of our findings are the following: a) *Sensilla of the head capsule:* all are *tactile sensilla*, discriminated by function after Neuffer (1954) into *typical tactile setae, position setae* and *pressoceptive setae*. b) *Sensilla of the mouthparts:* in the labrum, thick walled chemoreceptors only, and in the labium, typical tactile setae and thick-walled chemoreceptors. c) *The antennal sensilla: tactile setae* (typical tactile setae and position setae) and *chemoreceptors* (placodean sensilla, coeloconic sensilla and setae and pegs are found (thick and thin-walled chemoreceptors). Regarding the lingual sclerites and the water-uptake system as well as the different kinds of sensilla cited above, all are remarkably similar in morphology and number in adults and all nymphal stages, the only noticeable difference being the size attained.

RESUMEN: Se estudian en este trabajo la morfología externa de los diferentes tipos de sensilos y las distintas partes que componen el sistema de captación hídrica que se hallan en la cabeza de *Vernoniella bergi* (Kellogg 1906), mediante técnicas combinadas de microscopía electrónica de barrido y microscopía óptica convencional. El estudio ha sido llevado a cabo en forma comparativa, analizando las variaciones cuali y cuantitativas de las estructuras citadas en los tres estadios ninfales y los ímagos macho y hembra. Por una razón de conveniencia, la cabeza ha sido dividida topográficamente en: cápsula cefálica, antenas y partes bucales, estudiándose sus sensilos en forma separada. El sistema de captación hídrica tiene un tratamiento independiente, y su mecanismo básico de acción ha sido investigado a partir de piojos criados en cápsulas de Petri, en laboratorio. Los tipos de sensilos hallados son: a) *de la cápsula cefálica:* todos son *sensilos táctiles* (setas táctiles típicas, setas de posición y setas presoceptivas); b) *de las partes bucales:* en el labro únicamente quimioreceptores de paredes gruesas, en el labio setas táctiles típicas y quimioreceptores de paredes gruesas; c) *en las antenas*: setas táctiles (setas táctiles típicas y setas de posición) y quimioreceptores (sensilos

placodeos, sensilos celocónicos, y sensilos setiformes). Tanto los distintos tipos de sensilos arriba citados como las diferentes partes que componen el sistema de captación hídrica se han mostrado muy similares en morfología y número tanto en los adultos como en las formas ninfales, siendo su principal diferencia el tamaño absoluto de cada uno de ellos.

INTRODUCTION

The present contribution deals with the different kinds of sensilla present in the head of *V. bergi* (Kellogg 1906) (cephalic capsule, mouthparts and antennae), with brief comments on the morphology of the anatomical devices of the water-uptake system.

The literature concerning the ultrastructural features of lice belonging to the genus *Vernoniella* Guimaraes 1942 (Insecta: Phthiraptera; Philopteridae) is restricted to the papers published by us, dealing with the egg morphology (Abrahamovich & Cicchino, 1985, 1986 and 1987).

The most relevant studies concerning several aspects of structure and function of the head sensilla of different Ischnoceran genera of Phthiraptera are cited below, in chronological order.

Clay (1951) proposed a code of nomenclature for the cephalic setae, except for those found on the antennae and mouthparts of the Ischnocera, which is followed here.

Neuffer (1954) studied the sensilla of three Ischnoceran genera: *Philopterus, Brueelia* and *Bovicola* (in addition to the Amblyceran genera *Menacanthus* and *Trimenopon*), he grouped the sensilla into Tactile setae ("taktile sinneshaare") and Chemoreceptor sensilla ("chemische Sensillen"). The former kind of sensilla was also discriminated on a functional basis.

Clay (1970) illustrated by means of Scanning Electron Microscope pictures the antennal flagellum of three Ischnoceran genera: *Goniodes, Naubates* and *Trichodectes,* and pointed out that these have two "saucer-like sensilla" on antennal segment V (in addition to one coeloconic sensillum), and one on IV.

Slifer (1970) provided a review of the chemoreceptors known to occur in Insecta and other arthropoda, and later (1976) she studied the sensilla of the antennal flagellum of the Ischnoceran *Craspedorhynchus americanus* Emerson.

Eichler *et. al.* (1976) showed a SEM picture of the last antennal segment of *Columbicola columbae columbae* (L), but no comments about their number, size and functions are given.

Zacharuk (1980) revised the ultrastructure and function of insect chemosensilla, simplifying the typology formerly proposed by Altner (1977).

Rudolph (1982, 1983) reviewed the literature and on experimental grounds settled the functions and mechanisms of the different devices of the athmospheric water-uptake system.

Zlotorzycka and Kassner (1986) examined the antennal sense organs of the antennae of fourteen Ischnoceran species, discriminating them into six groups (A-F) on the basis of the morphological features of the sensilla investigated, and concluding that their morphology can be used not only for systematics but also for the special sense physiological peculiarities of these parasites.

An excellent study concerning the antennal sense organs located in the antennae of post-embryonic development stages of the human louse *Pediculus humanus humanus* (L.) (Anoplura: Pediculidae) has been carried out by Szczesna (1985).

As a result of careful analysis of the literature cited above in addition to several experimental data and biological observations, it is our purpose to provide a survey of all external sensilla, as well as the different parts of the water-uptake system, present in the head of adults and the three nymphal instars of *Vernoniella bergi,* not satisfactorily known to date.

MATERIAL AND METHODS

All specimens were obtained alive directly from the type host, *Guira guira* (Aves, Cuculiformes, Cuculidae, Crotophaginae) shot at La Plata and neighbouring areas (Buenos Aires Province, Argentina). All them were fixed in an ethanol-acetic mixture (1:1 vol/vol). Individuals for scanning study (adult males and females, and the three nymphal instars) were washed in distilled water, cleaned during 20-30 seconds in an ultrasonic vibrator, and dehydrated through a graded acetone series. After three changes in 100% acetone they were critical point dried in liquid CO_2 in a Sorvall Critical point drying apparatus. Then, the specimens were mounted on several stubs in different positions, coated with gold-palladium in a Jeol vacuum metallizer, and subsequently examined with a Jeol JSM U3 Scanning Electron Microscope.

Specimens for optical microscopy were cleared in phenol-ethanol 4:1 (vol/vol) and examined in a Wild M21 microscope with drawing apparatus.

For testing the presence of pores in the walls of the sensilla here studied, we used a solution of crystal violet applied to their external surface, following Slifer (1960).

Measurements: with the SEM, by means of the digital scale given at different magnifications, and with the light microscope, using an suitably calibrated eyepiece. All measurements are given in micrometers.

Pictures: for the SEM photographs a Kodak Verichrome pan ^{R} VP 120 (ASA 125/22 DIN) film was used. Drawings (except as otherwise stated) were done by means of a *camera lucida*, inked and photographed. All SEM pictures were stored in the iconographic collection at the La Plata Museum and are available from the authors.

RESULTS

For a reason of convenience, the louse head has been divided into the following regions: the head capsule, the mouthparts (labrum and labium), the antennae, and the water-uptake system. These gross anatomical structures of the head are extensively treated, among others, in the works by Blagoveshchenskyi (1959), Séguy (1944, 1951), Da Costa Lima (1939), Snodgrass (1896), Symmons (1952), Matsuda (1965), Clay (1951) and Rudolph (1982, 1983) We add drawings of male and female heads of *V. bergi* (figs. 24 y 25) in order to clarify the nomemclature followed here. A careful study of the external morphology (including morphometry), number and location of all sensilla has been carried out, with the following results:

I) Sensilla of the cephalic capsule (excluding those of the antennae and mouthparts, figs. 1-3 and 24-25)

All the sensilla examined are different kinds of setae, whose function will be discussed further. Their nomenclature (following Clay 1951), position and size in *V. bergi* are listed below:

pcs: *preconal seta*, medium long, ventral in position, arising just anterior to the conus.

mds: *mandibular seta*, medium long, ventral, arising between the conus and the mandibular framework.

pas: *preantennal seta*, small, dorsal, near the antennal socket.

pns: *postnodal seta*, small in the male, minute in the female; dorsal, posterior to the preantennal nodus.

os: *ocular seta*, medium long, dorsal, on the surface of the lens of ocellum.

av: *anterior ventral seta*, numbered I to III, in *Vernoniella*, as in genera such as *Bruelia*, *Philopterus* and *Saemundssonia*; av_I and av_{II} arise closer together than av_{III}. av_I and av_{II} are long, and av_{III} very long.

vsm: *ventral submarginal setae*, medium long,

numbered as I and II. vsm_I, arise near the marginal carina, and vsm_{II} just lateral to the ventral anterior plate.

as: *anterior setae,* medium long, numbered I to III. In *Vernoniella,* these setae arise on the anterolateral margins, at level of vsm_I.

ads: *anterior dorsal seta,* small, dorsal, associated with the dorsal preantennal suture.

dsms: *dorsal submarginal seta,* long, dorsal, near the marginal carina.

t: *temporal setae,* numbered I to VI. All them arise on or near the margins of the temples. t_I minute, t_{II} medium long, t_{III} minute, t_{IV} very long, t_V and t_{VI} minute.

pts: *postemporal seta,* small in the male, minute in the female, placed near the occipital margin.

