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BULLETIN
OF THE
AMERICAN MUSEUM OF NATURAL HISTORY
NUMBER 228 NEW YORK : 1996

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LARVAL MORPHOLOGY OF THE SEPSIDAE (DIPTERA: SCIOMYZOIDEA), WITH A CLADISTIC ANALYSIS USING ADULT AND LARVAL CHARACTERS

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BULLETIN OF THE AMERICAN MUSEUM OF NATURAL HISTORY
Number 228, 147 pages, 478 figures, 3 tables
Issued January 12, 1996
Price: $12.50 a copy

ISSN 0003-0090

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In contrast to their disgusting habitat the species are really beautiful little insects and with their curious habit of pirouetting about with extended vibrating wings they attract attention by their dainty dance.

—Melander and Spuler (1917: 11) on sepsids

ABSTRACT

A phylogenetic hypothesis based on larval and adult characters is proposed for the Sepsidae. The cladistic analysis employed 85 characters and 57 taxa and found 16 equally parsimonious cladograms. The strict consensus tree and a preferred tree are presented, the region of the tree in which the parsimonious cladograms differ is indicated, and the competing arrangements of taxa are shown. Outgroup representatives included two species of ropalomerids (*Ropalomera* sp., *Willistoniella pleuropunctata*), two species of coelopids (*Coelopa frigida*, *Chaetocoelopa sydneyensis*), and one species of dryomyzid (*Neuroctena caucasica*). Based on larval characters, the Coelopidae are the sister group of the Sepsidae. Based on both the adult and the combined data sets, the Ropalomeridae, which are generally regarded as the sister group of the Sepsidae, are confirmed as their closest living relatives. Two new morphological autapormorphies related to the posterior spiracles are described for the Sepsidae. The following phylogenetic hypothesis is proposed based on the combined data set: (*Orygma* (*Ortalischema* (*Paratoxopoda* (*Themira* (*Decachaetophora* ((*Saltella Susanomira*) (*Nemopoda* (*Lasionemopoda* ((*Meroplius Xenosepsis*) (*Palaeosepsis* (*Palaeosepsis* (*Parapalaeosepsis* (*Dicranosepsis* (*Sepsis* (*Australosepsis Sepsis*)). The genus *Xenosepsis* is synonymized with *Meroplius* (syn. nov.), and the genus *Australosepsis* with *Sepsis*. The history of sepsid classification is briefly discussed, and the most influential systems are compared with the results of the cladistic analysis. The phylogenetic relationships of the genera for which the larvae are unknown are inferred from adult characters.

Larvae for the following genera are described based on a comprehensive scanning electron microscopical study: *Australosepsis* (1 sp.), *Decachaetophora* (1 sp.), *Dicranosepsis* (1 sp.), *Lasionemopoda* (1 sp.), *Meroplius* (2 spp.), *Nemopoda* (3 spp.), *Ortalischema* (1 sp.), *Orygma* (1 sp.), *Palaeosepsis* (4 spp.), *Parapalaeosepsis* (2 spp.), *Paratoxopoda* (1 sp.), *Saltella* (3 spp.), *Sepsis* (20 spp.), *Susanomira* (1 sp.), *Themira* (10 spp.), and *Xenosepsis*. Except for two species of *Nemopoda* for which the cephalic region could not be studied, drawings of the following structures are supplied: cephalic region (ventral and lateral), maxillary palp, anterior spiracle, ventral creeping welt, last segment (ventral, lateral, and dorsal), and spiracular plate of the posterior spiracle. Keys are presented that allow the identification of all genera and most species within the genera. However, the morphological differences between some species within *Sepsis* and *Themira* are so subtle that species identifications are difficult or even impossible. The literature on larval morphology, biology, and distribution of the species is briefly summarized.

INTRODUCTION

Dipterists with an interest in the phylogenetic relationships of higher flies (Cyclorrhapha) have traditionally devoted little time to the study of immatures (but see Okada, 1968; O'Hara, 1989). In part this was due to the difficulty of obtaining immature stages. Even large insect collections house few larvae and systematic collecting of eggs and larvae has been largely neglected. Undoubtedly, acquiring larvae can be quite labor intensive because it is generally difficult to identify immatures to species without establishing cultures. However, as soon as rearing methods are developed, much interesting information about the biology of the species and its various semaphoronts can be gained. I am convinced that developing culture techniques for species with saprophagous larvae will frequently be easy and the results will justify the efforts (e.g., see publications on sciomyzid biology and additional publications by B. A. Foote as listed in Ferrar, 1987).

Larval characters have been crucial for the reconstruction of the higher-level relationships in the Diptera. In the third volume of the "Manual of the Nearctic Flies" on the phylogenetic relationships of the Diptera, 60 of 84 characters for the Nematocera and 20

of 60 for the "orthorrhaphous" Brachycera came from immatures (Wood and Borkent, 1989; Woodley, 1989). However, the proportion of larval characters in the Cyclorrhapha chapter was considerably lower. I am convinced that some of the uncertainty over the phylogenetic position of some families and superfamilies in the Cyclorrhapha could be resolved by larval characters, although Ferrar (1987) was more pessimistic after a study of the published literature: "I still believe that to some extent one can draw conclusions on such [phylogenetic] relationship from immature stages, but I now consider that larval morphology is predominantly functional and that larvae show a number of interesting examples of parallel evolution." (Ferrar, 1987). The conflicting points of view are partly due to a different kind of study that Ferrar and I are referring to. Traditionally, only a small number of characters like the arrangement of spiracle openings, general body shape or the cephalopharyngeal skeleton were studied. The latter even became the embodiment of papers on the morphology of "maggots." There was often rather little variation in these character systems. Phylogenetic analyses must be based on considerably more characters, which in the case of the Sepsidae involves the ultrastructure of the cephalic region and the anal segment. Both can only be adequately explored with the aid of scanning electron microscopy (Grodowitz et al., 1982; Colwell and Kokko, 1986; Ferrar, 1987; Ruiz-Martinez et al., 1989, 1990). Unfortunately, the use of SEM for the study of immature Cyclorrhapha is in its infancy and cladistic evaluation of the morphological information is exceedingly rare (but see O'Hara, 1989). Most SEM studies are exclusively descriptive and involve only one or a few selected species.