II) Sensillae of the mouthparts (figs. 3, 18 y 22)

All are setae. Three morphological types are recognized:

1) *Long and slender setae:* they are the longest setae found in the labium (see figs. 18 and 22). They correspond to *typical tactile setae,* and their location, number and probable function are shown in table I.

TABLE I

NAME, LOCATION, NUMBER AND PROBABLE FUNCTION OF THE LABRAL AND LABIAL SENSILLAE OF *V.BERGI* (KELLOGG 1906).

NAME	LOCATION	NUMBER	PROBABLE FUNCTION
LABRAL THICK WALLED CHEMORECEPTORS (fig. 3)	Distal edge of the labrum	12	Chemoreceptors (Neuffer)
LABIAL PALP THICK WALLED CHEMORECEPTORS (figs. 18, 22)	Apical third of labial palpi	6 (each palpus)	Chemoreceptors
LABIAL THICK WALLED CHEMORECEPTORS (fig. 22)	Prementon of labium	4	Chemoreceptors
LABIAL POSITION TACTILE SETAE (fig. 22)	Medial fold of prementon and outer edge of labial palpi, near their bases	4 (2 labial, 1 each palpus)	Mechanoreceptors, sense of position ("Stellunghaare", Neuffer)
PROBABLE POSITION TACTILE SETAE (fig. 22)	Prementon, outside the labial thick walled chemoreceptors	2	Mechanoreceptors ? Free ends of sensitive dendrites ?
LABIAL TYPICAL SETAE (figs. 18 and 22)	Prementon, backward the labial position tactile setae	2	Mechanoreceptors, typical tactile, setae

2) *Minute setae:* difficult to see with optical microscope because of their very small and slender dimensions. Two of these (fig. 22) need additional observations due to the possibility that they be free ends of sensitive dendrites as supposed by Neuffer (1954: 499, fig. 36). The correspond to *position tactile setae* (see table I).
3) *Stout and blunt-tipped setae:* easily recognizable by their typical silhouette (figs. 3, 18 and 22). They correspond to *labral* and *labial thick-walled chemoreceptors* (see table I).

III) The antennae and antennal sensilla (figs 4-17, 19-21 and 24-25).

The antennae are filiform and five-segmented in both adults and nymphs. The male and female antennae are strongly dimorphic. Those of the male (figs. 2,19 and 24) have the scape, pedicel and first segment of the flagellum adapted for pairing, like the illustrations given by Séguy (1944, 1951) for *Perineus diomedeae* (J. C. Fabricius 1775), and by Werneck (1936) for *Eutrichophilus cordiceps* Mjöberg 1910.

The scape in the male is the largest segment, as long as the pedicel and the first two segments of the flagellum together. The pedicel is articulated in angle with the scape, and almost as long as the two last segments of the flagellum together. The first segment of the flagellum has an apophysis directed inwards for clasping the female during pairing, at level of the thoracic-abdominal intersegmental membrane. The last two segments do not participate in the pairing, being directed up and outwards (see fig. 2). The female antennae (fig. 20 and 25) show very different proportions, the largest segment being the pedicel. The morphometry and proportions of each antennal segment vary among different nymphal instars and imagoes, as shown in tables II and III.

TABLE II

MORPHOMETRY OF THE ANTENNAL SEGMENTS OF THE THREE NYMPHAL INSTARS OF *V. BERGI* (KELLOGG 1906). VALUES REPRESENT THE MEAN. MEASUREMENTS IN MICROMETERS (μm)

	FIRST INSTAR		SECOND INSTAR		THIRD INSTAR	
ANTENNAL SEGMENT	LENGTH	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH
I	26,25	28,12	27,65	28,82	37,14	27,86
II	26,25	26,25	33,53	25,88	42,14	25,71
III	17,50	20,0	20,59	20,0	24,29	21,43
IV	18,75	20,0	18,82	20,82	27,14	22,86
V	26,25	19,37	27,65	18,47	28,57	20,71

TABLE III

MORPHOMETRY OF THE ANTENNAL SEGMENTS OF MALE AND FEMALE OF *V. BERGI* (KELLOGG 1906). MEASUREMENTS INCLUDE THE RANGE AND, WITHIN PARENTHESIS, MEAN AND STANDARD DEVIATION. MEASUREMENTS IN MICROMETERS (μm).

	MALES	
ANTENNAL SEGMENT	LENGTH	WIDTH
I	203,35–210,70 (205,80 ± 4,2)	58,80–61,25 (60,03 ± 1,7)
II	85,75–88,20 (86,98 ± 1,7)	45,33
III	58,80–61,25 (60,03 ± 1,7)	29,40
IV	44,19–53,90 (49,0 ± 4,9)	31,85
V	41,65–49,0 (46,55 ± 4,2)	28,18–29,40 (28,59 ± 0,7)

	FEMALES	
ANTENNAL SEGMENT	LENGTH	WIDTH
I	68,60–73,50 (71,05 ± 3,5)	49,0 –53,90 (51,45 ± 3,5)
II	93,10–100,45 (96,78 ± 5,2)	37,98–41,65 (39,82 ± 2,6)
III	60,03–71,05 (65,54 ± 7,8)	34,30
IV	44,10–56,35 (50,23 ± 8,7)	30,63–33,08 (31,86 ± 1,7)
V	46,55–49,0 (47,78 ± 1,7)	29,89

Four morphological kinds of sensilla are found in the antennae of adults and nymphs are listed below:

1) *Small setae* (figs. 10, 13-15 and 19-21): minute setae, located on the intersegmental membranes of all antennal segments, and the two short tactile setae placed on the dorsal surface of segment V also probably belong here. They correspond to *position tactile setae* and *short tactile setae* (see table IV).

2) *Slender setae* (figs. 8, 9, 12 and 19-20): sharply pointed medium long setae, with general distribution pattern as shown in figures 19 and 20, more or less variable between the two sexes: 19-24 in the male and 18-21 in the female. The three nymphs show similar range and distribution pattern as for the female. The two small setae present on the dorsal surface of segment V marked with and "n" in fig. 21 may be interpreted as *small setae* as well as *slender setae*. They correspond to *medium to long tactile setae* (see table IV).

TABLE IV

NAME, POSITION, NUMBER AND PROBABLE FUNCTION OF THE ANTENNAL SENSILLA OF *V. BERGI* (KELLOGG 1906).

NAME	POSITION	N^{er}	PROBABLE FUNCTION
POSITION TACTILE SETAE (figs. 19-20)	Scape	3	Mechanoreceptor, position of scape.
	Pedicel	1	Mechanoreceptor, position of pedical.
	Intersegmental membrane of II–III	1–2	Relative position of both segments.
	Intersegmental membrane III-IV	1	Relative position of both segments.
MEDIUM TO LONG TACTILE SETAE (figs. 8, 9, 12, 19, 20)	Segments I to V	18–24	Mechanoreceptors, tactile.
SHORT TACTILE SETAE (figs. 10, 13, 14, 15, 21)	Dorsal surface of segment V	2	Mechanoreceptors, tactile or position of segment V.
	Antennal tuft	1	Mechanoreceptor, tactile
PLACODEAN SENSILLA (?) OF SCAPE AND PEDICEL (fig. 19)	Basal third of scape	1	Chemoreceptor, olfactive?
	Distal third of pedicel	1	Chemoreceptor, olfactive?
COELOCONIC SENSILLA OF FLAGELLUM (figs. 4-12, 16-17, 19-20)	Segment IV	1	Chemoreceptor.
	Segment V	1	Chemoreceptor.
PLACODEAN SENSILLA ("PORE ORGANS") (figs. 4-6, 9-12, 16-17, 19-21)	Segment IV	1	Chemoreceptor, olfactive?
	Segment V	2	Chemoreceptor, olfactive?
THICK WALLED CHEMORECEPTORS (figs. 6, 10, 12, 13, 19, 20)	Basal third of segment V	1	Chemoreceptor.
	Antennal tuft	7–8	Chemoreceptor.
THIN WALLED CHEMORECEPTORS (figs. 10, 13, 14, 15)	Antennal tuft	2	Chemoreceptor.

3) *Blunt-tipped setae* (fig. 6, 10, 12-15 and 19-20): much stouter than the preceding ones. Only those present on the antennal segment V are here studied in detail with the SEM. Probably the stout setae on scape and pedicel (marked with "q", figures 5-6, 19-20) belong here, but this assertion deserves further studies. They correspond to *thick-walled chemoreceptors* (tq) whose number and position are shown in table IV. Their measurements (length and width) increase arithmetically throughout the three nymphal instars (see table VII), and those found in the imagoes essentially match the morphometry for third nymphal instar.

4) *Pegs* (figs. 10, 13-15): readily distinguished by their rounded tipped and stout silhouette, and restricted to the apical tuft of segment V. They correspond to *thin walled chemoreceptors* (hq) (table IV). Their dimensions (length and width) do not exhibit significant variations within the nymphs (see table VII) and imagoes.

5) *Placodean sensillà* (figs. 4-6, 9-12, 16-17 and 19-21): nearly circular, and placed into a "plate like" structure (see figs. 6, 9 and 17). The first nymphal instar lacks sensilla placodea on IV, whilst it is present in the second and third instars and male and female adults. Probably the sensorial areas, marked with "z" in figure 19, found on the scape and pedicel must be included here. Number and position are shown in table IV. Their size increases proportionally through the three nymphal instars (see table VI), remaining almost unchanged from nymph III to imagoes.

6) *Coeloconic sensilla* (figs. 4-12, 16-17 and 19-20): with classical structure: a chamber containing a round-tipped peg (not shown in the SEM pictures, but studied with light mi-

TABLE V

DIAMETER (MEAN) OF THE EXTERNAL OPENING OF THE COELOCONIC SENSILLA OF SEGMENTS IV AND V OF THE THREE NYMPHAL INSTARS OF *V. BERGI* (KELLOGG 1906). MEASUREMENTS IN MICROMETERS (μm).

ANTENNAL SEGMENT	FIRST INSTAR	SECOND INSTAR	THIRD INSTAR
IV	1,2	1,09	1,89
V	1,51	1,54	1,4

TABLE VI

DIAMETER (MEAN) OF THE PLACOID SENSILLA OF SEGMENTS IV AND V OF THE THREE NYMPHAL INSTARS OF *V. BERGI* (KELLOGG 1906). MEASUREMENTS IN MICROMETERS (μm).

ANTENNAL SEGMENT	FIRST INSTAR	SECOND INSTAR	THIRD INSTAR
IV	–.–	5,88	6,42
V	5,95	6,24	7,4

TABLE VII

RANGE OF MEASUREMENTS OF TACTILE SETAE AND CHEMORECEPTORS OF THE APICAL TUFT OF ANTENNAL SEGMENT V OF THE THREE NYMPHAL INSTARS OF *V. BERGI* (KELLOG, 1906). MEASUREMENTS IN MICROMETERS (μm)

	FIRS INSTAR		SECOND INSTAR		THIRD INSTAR	
KIND OF SENSILLA	LENGHT	WIDTH	LENGTH	WIDTH	LENGTH	WIDTH
ts	5,48	0,53	3,51–6,67	0,51	6,22	1,03
tq	5,75–13,70	1,01–1,64	5,13–12,70	1,03–1,35	6,62–14,19	1,08–1,22
hq	4,38–5,07	1,10–1,37	5,00–5,13	1,12–1,35	4,49–5,54	1,30–1,76

croscope), and a nearly circular external opening. They are restricted to the last two segments, and conspicuous in number: one sensilla on segment IV and one on V, in both nymphs as imagoes (see table IV). Their size remains essentially unchanged along the nymphs (see table V) and imagoes.

IV) *The lingual sclerites and the water-uptake system (figs. 3, 23 and 25).*

The structural components of this peculiar system (fig. 23) are:

a) two *lingual sclerites,* more or less ovoid in form, with a medial shallow groove each one.
b) a *tubular filament,* branched apically in connection with the lingual sclerites. Basally, it opens into the cibarium.
c) a *cibarial sclerite,* heart-shaped.

When inactive, these components are retracted inside the cibarium. When active, the lingual sclerites expose in full to the air. SEM picture 3 shows a female fixed a few seconds previous to the full exposition of these sclerites.

The morphology of lingual sclerites, duct and pharyngeal sclerites is remarkably similar in adults and all nymphal stages, the only noticeable difference being, in each case, the size attained.

DISCUSSION

Clay (1951) proposed a code of nomenclature for setae (except for those found on the antennae and mouthparts) of the Ischnocera, but no function is attributed to them.

Neuffer (1954) studied the sensilla of three Ischnoceran and two Amblyceran genera, groupping their sensilla into Tactile setae ("taktile Sinneshaare") and Chemoreceptor sensillae ("chemische Sensillen"). The former kind of sensilla was also classified on a functional basis as follows: Tactile setae into typical tactile setae, position sensilla ("Stellungshaare") and pressoceptors ("Drucktasthaare").

Clay (1970) pointed aut that there are two "saucer-like sensilla" (= placodean sensilla) on antennal segment V, and one on IV. This critherium has been followed by Kim & Ludwing (1978, 1982)..

Slifer (1970) reviewed the chemoreceptors present in the Insecta and other Arthropoda, grouping them into thin-walled and thick-walled chemoreceptors. Later (1976), she followed the same classification when studying the sensilla of the antennal flagellum of the

Philopterid *Craspedorhynchus americanus* Emerson.

Zacharuk (1980) divided the chemosensilla into Uniporous chemosensilla (UP) and Multiporous chemosensilla (MP), both similar in structure and function to the thick-walled and thin-walled categories of Slifer (1970).

Zlotorzycka & Kassner (1986), discriminated into six groups ("A" to "F") the different arrangements of the placodean and coeloconic sensilla observed in the antenna of fourteen Ischnoceran species; they pointed out that their morphology reveals defferent physiological peculiarities of these lice, keeping in mind that they used the german term "Grubenkegel" for coeloconic sensilla and "Porenorgane" for "pore organs" (= sensilla placodea).

As has been indicated by Slifer (1970) and Zacharuk (1980), a close correlation exists between the typology and gross function of each kind of sensillum. As a complement we tested the presence of pores in the setae and pegs by means of a solution of crystal violet applied to their external surface (Slifer, 1960) Due to this reason, we employ in this paper a functional-morphological approach, because it is widely used in most arthropodological articles and textbooks.

Consequently, for *tactile setae* we follow Clay (1951), and Neuffer (1954) for those not covered by her. The *chemoreceptors* were discriminated into *thin-walled* and *thick-walled chemoreceptors* following Slifer (1970, 1976), and into *Uniporous* (UP) and *Multiporous chemosensilla* (MP) following Zacharuk (1980) The "saucershaped pore organs" are derived from large sense pegs often found in the cavity of coeloconic sensilla found in the Amblycera (Kim & Ludwing, 1982) being a type of *placodean sensilla* (Kim & Ludwing, 1878), and so treated here. The *coeloconic sensilla* are like those described by Snodgrass (1935: 520-521) and Richard & Davis (1983: 148) and here referred to as such. Equivalences between Slifer's (1970) and Zacharuk's (1980) systems are provided in a number of cases.

The following approach is used in this paper, adding the equivalences into Neuffer's (1954), Slifer's (1970) and Zacharuk's (1980) system for those who prefer to use them and to interpret in those terms the nomenclature here used.

Therefore, with this approach we offer pertinent comments about the probable function of the sensilla found on the head of *V. bergi*, being groupped in topographic regions, as well as the water-uptake system.

I) *Sensilla of the cephalic capsule:* all the sensilla examined are tactile setae, and their morphology and distribution pattern are reminiscent of those found in *Brueelia rotundata* (Osborn 1896), a species studied by Neuffer (1954). These sensilla may be discriminated as follows.

a) *typical tactile setae:* mds, os, $av_{I\text{-}III}$, $vsm_{I\text{-}II}$ $as_{I\text{-}III}$, dsms, t_{II} and t_{IV}. In *B. rotundata*, os and t_{II} are much shorter, being position setae.

b) *position setae:* pcs, pas, pns, t_I, t_{III}, t_V and t_{VI}.

c) *pressoceptive seta:* ads.