THE PHYLOGENETIC RELATIONSHIPS OF THE SEPSIDAE

The Sepsidae are a small family of acalyptrate flies in the Sciomyzoidea (Hennig, 1971, 1973; McAlpine, 1989). The classification of the family is characterized by a large number of very small genera. *Sepsis* and *Themira* comprise far more than half of the 240 described species (Pont, 1979). At the same time, at least 13 accepted genera include fewer than four species each. In some cases, Hennig (1949) already recognized that some of the genera could be synonymized but his suggestions, often not convincingly supported by characters, have been largely neglected in the literature. One goal of my study was to elucidate which of the small genera have to be maintained due to their special position in the phylogenetic system of the Sepsidae and which can be safely synonymized.

The early classificatory history of the Sepsidae is summarized by Duda (1925, 1926). It was through his and Melander and Spuler's (1917) contributions that the Sepsidae and Piophilidae were recognized as different families and that misplaced genera were removed. Hennig (1937) completed this task when he added *Orygma luctuosum*, which had been incorrectly classified in the Coelopidae, to the Sepsidae.

Within the Sciomyzoidea, the Sepsidae and Ropalomeridae are considered sister groups. According to McAlpine (1989), this sister-group relationship is based on eight synapomorphies. However, McAlpine determined the character polarities with respect to the groundpattern of the Sciomyzoidea (although it is uncertain whether the superfamily is monophyletic). Some of the characters occur not only in the Sepsidae and the Ropalomeridae but also in other families within the "superfamily." When all the characters for which this is the case are eliminated, only four unambiguous synapomorphies supporting the sister-group relationship between the Ropalomeridae and the Sepsidae remain: (1) One or more subvibrissal setae tend to be enlarged and vibrissa-like. This is certainly not a convincing character since the subvibrissae are often enlarged in other acalyptrates and the character may even be continuous upon closer inspection of many taxa. (2) Vein A_2 is absent. Again, this in itself would not constitute good evidence since loss of this vein has occurred many times independently within the Acalyptrates. (3) Aedeagal apodeme is fused to hypandrium, i.e., cuneiform. Unfortunately the apodeme has only been studied for a few species (the ropalomerid *Rhytidops floridensis* and the sepsids *Orygma luctuosum*, *Themira putris*, *Nemopoda nitidula*, *Sepsis vicaria*). It may constitute an im-

portant synapomorphy. (4) Posterior thoracic spiracle has one or more distinct setae on posterior margin. This last character is certainly the strongest synapomorphy for the sister-group relationship between the Ropalomeridae and Sepsidae. It is unique within the Sciomyzoidea and very rare within the remaining Cyclorrhapha (it also occurs in some Muscidae and possibly some Oestroidea; Pont, in litt.). In 1973, Hennig argued that the Eurychoromyiidae have a similar seta, but since the seta of *Eurychoromyia* is well posterior to the margin of the metathoracic spiracle, the Eurychoromyiidae are no longer included in the Sciomyzoidea.

The monophyly of the Sepsidae has never been seriously questioned (Hennig, 1973; Griffiths, 1972; McAlpine, 1989). Griffiths (1972) mentioned six autapomorphies. The palpi are reduced, the 6th and 7th abdominal spiracles of the female lie within their respective tergites (Hennig, 1958), the surstyli are fused with the epandrium, the 6th abdominal spiracle of the male lies within the 6th tergite, the 7th sternite of the male is not delimited (either lost or fused with 8th sternite), and the anal (A_1) vein is shortened, not reaching the wing margin (Hennig, 1958; Griffiths, 1972; McAlpine, 1989). McAlpine (1989) added a prominent median facial keel as a 7th autapomorphy. Some of these characters probably do not constitute valid autapomorphies for the family. For example, the fusion of the surstyli to the epandrium is restricted among the basal sepsids to *Orygma* and the Toxopodini. Most other basal sepsids still have free surstyli so that fusion has probably occurred several times independently and may not furnish support for the monophyly of the Sepsidae. Also, the palpi of *Orygma* are not smaller than those of the Ropalomeridae, so that minute palpi probably evolved within the Sepsidae and do not constitute an autapomorphy for the family (for a more detailed discussion, see Meier, submitted).

Neither the apomorphies mentioned for the Sepsidae nor most of those supporting the sister-group relationship of the Sepsidae to the Ropalomeridae are particularly convincing. Most also occur in other presumably more distantly related "Acalyptrates" and the characters appear prone to homoplasy. Thus, these relationship hypotheses are mainly convincing based on the comparatively large number of characters supporting them.

Three different classification schemes have been proposed for the Sepsidae. They are discussed in more detail in Meier (submitted) and summarized in table 1. Except for Duda's (1925) proposal the systems were used to classify the species of individual biogeographic regions, and it is difficult to infer where the authors would have placed other genera not occurring in that region. Duda's (1925) and Zuska's (1980) system, later modified by Steyskal (1987), were probably intended to reflect only loosely phylogenetic relationships. Only Hennig's classification (1949) is explicitly phylogenetic. However, at the time he prepared the manuscript he had not yet developed his phylogenetic method (Richter and Meier, 1994), and some of the proposed monophyletic groups are not supported by any apomorphy found throughout the genera composing the taxon (see Meier, submitted, for a detailed discussion). Also, some of his species groups are obviously supported by plesiomorphies since he uses both the absence of a structure as well as its presence to support different taxa (lack of osmeteria and tufts on the fourth sternites to support the *Sepsis*-, and presence of these structures to support the *Themira* group).