II) *Sensilla of the mouthparts:* they are found in the labrum and labium, and they are:

a) *typical tactile setae:* two in number and often called premental setae, they are consistent with the morphology and negative crystal-violet of the cephalic capsule setae.

b) *probable position tactile setae:* two minute setae, very difficult to see because of their minute size, so it is not clear whether they are free ends of sensitive dendrites, as supposed by Neuffer (1954) for *Brueelia rotundata*, or true position setae.

c) *position tactile setae:* these four small setae are crystal violet-negative, and they agree with the morphology and location found in a number of Ischnoceran genera (*Brueelia, Philopterus, Aquanirmus*).

d) *thick-walled chemoreceptors:* they are located in the labrum (twelve) and la-

TYPOLOGY	Neuffer (1954)	Slifer (1970)	Zacharuk (1980)	Present study
Slender setae	Typische taktile Sinneshaare	—.—	—.—	Typical tactile setae
Small setae	Typische taktile Sinneshaare	—.—	—.—	Typical tactile setae
Minute setae	Stellungshaare and Drucktasthaare	—.—	—.—	Position or pressoceptive setae
Blunt-tipped setae	Chemische Sensillen	Thick-walled chemoreceptors	UP (uniporous) chemosensilla)	Thick-walled chemoreceptors (UP)
Pegs	Chemische Sensillen	Thick-walled chemoreceptors	MP (multiporous chemosensilla) (MPP, multiporous pitted chemosen).	Thin-walled chemoreceptors (MP) or (MPP)
Placodean sensilla	—.—	Thin-walled chemoreceptors plate organs	MP Placodean sensilla	Placodean sensilla
Coeloconic sensilla	—.—	Thin-walled chemoreceptors, pegs in pits	MP Coeloconic sensilla	Coeloconic sensilla

bium (sixteen) and are consistent in morphology and crystal violet test with that of thick-walled chemoreceptors (Slifer 1970, 1973) and uniporous sensilla (UP) (Zacharuk, 1980).

III) *Sensilla of the antennae:*

a) *typical tactile setae:* general structure much as those of the cephalic capsule. As they are present in all antennal segments this fact denotes an important rôle of the antennae as tactile organ.

b) *position sensilla:* as they are placed in the intersegmental membranes, as well as in the scape and pedicel, this indicates the relative position of the antennal segments among themselves, as well as the position of the whole antenna respect to the head.

c) *placodean sensilla:* the first nymphal instar lacks sensilla placodea on segment IV, whilst it is present in the second and third instars, as well as in the male and female adults.

d) *coeloconic sensilla:* restricted to segments IV and V. The sensorial pegs do not reach the antennal surface (2,4-3,6 μm in length). The peculiar arrangement of the placoid and coeloconic sensilla into a "plate-like" structure is typical of the "Gruppe F" after Zlotorzycka & Kassner (1986) and only known to date for the genus *Aquanirnus* Clay & Meinertzhagen 1939 (Philopteridae).

e) *thick-walled chemoreceptors:* they are characterized by a wall that is relatively thick when compared to the diameter of the hair (Slifer 1970, 1973, 1976), and are crystal violet-positive (Slifer 1960).

f) *thin-walled chemoreceptors:* readily distinguishable by their very thin and perforated wall (Slifer 1970, 1973, 1976). The arrangement of thin-walled and thick-walled chemoreceptors –in addition to a tactile seta– clustered in an apical tuft is typical, at least, for the family Philopteridae (Ischnocera).

IV) *The lingual sclerites and the water-uptake system:* active uptake of water-vapour from subsaturated athmospheric air is known to occur in a large number of systematically unrelated insects ranging from the Apterygota to the Endopterygota (see Rudolph 1983).

The water-uptake devices have formerly received –within the Psocodea– a variety of different interpretations, e. g. as representing a grinding or transport device for the food materials, or as a transfer system for the conveyance of saliva from the salivarium to the preoral food cavity (Haub 1972, 1973; Kéler 1966, 1969; Risler 1951; Symmons 1952; Weber 1936).

The structural components of this system: the lingual sclerites connected by a "Y" –shaped filamentous duct to the cibarial sclerites, have been properly identified as such by Rudolph (1982, 1983, see also Lyal 1985).

Water vapour is condensed on the lingual sclerites from subsaturated air, and pumped by the action of the cibarial pump through the duct. This mechanism is an unique acquisition of the Psocodea (Rudolph 1983, Lyal 1985), and it is accepted by Lyal (1985) as apomorphic for the Psocodea, despite the fact that it is absent in the highly-modified Rhynchophthirina and Anoplura.

The movements of the lingual sclerites, in relation to the mouthparts during water-vapour absorption in *Vernoniella bergi* (Kellogg 1906) –as observed by us in living specimens reared in Petri-dishes– match those described by Rudolph (1982). Figure 3 shows a female specimen fixed just during the moving of the mandibles in the transverse plane, together with a slight backwards movement of the labium, a few seconds previous to the full exposition of the lingual sclerites.

It is an unfortunate fact that, due to lack of adequate instruments, it has not been possible to evaluate quantitatively the water absorption, in order to compare it with the data obtained from other louse species (Rudolph 1983).

CONCLUSIONS

In the head of *V. bergi* we found two kinds of sensilla:

1) Tactile sensilla: we classified them following Neuffer (1954) into:
   a) Position sensilla
   b) Pressoceptive sensilla
   c) Typical tactile setae
2) Chemoreceptors: they are groupped by their gross external morphology following Snodgrass (1935) on classical grounds, and secondarily, their ultrastructural equivalences, in Slifer's (1970, 1973, 1976) and Zacharuk's (1980) systems whenever possible.
   a) Placoid sensilla
   b) Coeloconic sensilla
   c) Setae and pegs.

For a reason of convenience, the louse head has been divided into the following regions: the head capsule, the mouthparts (labrum and labium) and the antennae. A careful study of the external morphology (including morphometry), number, location and probable function of all sensilla has been carried out, with the following results:

1) The sensilla of the cephalic capsule: all them are Tactile Setae discriminated by function following Neuffer (1954) into:
   a) typical tactile setae.
   b) position setae
   c) pressoceptive setae.

For nomenclature of these setae, we follow Clay (1951).

Their morphology, number and position are virtually identical in both imagoes and nymphal instars. As pointed out by Clay (1951), the setae of the head are remarkably constant in position and number throughout the Ischnocera, and can frequently be used as guides to certain parts of the head, elucidating the homologies of special structures such as different sutures or adaptations of whole parts of the head.

2) The sensilla of the mouthparts (labrum and labium):
   a) Tactile sensilla: restricted to the labium, belonging to the typical tactile setae and position setae.
   b) Chemoreceptors: present in both labrum and labium. Following Slifer's (1970) system they belong to the thick-walled chemoreceptors, (UP) of Zacharuk (1980).
   Their number and position are essentially the same in both adults and nymphs.
3) The antennal sensillae:
   a) tactile setae: in all antennal segments, and classified as follows:
   – typical tactile setae
   – position setae
   b) chemoreceptors: present in all segments:
   – placodean sensilla: on antennal segments IV and V in nymphal instars II, III, male and female, only on V in nymphal instar I.
   – Coeloconic sensilla: on antennal segment IV and V in all nymphs and adults.
   – setae and pegs:
   • thick walled chemoreceptors (Slifer 1970, 1976): probably in all antennal segments. They are uniporous (UP) in Zacharuk's (1980) system.
   • thin walled chemoreceptors (Slifer 1970, 1976): only two in number, and restricted to the apical tuft of segment V they belong to the MPP chemoreceptor of Zacharuk (1980).
   The number and position of these sensilla remains essentially unchanged during all stages of development.

Regarding the lingual sclerites and the water-uptake system, we found that the morphology and the water-vapour absorption mechanisms, as exhibited by living specimens reared in Petri-dishes, match those described by Rudolph (1983).

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LEGENDS PLATE I

Fig. 1: Scanning electron micrograph of preantennal portion of the male head, lateral view, showing the conus (*co*), basal portion of scape (*I*), and the mechanoreceptive setae. For explanation of abbreviations see below (300 X, scale equal to 100 μm).

Fig. 2: Scanning electron micrograph of the postantennal portion of male head, showing the conus (*co*), the five antennal segments (see figure 19 for explanation), the ocellum (o), and the mechanoreceptive setae. For explanation of abbreviations see below (360 X, scale = 100 μm).

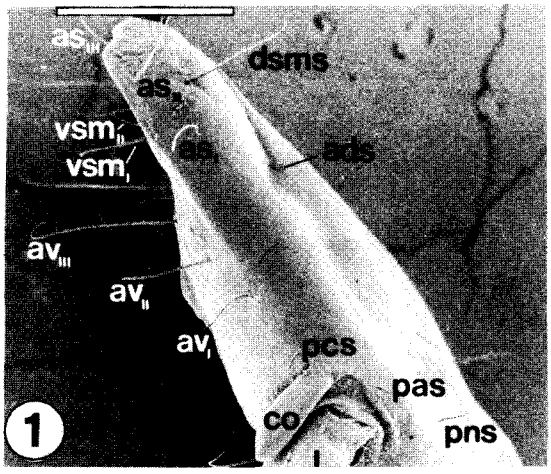
Fig. 3: Scanning electron micrograph of female head, ventrolateral view. Note the pulvinus (*pu*), labrum (*lr*), mandibles (*md*), the lingual sclerites of the water vapour-uptake (*ls*, see figure 23 for further explanation), the labial palpi (*lp*), and the different tactile setae and chemoreceptors. For abbreviations see below, and for further explanation see text, (300 X, scale = 100 μm).