BIOLOGY AND NATURAL HISTORY OF THE SEPSIDAE

For many years, the biology of the Sepsidae has received little attention, and Melander and Spuler (1917) observed: "Possibly because of the commonness and the familiarity of the species, possibly because of their filthy habits, the group has never been adequately studied." Common, they are indeed. The larvae and adults of this group are exclusively saprophagous with most species living on mammal feces (Hafez, 1939, 1947, 1948; Hammer, 1941). Cow dung is the preferred substrate of the most abundant species in the *Sepsis* group and in the genus *Saltella* (Hammer, 1941; Mohr, 1943; Pont, 1979). Many species of the *Themira* group also live on decaying plant matter, carcasses, sludge, and fungi (Hennig, 1949). Little is known about the ecology of species of the *Toxopoda* group

TABLE 1
Comparison of Three Previous Classifications of the Sepsidae

DUDA 1925	HENNIG 1949, 1965	ZUSKA 1977, 1980; STEYSKAL, 1987
Orygma was not yet included in the family	*Orygma luctuosum* as sister group of remaining sepsids	*Orygma* not included****
Saltellinae*: *Saltella**, *Australosepsis**	*Saltella* in *Themira* group *Australosepsis* classified in *Sepsis* group	**Saltellinae**: *Saltella* *Australosepsis* in the Sepsinae
Toxopodinae: *Toxopoda*, *Paratoxopoda*, *Platytoxopoda***	***Toxopoda* group**: *Toxopoda*, *Paratoxopoda***, *Platytoxopoda***	**Toxopodinae:** *Toxopoda*, *Paratoxopoda*, *Platytoxopoda*
Themirinae: *Ortalischema**, *Themira* (*Enicita*, *Enicomira*, *Cheligaster*)	***Themira* group**: *Saltella*, *Ortalischema*, *Themira*, *Susanomira***, *Zuskamira***	**Sepsinae**: *Ortalischema***, *Themira***, *Susanomira***, *Zuskamira***
Meropliinae: *Decachaetophora*, *Meroplius**, *Xenosepsis**	*Decachaetophora*, *Meroplius**, *Xenosepsis**	*Decachaetophora*** *Meroplius*, *Xenosepsis*,
Nemopodinae: *Perochaeta*, *Lasionemopoda*, *Nemopoda*, *Sepsis** (*Sepsidimorpha*)	*Perochaeta***, *Lasionemopoda***, *Nemopoda*, *Sepsis* (*Sepsidimorpha*) classified in *Sepsis*	*Perochaeta***, *Lasionemopoda***, *Nemopoda*, (*Sepsidimorpha*)
Sepsinae***: *Meropliosepsis*, *Lasiosepsis*	***Sepsis* group**: *Meropliosepsis* (as part of *Palaeosepsis*), *Lasiosepsis* (in *Sepsis*)	*Meropliosepsis***, *Lasiosepsis*
Palaeosepsinae***: *Palaeosepsis* *Dicranosepsis*, *Parapalaeosepsis**	*Palaeosepsis*, *Dicranosepsis*, *Parapalaeosepsis** (the last 3 as *Palaeosepsis*)	*Palaeosepsis***, *Dicranosepsis*, *Parapalaeosepsis***
Neosepsinae***: *Leptomerosepsis*, *Sepsis* s. str.	*Leptomerosepsis*, *Sepsis* s. str. (including *Sepsidimorpha* and *Australosepsis*)	*Leptomerosepsis*, *Sepsis* s. str., *Australosepsis*

* Name of genus or subfamily adjusted to modern nomenclature.

** Genus not included in original classification but placement here likely to reflect author's opinion.

*** Duda probably considered the Palaeosepsinae and Neosepsinae subgroups of the Sepsinae although his original table assigns the same rank to all three groups (see Hennig [1949] for similar comments).

**** Classification was presented in the Catalogue of Afrotropical Diptera and *Orygma* is Holarctic.

but some have been attracted to and reared from cc w dung (Cuthbertson, 1937; personal obs.) while others apparently visit carcasses (Braack, 1981). *Orygma luctuosum* is the only sepsid exclusively occurring on decaying sea wrack (Egglishaw, 1960).

For a long time little was known about the biology of the Sepsidae, although the behavior of some species attracted the attention of naturalists. Individuals of *Sepsis fulgens* have the tendency to form large swarms containing up to an estimated 50,000 individuals. Such swarms can be stationary for as long as 30 days (Pont, 1987b). The swarming of *Sepsis fulgens* has spawned numerous notes in entomological journals (see Pont, 1987b) and is today interpreted as a hibernation phenomenon (Pont, 1987b), although similar swarming has also been observed in at least one tropical species in Costa Rica (Grimaldi, personal commun.). In this case, the swarms mainly contained pharate adults and may have been the result of mass emergence.

The other aspect of sepsid biology that has been studied extensively is courtship and mating behavior. The precopulatory guarding by males of *Sepsis cynipsea* has been the subject of important sociobiological studies (Foster, 1967; Parker, 1972 a, 1972 b; Ward, 1983). In precopulatory guarding, the males mount the females prior to egg deposition and copulation takes place only after the female has laid her eggs. Therefore, the deposited batch of eggs is fertilized by sperm that, during previous copulations, had been transmitted into the spermathecae by other males. Interestingly, precopulatory guarding is observed in a number of sepsids, although it had only been described for two species by Parker (1972a, 1972b; *Sepsis cynipsea*, *S. punctum*). Katja Schulz and I also observed this behavior in *Sepsis thoracica* (Zimbabwan population, possibly new species), *Saltella sphondylii*, *Xenosepsis fukuharai*, *Palaeosepsis mitis*, and *Palaeosepsis pusio*. Eberhard (personal commun.) also observed precopulatory guarding in *Palaeosepsis diversiformis* and two other unidentified species of *Palaeosepsis*.

Information on the economic importance of sepsids is scarce, suggesting that it is probably minor. Many species are synanthropic and, unfortunately, the natural history notes containing collecting and rearing records are scattered throughout the literature. I have collected much biological information, which is summarized in a short paragraph following the larval descriptions of each species. Immature sepsids play a major role in the decomposition of cow dung, a process of great importance for dairy farming, which was only realized recently when the use of pesticides disturbed it sufficiently to cause various problems (e.g., Roncalli, 1989; Waterhouse, 1974). Probably more significant is the role of sepsids as disease vectors (Zuska, 1960; Zuska and Laštovka, 1969; Greenberg, 1971). Sepsids have been shown to carry bacteria and spores of fungi (Greenberg, 1971) and occur quite regularly in slaughterhouses (Zuska, 1960; Greenberg and Bornstein, 1964). However, they are usually outnumbered by calyptrate flies, and little research on their potentially detrimental activities has been carried out. Also, adult sepsids rarely visit food that is intended for human consumption, which reduces the risk of disease transmission.

THE MORPHOLOGY OF SEPSID LARVAE

The small body of literature on the morphology of sepsid larvae (Brindle, 1965; Egglishaw, 1960; Hennig, 1949, 1952; Mangan, 1977; Ozerov, 1986a, 1987, 1991a; Schumann, 1962) is summarized in Ferrar (1987). Information on 20 species in 7 genera is available. They were studied using light-microscopical techniques. The morphology of the cephalic region, consisting of head and thoracic segments, has received very little attention in the sepsid and in the remaining literature on the morphology of cyclorrhaphan larvae (but see Hennig, 1949). It is here that the advent of SEM (scanning electron microscope) may have its biggest impact. The quality of the larval descriptions of immature sepsids in the literature is uneven. For example, some small tubercles on the last segment were seen by some authors and missed by others, or the pattern of spines on the last segment was misidentified (e.g., *S. thoracica*, see Hennig, 1949). This made it very hard to evaluate the published information from a cladistic point of view. Fortunately, I was

able to study all previously described species (except for *Saltella orientalis*) and revise the descriptions. From my study I have to conclude that most published keys and identification tables should not be used since too much emphasis has been placed on the number of lobes on the anterior spiracles. Studied across a large number of species, this character is largely continuous. It can only be used for species identification within certain genera.

MATERIALS AND METHODS

The larvae of 52 species from 16 of the 23 sepsid genera were studied with the aid of the SEM (see table 3). Since only the larvae of every fifth described species of the Sepsidae was available for study, the larval apomorphies may not always refer to entire genera but only to species groups within the genera. Thus, the results of this study should "be regarded only as a provocation for further investigation" (Wood and Borkent, 1989).

For outgroup comparison, the immatures of two species of the putative sister group of the Sepsidae, the Ropalomeridae (*Willistoniella pleuropunctata*, and an unidentified *Ropalomera*), two species of the Coelopidae (*Coelopa frigida* and *Chaetocoelopa sydneyensis*), and a species of the Dryomyzidae (*Neuroctena caucasica*) were studied. Except for a brief description (Lopes, 1932), the larvae of the Ropalomeridae were not known prior to this work.

Larvae for some species were provided by K. Schulz (Berlin/Tucson) and immatures for many more species by Dr. A. L. Ozerov (Moscow). A list of species and collecting sites is provided in the descriptions. Larvae which I collected were preserved from cultures established by field-caught females. Normally, single females were placed in a container, provided with substrate, and allowed to lay eggs. Some of the larvae which hatched from the eggs were preserved and others were allowed to complete development. Males of the F_1 generation were used for species identification. It is very important that larvae be cleaned before being preserved in alcohol. The easiest and most efficient way is to use a solution of regular liquid household detergent or to let the maggots crawl through moist tissues. To prevent the retraction of the cephalic region of the larvae during fixation, they were either relaxed in a 10% solution of magnesium sulfate or quickly killed in near-boiling water, the latter technique being more effective.

The fixation of larval Schizophora for SEM has been described as problematic (Grodowitz et al., 1982; Colwell and Kokko, 1986; Ferrar, 1987; Ruiz-Martinez, 1989), and several different techniques have been proposed. Some are technically complicated and expensive (Colwell and Kokko, 1986), others involve extremely toxic chemicals (Grodowitz et al., 1982). I found that preserving larvae in a traditional fixative, alcoholic Bouin, or even 70% alcohol yielded good results with very little distortion of even the delicate structures. After leaving the larvae for at least 2 hours in the fixative, they were transferred in 10% steps into 100% ethanol, critical-point-dried, and sputter coated.

For each species the same nine views of the same larval structures were studied under a SEM (Philips SEM 515): cephalic region, ventral and lateral view; anterior spiracle; posterior spiracle; maxillary sensory organ; last abdominal segment, ventral, lateral, and dorsal; creeping welt. Illustrations were prepared from 18 × 13 cm micrographs, since the preservation and cleanliness of the larvae were too uneven to document the morphology for all species and genera with micrographs. For *Nemopoda speiseri* the cephalic region could not be studied because it was retracted in all specimens. Only partial views of the cephalic region were available for *Nemopoda pectinulata*. Drawings of the cephalopharyngeal skeletons will be forthcoming in Ozerov and Meier (1995).

Measurements were taken with the aid of an electronic measurement board. Arithmetic means and standard deviations are given only when more than five specimens were available for study. The size of third instar larvae can vary considerably because most of the larval growth takes place during this life stage. Also, sepsids are known for their considerable size variability within a species. Depending on the availability of food, the weight of individuals within *Sepsis punctum* can vary by a factor of ten (Zerbe, 1993). Most measurements reported in this study were taken

on late third-instar larvae so that in most cases the reported range is inaccurate at the lower end.