Fig. 4-6: Scanning electron micrograph of the antennae of nymphs I-III, ventral view. For explanation of abbreviations see below.

Fig. 4, nymph I (910 X, scale = 10 μm); fig. 5, nymph II (860 X, scale = 10 μm); fig. 6, nymph III (660 X, scale = 10 μm).

The following abbreviations have been used troghout the figures:

c = coeloconic sensillum (probably MP).
cl = claws
cr = circular ridge
cy = cybarium
co = conus
f = femur
hq = thin walled chemoreceptor (= MP) (see text).
lb = labium
lp = labial palpus
lr = labrum
ls = lingual sclerite
md = mandible
o = ocellum
p = placodean sensillum = pore organ (see text).
pts = position tactile seta.
pts? = probably position tactile seta.
pu = pulvinus
r = ridges of antennal segments.
sal = salivarium
t = tarsus
ti = tibia
tq = thick walled chemoreceptor (= UP) (see text).
tr = tronchanter
ts = tactile seta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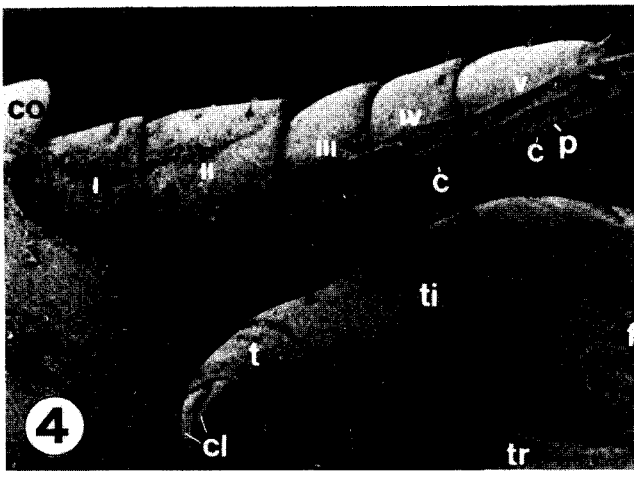
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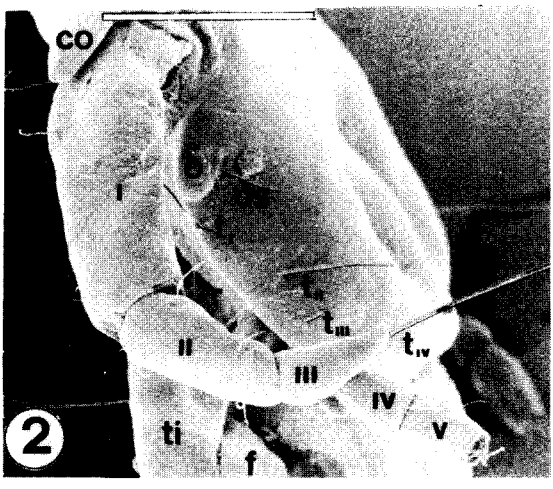
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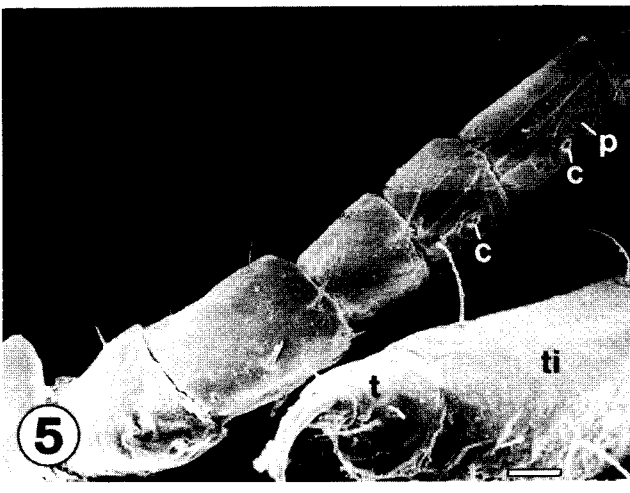
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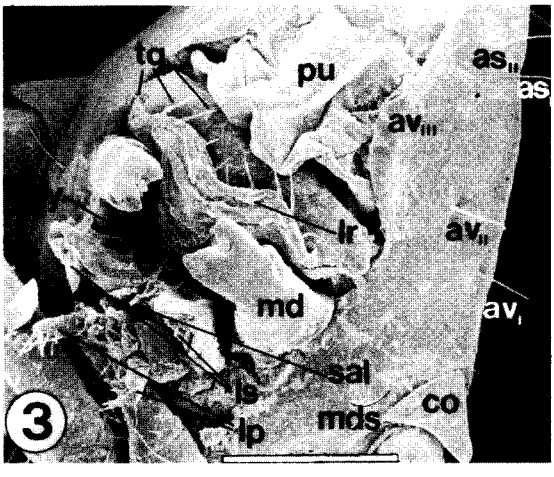
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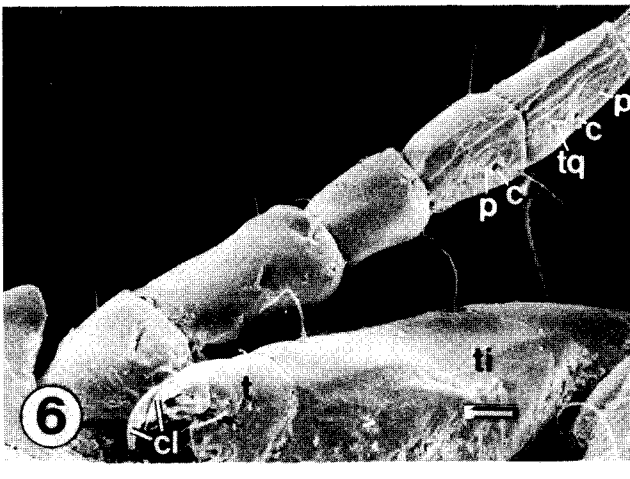
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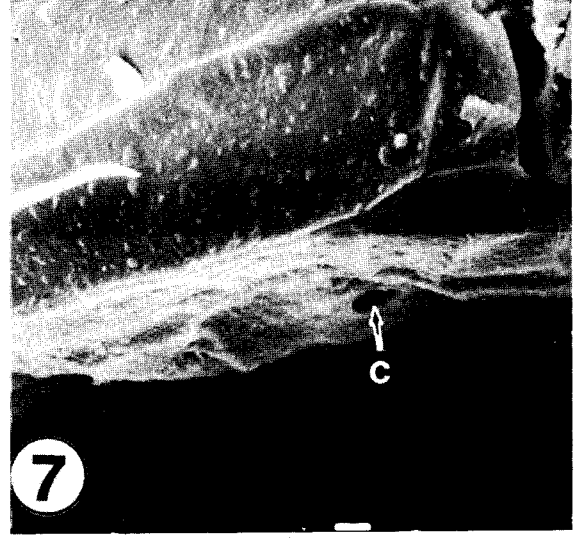
LEGENDS PLATE II

Fig. 7-9: Scanning electron micrograph of the second segment of flagellum of the left antennae of nymphs I-III, ventrolateral view. Fig. 7, nymph I, note the single pit of the coeloconic sensillum (*c*); (4400 X, scale = 1 μm); fig. 8, nymph II, showing the coeloconic sensillum (*c*) (there is also a placodean sensillum, although not easily visible in the photograph) and two tactile setae (*ts*) (3200 X, scale = 10 μm); fig. 9, nymph III, showing the placodean (*p*) and coeloconic (*c*) sensilla, as well as two tactile setae (*ts*) (2600 X, scale = 10 μm).