ACKNOWLEDGMENTS

I started my work on the larvae of the Sepsidae four years ago. During the past years numerous colleagues assisted with advice and material. Foremost, I would like to thank Dr. A. L. Ozerov for providing specimens of many species that he reared during fieldwork in the former Soviet Union. The very valuable ropalomerid larvae were kindly loaned to me by W. N. Mathis from the National Museum of Natural History. Additional specimens and a first introduction into "Sepsidology" was provided by K. Schulz. K. Kiontke was a steady source of information on how to efficiently operate the SEM facilities and Dr. W. Sudhaus kindly provided access to the facilities at the Institute of Zoology at the Freie Universität Berlin. The less than pleasant scents of sepsid breeding substrates were patiently tolerated by J. V. McHugh, K. Kiontke, M. J. McDonald, T. R. Schultz, K. Schulz, S. Richter, T. U. Grafe, H.-J. Uffhaus, my mother and various members of the Wheeler and Sudhaus lab in Ithaca and Berlin. Hamish Armour kindly provided housing and permission to work on the Claremont orchard during my visit in Zimbabwe. Advice and continuous encouragement came from Drs. W. L. Crepet, J. I. Davis, D. A. Grimaldi, A. L. Ozerov, A. C. Pont, W. Sudhaus, Q. D. Wheeler, and J. Zuska. The excellent habitus illustrations were prepared by Frances L. Fawcett (Ithaca, NY). For additional information on various aspects of my study, I owe thanks to Drs. P. Ferrar, B. A. Foote, H. Schumann, and M. von Tschirnhaus.

Fellowships to the author were provided by the German National Scholarship foundation and the A. D. White and Olin fellowships of Cornell University. Further generous financial assistance for material and travel expenses came from the Grants-in-Aid of Research program of Sigma Xi, the local chapter of Sigma Xi, the Grace Griswold fund, the Theodore Roosevelt Memorial Fund, the Graduate School of Cornell University, a dissertation improvement grant of the National Science Foundation and a grant from the W. Arthur and Alma D. Rawlins endowment to the Department of Entomology, Cornell University.

DESCRIPTIONS

Hennig (1948–52) and Schumann (1962) characterized the larvae of the Sepsidae by (1) the bulbous swelling of the last segment in preserved specimens, (2) felt-like hairs and strong spines on the last segment, (3) two separate spiracle mountings, (4) ventral and dorsal tubercles on the last abdominal segment and (5) the treelike arrangement of lobes along a central axis of the anterior spiracle. Unfortunately, none of these characters is consistently found in all species, but if a combination of them is encountered the immature is likely to belong to the Sepsidae. This is especially true for the bulbous last segment in combination with the treelike anterior spiracles.

Recently, three keys for the identification of Diptera larvae to families have been published (Ferrar, 1987; Teskey et al., 1991; Teskey, 1981). However, the one by Teskey et al. in Stehr's "Immature Insects" (1991) is, with respect to the Sepsidae, an unmodified version of Teskey's key originally published in the "Manual of the Nearctic Diptera" (Teskey, 1981), so that only two keys are actually available for the identification of sepsid larvae to family. When the keys were originally devised the immatures of only a few genera were known. It does not come as a surprise that the keys have to be modified in order to accommodate some of the immatures newly described in this paper.

In couplet 72, the key (Teskey, 1981) states ". . . shorter spiracular prominences when not forming respiratory tube usually each with tubercle located dorsally or dorsolaterally at base . . ." *Ortalischema* lacks this tubercle and since all the remaining attributes in this couplet also do not apply to this genus while the alternative characters of the couplet do, the

key leads to couplet 79, where *Ortalischema* may be mistaken for a milichiid because it has an arrangement of the slits on the posterior spiracles that resembles the one on milichiids. An additional couplet separating *Ortalischema* from the Milichiidae based on the long-oval shape of the posterior spiracular plate will correct the larval key for *Ortalischema*.

Couplet 77, leading to the Sepsidae, states: "Spicules and pubescence extensively covering terminal abdominal segment only . . . Posterior spiracles usually with well-defined spiracular setae (in *Orygma* resembling *Coelopa* . . .); anterior spiracle with buds projecting to either side of a more or less elongate central axis . . ." None of these features applies to all sepsid larvae. The pubescence is missing in *Orygma* and covers all abdominal segments in *Nemopoda*. *Ortalischema* and *Paratoxopoda* have inconspicuous spiracular hairs. Even given that *Ortalischema* was to key out earlier as suggested above, the problem with *Paratoxopoda* remains. The morphology of the anterior spiracles here ascribed to all sepsids is found in most genera except for *Orygma*, *Ortalischema*, and *Paratoxopoda* (and likely the entire *Toxopoda* clade with roughly 40 species; see Discussion). I think it is necessary to modify the couplet as follows: "usually spicules and pubescence extensively covering terminal abdominal segment only; if pubescence also on other body segments, then with dorsal transverse row of spines on last segment (*Nemopoda*). Posterior spiracles usually with well-defined spiracular setae (in *Orygma* resembling *Coelopa* . . .); if not, posterior spiracular slits on separate elevations (*Paratoxopoda*); anterior spiracle usually with buds projecting to either side of a more or less elongate central axis, if fanlike (*Orygma*, *Paratoxopoda*) check for agreement with special features for these taxa described above."

It is more difficult to accommodate Ferrar's key (1987) where the Sepsidae key out in various places. The key emphasizes the shape of the spiracular slits on the posterior spiracles: "63: Posterior spiracular plates with three straight or virtually straight slits . . ." versus "Posterior spiracular plates with distinctly curved or sinuous slits." This character varies somewhat continuously within the Sepsidae. Due to the very sinuous and curved slits of *Orygma*, *Paratoxopoda*, and *Ortalischema*, one may key out some of these genera (*Paratoxopoda*) as muscids. In one of the couplets leading to the sepsids the last segment is described as "distinctly bulbous compared to rest of body." Here, the word "usually" should be added to accommodate species like *Sepsis indica* or the *Nemopoda* species. Also, in a later couplet (98) leading to the sepsids, an anterior spiracle with a central axis is required. Even given that all the species with a fanlike spiracle are keyed out earlier (since they have sinuate or C-shaped spiracular slits), *Susanomira* with its "spiracle field" would have to be accommodated.