Fig. 10-12: Scanning electron micrograph of the terminal segment of flagellum and apical tuft of nymphs I-III, showing the tactile setae (*ts*) and the different chemoreceptors (for explanation of abreviations see references under) figs. 1-6. Except for the increae of distance between the placodean and coeloconic sensillae, note the remarkable uniformity in number and position of all sensillae. Fig. 10 (1800 X, scale = 10 μm); fig. 11 (2600 X, scale = 10 μm); fig. 12 (2000 X, scale = 10 μm).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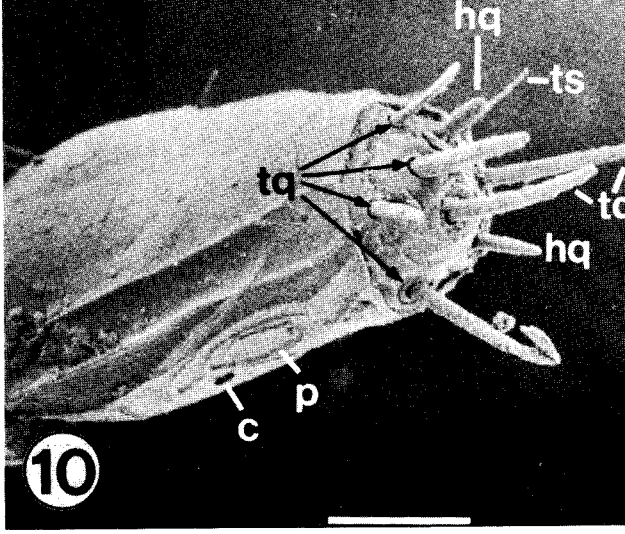
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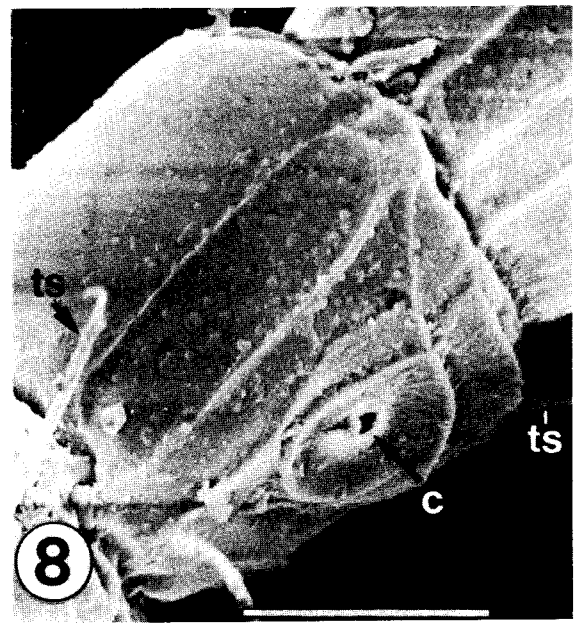
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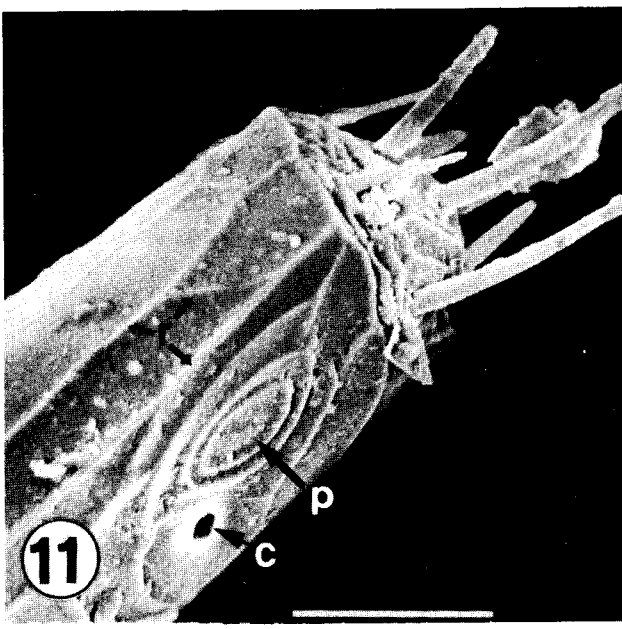
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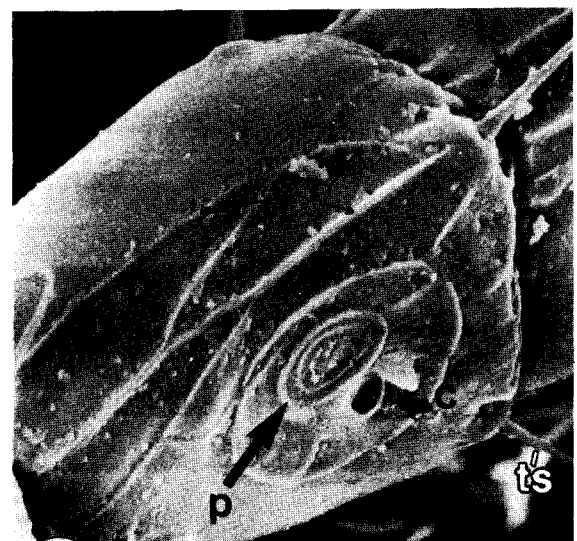
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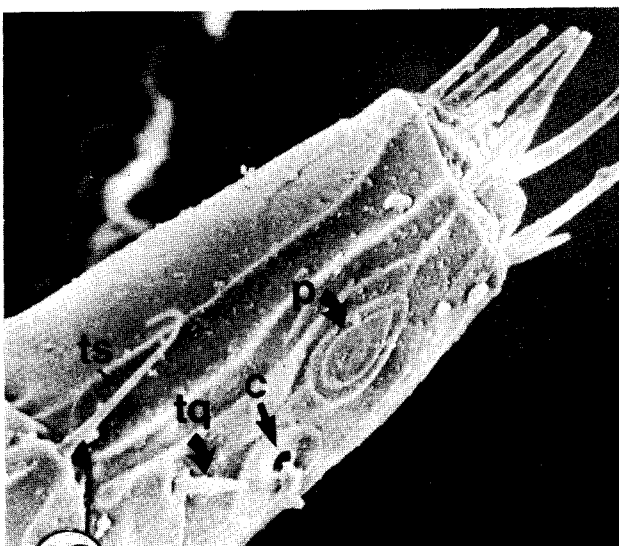
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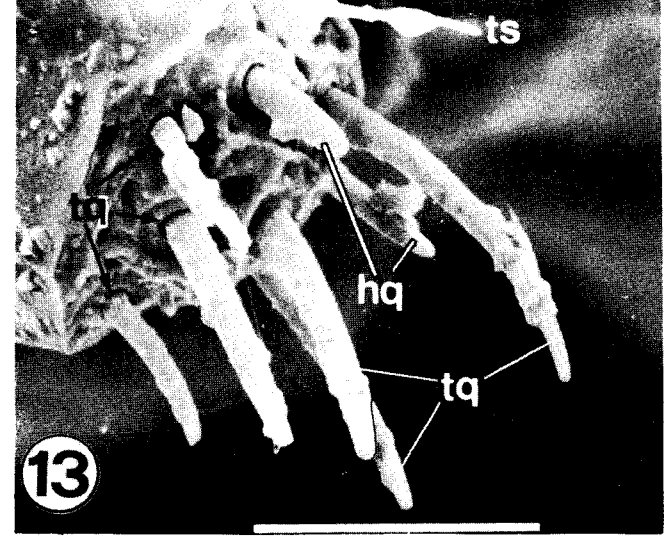
LEGENDS PLATE III

Figs. 13-15: Scanning electron micrograph of the apical tuft of last segment of antennal flagellum of nymphs I-III, ventrolateral view. For explanation of abbreviations see references under figs. 1-6. Note the single tactile setae (*ts*), two round-tipped thin walled chemoreceptors (*hq*) and 6-9 blunt-tipped chemoreceptors (*tq*). For further explanations see text. Fig. 13 nymph I, (3600 X, scale = 10 μm): Fig. 14 nymph II (3600 X, scale = 10 μm); fig. 15 nymph III (3600 X, scale = 10 μm).

Fig. 16: Scanning electron micrograph of the placodean (*p*) and coeloconic (*c*) sensilla of antennal segment V of nymph I, (4400, scale = 1 μm).

Fig. 17: Scanning electron micrograph of the placodean (*p*) and coeloconic (*c*) sensilla of antennal segment IV of nymph III, (6000 X, scale = 1 μm).