DESCRIPTION OF SEPSID LARVAE

Body cylindrical, tapering toward head; last segment often appears bulbous since the abdominal segments immediately preceding last segment are narrower than last segment; length normally between 4 and 10 mm, rarely as short as 3 or as long as 17 mm; width usually between 0.5 and 1.2 mm, rarely as narrow as 0.4 mm or as wide as 2.5 mm.

CEPHALIC REGION: Ranging from short and wider than long (basal taxa) to very slender, much longer than wide (e.g., *Saltella*, *flavimana* species group in *Sepsis*); normally with two cephalic lobes rarely fused (but see *Australosepsis* and *flavimana* species group); one sensory organ to either side of the mouthhooks, either papilliform (e.g., fig. 463) or in derived taxa papilla incorporated into a comb (e.g., fig. 464); most species also with a posterior sensory pore on a lower lobe at base of mouth opening (e.g., figs. 1, 10); with two fleshy ridges in the middle of mouth opening (brace) either gaping (e.g., figs., 77, 454) or partly fused (e.g., figs. 391), anterior tips often distinctly enlarged into bulbous hooklike projections (e.g., figs. 95, 104); few to numerous combs covering cephalic region anterior to facial mask (e.g., figs. 158, 167) or even the entire facial mask (e.g., fig. 391); combs in some species with bifurcated tips (e.g., figs. 37, 46); facial mask usually with at least some ridges, which within *Sepsis* are arranged into "blocks" (e.g., fig. 294); within *Sepsis* group two ridges on either side of

mouth opening large and fused to each other at anterior end (e.g., fig. 292).

MAXILLA: Composed of five compound papillae often arranged into two groups of two and three (e.g., fig. 86); groups sometimes separated by a wide fleshy fold (e.g., fig. 86); four papillae consisting of two superimposed lobes, one composed of three superimposed lobes (e.g., fig. 38).

ANTERIOR SPIRACLE: Lobes arranged into a row (e.g., fig. 91), along a central axis (e.g., fig. 396), or a spiracle field (fig. 360); usually 5–20 lobes, rarely as few as three or as many as 40.

CREEPING WELTS: Usually, with spinules on either side of the ventral fold indicating the border between the cephalic- and thoracic segments; first seven body segments with rows of spinules laterally and dorsally; ventrally, first four welts normally consisting of spinules and six additional welts with two long ventral rows of reclinate spines and multiple additional rows of spinules anterior and posterior to rows of spines (e.g., fig. 317); rarely with three rows of spines (e.g., figs. 93, 362) and/or seven welts with spines; on first row of spines, the median ones missing or reduced in size (e.g., fig. 44); often with up to eight anteromedian spines forming a short row of spines anterior to complete rows (e.g., fig. 317). Except for last abdominal segment, integument not pubescent (but see *Nemopoda*).

LAST ABDOMINAL SEGMENT: Often distinctly bulbous at anterior end (e.g., fig. 110); usually with many hairs and/or warts (e.g., figs. 108, 110); in most species somewhat longer than wide (e.g., fig. 110), but sometimes extremely elongated (e.g., *Lasionemopoda*; e.g., figs. 32, 34); anal plate either reduced (*Orygma*; fig. 90), simple (e.g., *Meroplius*; fig. 41), swollen with diagonal fold (e.g., most *Themira*; fig. 368), or wing-shaped (*Nemopoda*; fig. 73; *Sepsis* group; e.g., fig. 278); postanal protuberance ranges from absent (e.g., fig. 90) to very well developed, tongue-shaped, and spiny (e.g., fig. 99); often with preanal row of spines along anal plate, spines sometimes fused to form a button (e.g., figs. 368); usually with a pair of subanal tubercles which can be small and bare (e.g., fig. 99) or large and hairy (e.g., fig. 66); always with a subanal sensory organ posterior to the tubercle (e.g., fig. 5), like the following organs consisting of a papilla and two or—rarely three—sensory hairs; usually with one or two pairs of ventral tubercles at the base of spiracle mountings (e.g., figs. 5, 162); usually with a pair of ventral sensory organs at the base of ventral tubercles (e.g., fig. 5); between bases often with a distinct depression; hairs posterior to postanal protuberance in the *Sepsis* group transformed into warts (e.g., fig. 99); last segment usually spiny with spines arranged into an anterior and a posterior band (e.g., fig. 101); area between bands normally pubescent (e.g., fig. 101), rarely bare or covered with warts (e.g., fig. 137); pair of lateral tubercles which are associated with a dorso- and a ventrolateral sensory organ (e.g., figs. 7, 9); spiracle mountings ranging from short (e.g., fig. 7), short and distinctly divided into three lobes (*Paratoxopoda*; fig. 153) to very long and slender (e.g., fig. 32); spiracle mounting usually with small dorsal tubercle (e.g., fig. 34); dorsal surface of last segment almost always with three longitudinal grooves, each bordered by a row of spines on either side (e.g., fig. 9).

POSTERIOR SPIRACULAR DISC: Flat to bulging, with three openings and usually four processes of spiracular hairs, which are rarely arranged along rim of spiracular plate (as in fig. 89); three processes are associated with openings, the unassociated one ("d" on figs.) is either similar in composition (e.g., fig. 58) or has only two very narrow, unbranched hairs (e.g., fig. 4); two spiracular openings either parallel with a third in a 90° angle (e.g., fig. 58), or opening in *Sepsis* arrangement with two slits extending beyond the spiracular plate and the third being characteristically bent (e.g., fig. 4); slits ranging from straight to crescent- or S-shaped; ecdysial scar not on spiracular plate but either just off edge (e.g., fig. 89) or in a dorsomedian position halfway between dorsal tubercle and spiracular plate (e.g., fig. 9, 45).

BIOLOGY: All known larvae are saprophagous. Most occur with little specialization on mammal feces but somes species appear to be restricted to either cow dung (some *Sepsis*) or horse droppings (e.g., *Ortalischema*). A few species are generalists and breed in carrion (*Meroplius*, *Xenosepsis*, *Nemopoda*). The widest range of breeding substrate is demonstrated by *Nemopoda nitidula* which breeds

on all kinds of decaying organic matter including feces and carrion, but also fungi (including slime molds). *Orygma luctuosum* is restricted to decaying brown algae.

DISTRIBUTION: Worldwide, with many species occurring across several biogeographic regions.

KEY TO SEPSID GENERA

The morphological study of the larvae was undertaken with the aid of a SEM. As far as possible, the following key is based on characters that can also be seen through a light microscope. It is often necessary to use 20× oculars. In any case, the morphology of the identified species should be carefully compared with the illustrations, descriptions, and information on breeding substrate and geographic distribution. Some genera can only be identified using characters for which a SEM is necessary. For characters based on the position of the spiracular slits, either a SEM can be used or microscopic slides can be prepared. This key is not intended to reflect phylogenetic relationships and applies only to third instars.

In the Sepsidae, third instars can be distinguished from the first two stages by the size and degree of sclerotization of the cephalopharyngeal skeleton as well as the morphology of the anterior spiracle. In first instars, the cephalopharyngeal skeleton is only partially pigmented and the spiracle openings consist of a single hole that is not placed on a lobe. In second instars the cephalopharyngeal skeleton is smaller and the anterior spiracle has only a single lobe. Only in third instars are at least three, but usually many more, lobes found on the spiracle and the cephalopharyngeal skeleton reaches its maximum size.

KEY TO GENERA OF SEPSID LARVAE

SIMPLIFIED KEY TO THE *SEPSIS* GROUP

More than half of all Sepsidae belong to Hennig's (1949) *Sepsis* group. All species in the *Sepsis* group that occur in Europe and most of those in North America belong to the genus *Sepsis*. To facilitate identification of *Sepsis* larvae, the following key can be used. It is difficult to devise a key that allows simple and fast identification of all *Sepsis* species. However, almost all specimens of all species have a wing-shaped anal plate which may be difficult to see in some specimens. Sometimes the "wing" is weakly differentiated, but only in *Sepsis indica* it is missing. Specimens with an anal plate that is difficult to classify must be run through the complete key, i.e., the following key is only applicable to larvae with a clearly wing-shaped anal plate.

1. Body densely hirsute (e.g., figs. 59, 61–63); last segment dorsal with transverse row of spines (e.g., fig. 63) ..... *Nemopoda*
– Body bare except for last abdominal segment and spinules around segmental borders; without dorsal transverse row of spines on last segment 2
2. With seven creeping welts consisting of a double row of spines, the seventh found immediately anterior to anal plate (e.g., fig. 386) ..... *Themira leachi*
– With six creeping welts consisting of ventrally complete double row of spines, i.e. without creeping welt immediately anterior to anal plate (e.g., fig. 269) 3
3. Last segment elongated with ventral tubercles not originating at base of spiracle mountings but further anterior (e.g., fig. 32) ..... *Lasionemopoda*
– When last segment elongated ventral tubercles originating at base of spiracle mounting (e.g., fig. 224) ..... *Sepsis* group, couplet 13 of complete key.

COMPLETE KEY TO SEPSID GENERA

1. Ventral tubercles distinctly bifurcated (e.g., fig. 162) ..... *Saltella*
– Ventral tubercles, if present, simple (e.g., fig. 5) at most with an additional small protuberance on the medioventral side (e.g., fig. 215) 2
2. Ventral tubercles missing (e.g., fig. 81); anterior spiracle consisting of row of lobes on body wall (e.g., fig. 82); spiracular slits of posterior spiracle on longoval plate (e.g., fig. 80) ..... *Ortalischema*
– Ventral tubercles present (e.g., fig. 5), anterior spiracle rarely consisting of row of lobes; instead lobes aranged along a central axis; spiracular slits not on longoval plate .. 3
3. Anterior spiracle composed of more than 30 lobes in a spiracle field (e.g., fig. 360) ..... *Susanomira*
– Anterior spiracle with at most 25 lobes per spiracle, not in a spiracle field (e.g., figs. 82, 91, 181, 414) 4

4. Anterior spiracle consisting of a row of lobes on body wall (complete spiracle must be visible) or fanlike (e.g., figs. 15, 82, 91, 154); spiracle large enough to be easily visible at low magnification 5
- Anterior spiracle consisting of lobes arranged along a central axis protruding from the body wall; at best with a few additional lobes along base of central axis (e.g., figs. 181, 414); spiracle small to large 7
5. Spiracular slits of posterior spiracle on three separate elevations (fig. 152) ..... *Paratoxopoda*
- Spiracular slits of posterior spiracle on single round spiracular plate (fig. 89) 6
6. Creeping welts consisting of three rows of dark spines (e.g., fig. 93); without lateral tubercle (e.g., fig. 92); last segment short (e.g., fig. 92); larvae exclusively in rotting brown algae in coastal habitats ..... *Orygma*
- Creeping welts consisting of two rows of spines (e.g., fig. 17); with lateral tubercle, last body segment elongated (e.g., figs. 14, 16, 18) ..... *Decachaetophora*
7. Entire body covered with hairs, giving body surface a dull appearance (e.g., figs. 59, 61–63); transverse row of spines on the last segment (e.g., fig. 63) ..... *Nemopoda*
- Body except for ventral area anterior to creeping welt shiny; without transverse row of spines on last segment 8
8. Last segment extremely elongated (e.g., figs. 32, 34, 36), ventral tubercles originate anterior of fold between last segment and root of spiracle mountings (e.g., fig. 32); cephalic region distinctly bilobed (e.g., fig. 28) ..... *Lasionemopoda*
- Last segment barely longer than wide, or if elongated [*Sepsis indica* (fig. 251), and *flavimana* species group within *Sepsis*; e.g., fig. 215], ventral tubercles originate at fold together with the spiracle mountings and except for *Sepsis indica* (fig. 47), cephalic region monolobed (fig. 211) 9
9. Last segment extremely elongated, anal plate swollen with diagonal fold (fig. 251) ..... *Sepsis* (*Allosepsis*) *indica*
- Last segment not elongated, or if elongated, with wing-shaped anal plate (e.g., fig. 215) 10
10. Ventrally, last segment with distinct preanal button consisting of spines (e.g., fig. 368); anal plate very large, covering almost entire width of segment (e.g., fig. 368) ..... *Themira* (subgenus *Enicita*)
- Ventrally last segment at best with row of spines along anterior margin of anal plate; anal plate usually much smaller (e.g., fig. 395) 11
11. Subanal tubercle large and hairy, much larger than spines on last segment (e.g., fig. 377); if subanal tubercle medium-sized (e.g., fig. 395), anterior spiracles long with at least 11 lobes along long central axis (e.g., fig. 396); cephalic region wider than long (e.g., fig. 391) ..... *Themira*
- Subanal tubercle small and usually bare, about as large as a spine (under a light microscope difficult to distinguish from spine; e.g., fig. 5); cephalic region longer than wide (e.g., figs. 1, 238) 12