Fig. 18: Scanning electron micrograph of the right labial palpus (*lp*), lateral view, showing the blunt-tipped thick walled chemoreceptors (*tq*), part of the prementon of labium (*lb*) and the long tactile setae (*ts*), apical portions of the right lingual sclerite (*ls*) and mandible (*md*), (2000 X, scale = 10 μm).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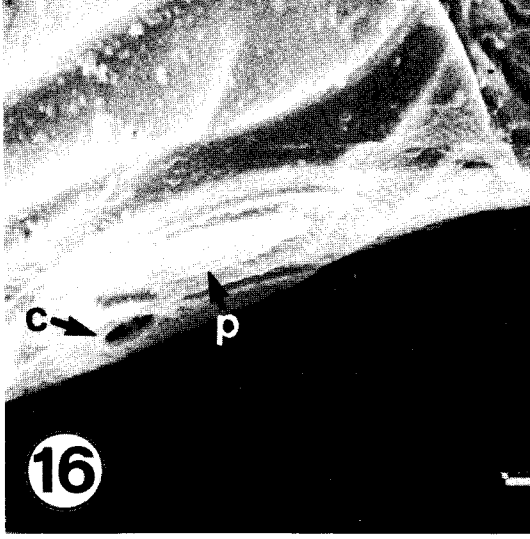
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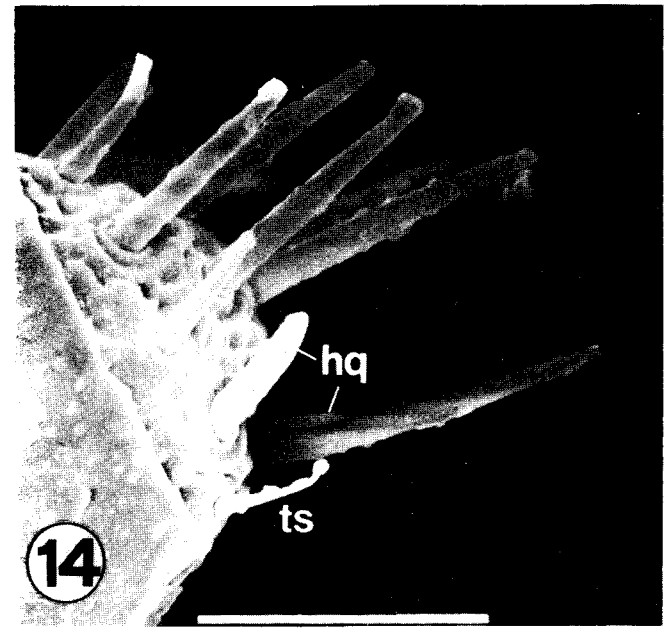
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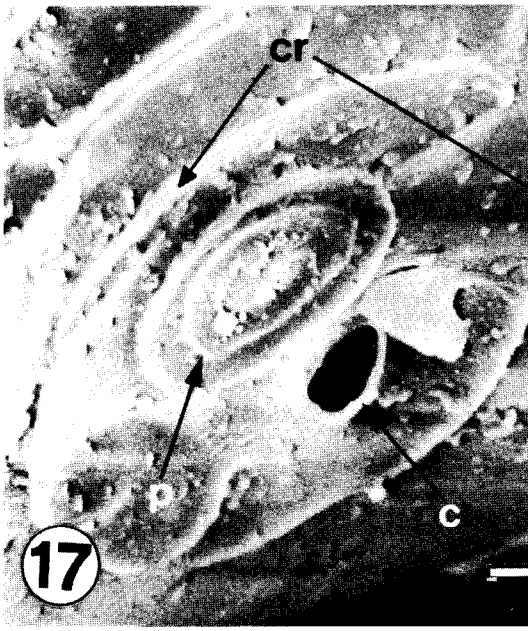
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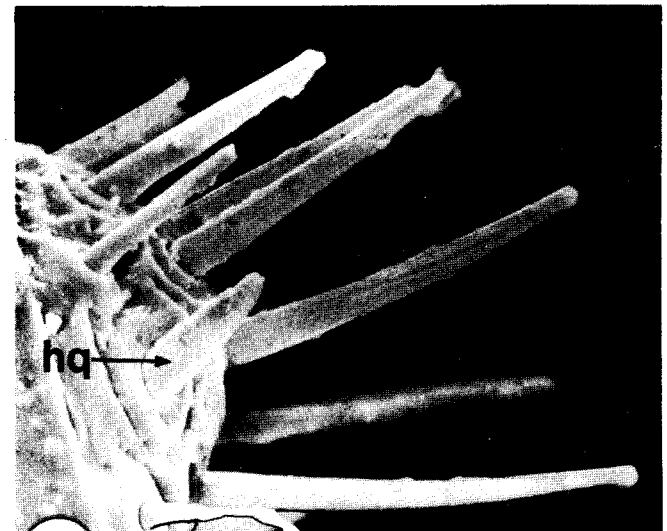
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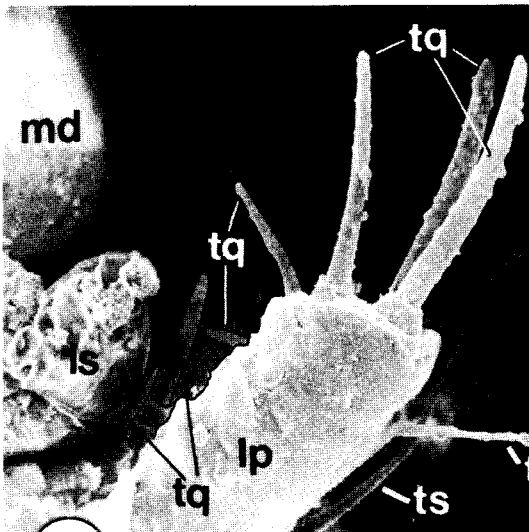
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LEGENDS PLATE IV

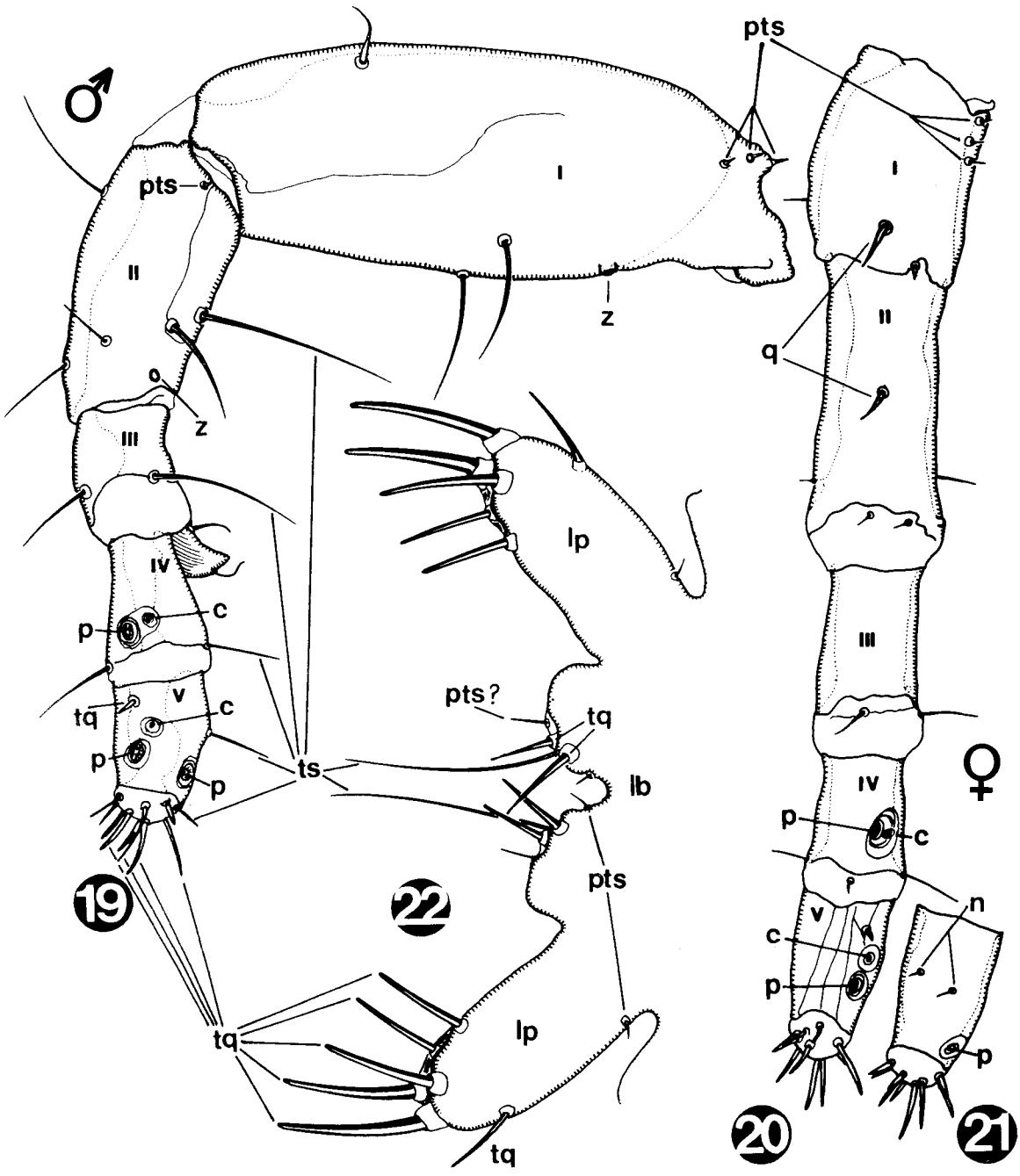
Fig. 19: Drawing of male right antenna, ventral view. Note the scape (*I*), pedicel (*II*) and the three segments of flagellum (III-V), and the sensilla located on them (450 X).

Fig. 20: Drawing of female antenna, (450 X).

Fig. 21: Drawing of female antenna, last segment of flagellum of left antenna, dorsal view (450 X).

Fig. 22: Drawing of labium, in frontal view. Note the labial palpi bearing the stout thick-walled chemoreceptors (*tq*) (450 X).

For explanation of abbreviations see legend of Plate I, and for further explanation of male and female antennae, see text.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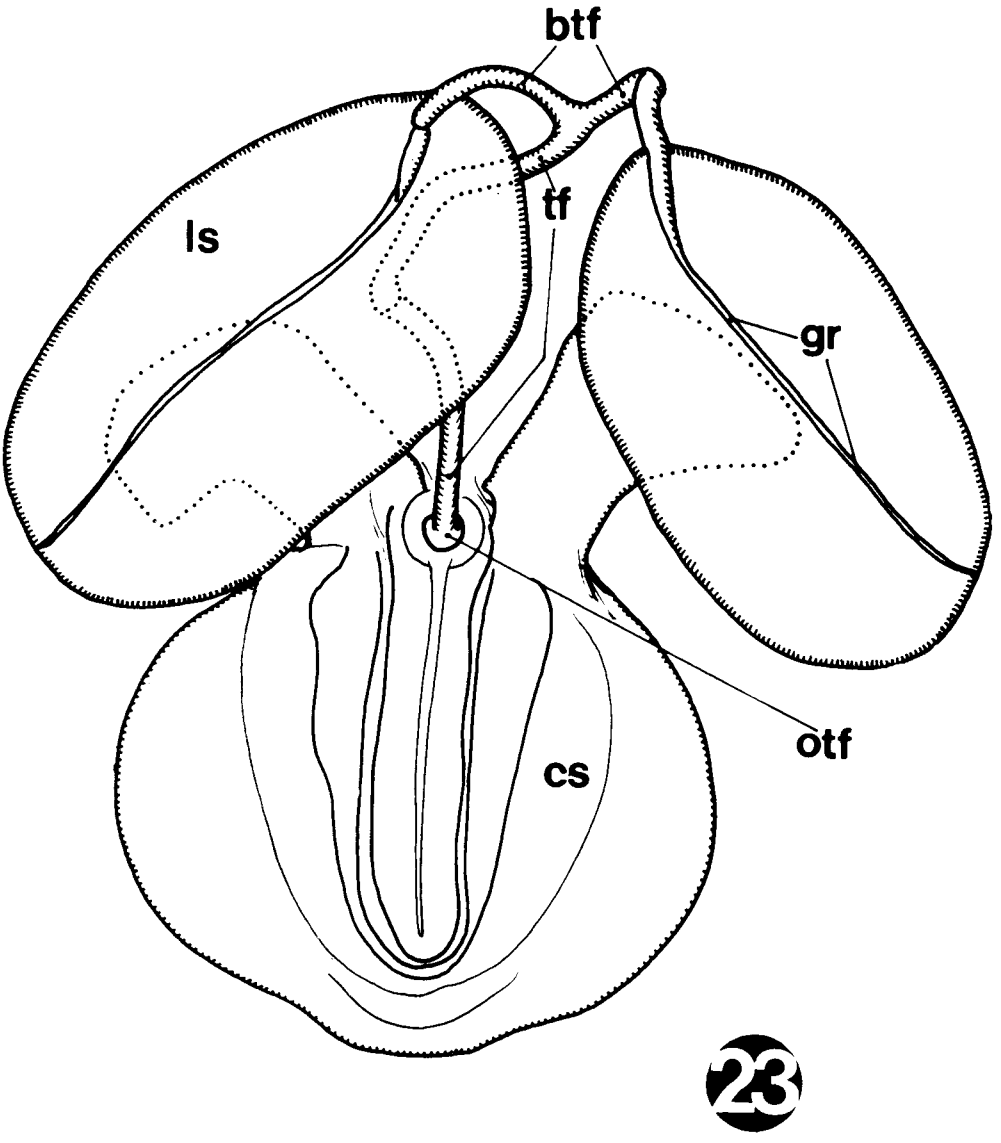
LEGENDS PLATE V

Fig. 23: Drawing of the head structures involved in water vapour-uptake (X 450). Nomenclature after Rudolph (1982 and 1983), by means of the following references:

btf = branches of the tubular filament.
cs = cybarial sclerite
gr = shallow groove
ls = lingual sclerite
otf = openning of the *tf* into the cibarium
tf = tubular filament



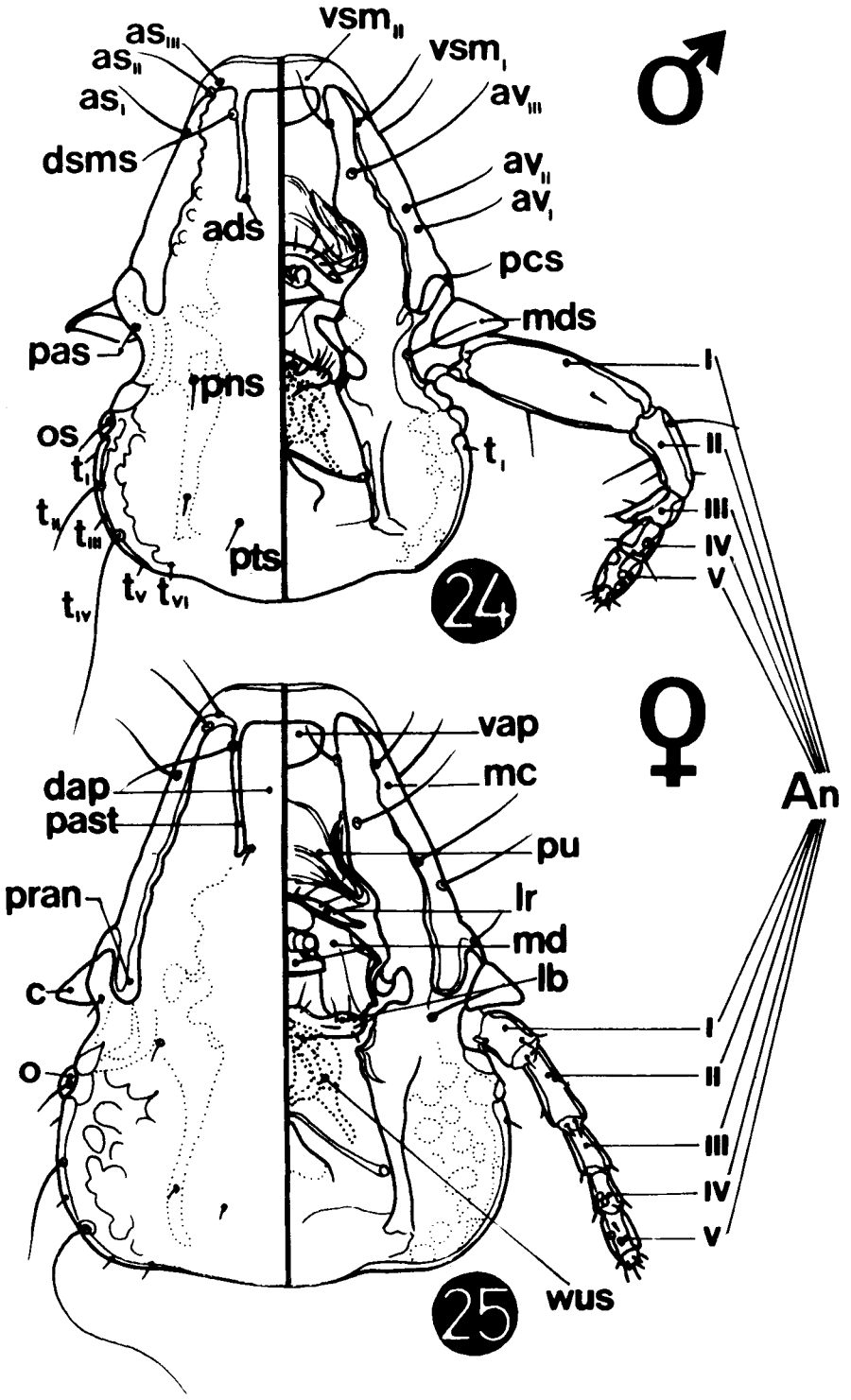
23

LEGEND PLATE VI

Fig. 24: Drawing of the male head of *V. Bergi* (X 200) (left: dorsal view, Right: ventral view) showing all the cephalic setae. Nomenclature after Clay (1951) by means of the following references:

An: antenna (includes antennal segments I to V).
dap: dorsal anterior plate.
past: preantennal suture.
pran: preantennal nodus.
c: conus
o: ocellum.
vap: ventral anterior plate.
mc: marginal carina.
pu: pulvillum.
lr: labrum
md: mandibles
lb: labium.
wus: water-uptake system (not exposed).

Fig. 25: Drawing of the female head of *V. bergi* (X 200) (left: dorsal view, right: ventral view) showing the anatomical features used in the text. References as above.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