The following character allows the identification of most specimens of species in the *Sepsis* group. In some specimens the "wing" of the anal plate is very weakly expressed and may be difficult to see. Such specimens will key to the *Sepsis* group at a later point in the key.

12. Last segment with wing-shaped anal plate (e.g., figs. 215, 314) ..... *Sepsis* group
- Last segment with simple anal plate (e.g., fig. 457) 13

The following genera can only be distinguished with some certainty using microscopical slides that document the arrangement of the openings of the posterior spiracle.

13. Slit of posterior spiracle not extending beyond spiracular plate or running along spiracle mountings (e.g., fig. 98) 14
- One slit distinctly arched at one end (e.g., fig. 4); two others extending beyond spiracular plate (e.g., fig. 4), one of which is very long and visible medioventrally on spiracle mounting (e.g., fig. 5) 16

Each of the following characters can only be seen with the aid of a SEM.

14. Brace between mouthhooks with swollen tip (e.g., fig. 95); ventrally last segment with small warts (e.g., fig. 99); facial mask usually with ridges (e.g., fig. 95) ..... *Palaeosepsis*
- Brace gaping, without swollen tip (e.g. figs. 37, 453); last segment covered with hairs (e.g., fig. 41) or very coarse and large warts (fig. 457); facial mask covered with coarsely toothed ridges (e.g., figs. 37, 453) 15
15. Last segment hairy, with one to several rows of spinules anterior to anal plate surrounding entire segment (e.g., figs. 41, 43, 45) ..... *Meroplius*
- Last segment bare except for very large warts (ventral side) and spines (fig. 458, 460, 462) ..... *Meroplius* (*Xenosepsis*)

16. Combs immediately anterior to facial mask with very blunt edge with no or very short fringes; cephalic lobes fused (e.g., fig. 1) ..... *Sepsis* (*Australosepsis*) *niveipennis*
- Combs always with long fringes (e.g., fig. 211); normally with two cephalic lobes (e.g., fig. 265), lobes rarely fused (as in fig. 211); if fused last segment elongated (except for *Sepsis dissimilis*; fig. 206) 17
17. Warts present between lateral bands of spines and dorsal double rows of spines (e.g., fig. 139); facial mask with two ridges along mouth opening that remain parallel and do not fuse (e.g., fig. 131) ....*Parapalaeosepsis compressa*, *P. plebeia*
- Warts, if present, restricted to ventral and lateroposterior and dorsoposterior parts of last segment; none between lateral rows of spines and on dorsal aspect of last segment between rows of spines (e.g., figs. 215, 217, 219); facial mask with two ridges along mouth opening, the lateral fused or attached to median ridge (e.g., figs. 211, 265) 18
18. Ridges of facial mask fringed, not arranged in blocks (e.g., fig. 21) ..... *Dicranosepsis*
- Ridges of facial mask never fringed (e.g., fig. 267), usually arranged in blocks (e.g., fig. 267) and if pattern indistinct, then cephalic lobes fused (e.g., fig. 213) ..... *Sepsis*

1. GENUS *AUSTRALOSEPSIS* MALLOCH, 1925

Australosepsis niveipennis (Becker, 1903)

Locality: Honde-Valley (Honde-Valley, Eastern Highlands, Zimbabwe), coll. R. Meier; 40 mi west of Cairns (Queensland, Australia), coll. R. Meier

Specimens examined: 18

Length: 4.26–5.07 mm ($\bar{x}$ = 4.53 0.30; n = 10)

Largest width of body segments: 0.59–0.78 mm ($\bar{x}$ = 0.68 0.07; n = 10)

Width of last segment: 0.65–0.83 mm ($\bar{x}$ = 0.73 0.06; n = 10)

CEPHALIC REGION (fig. 1: ventral view; fig. 3: lateral view): Longer than wide, monolobed, moderately large lower lip; anterior pore on one comb to either side of brace; combs with few or no teeth, combs with rounded posterior edges; posterior pore on distinctly bulbous lower lobe; brace with apical tips distinctly swollen into hooklike projections; facial mask composed entirely of smooth-edged ridges, two ridges next to either side of mouth opening attached to each other at tip; ridges organized into anterior and posterior sections separated by a midfurrow; anterior section organized into four "blocks," whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter, intercalary ridges; in Zimbabwen specimens the first block consisted of 3–4, the second of three, and the remaining of two ridges; in Australian specimens the last two blocks consisted of 2–3 ridges; posterior section of facial mask with five ridges in Zimbabwen specimens and about nine in Australian specimens; combs surrounding entire margin of facial mask.

MAXILLA (fig. 2): Consisting of five compound papillae not arranged in two distinct groups; four compound papillae (pap. 1–3, 5) consisting of two superimposed lobes, one (pap. 4) composed of three superimposed lobes.

ANTERIOR SPIRACLE (fig. 6): Consist of 5–6 lobes along a short central axis; some of the lobes are sometimes fused to body wall instead of being arranged around a central axis.

CREEPING WELTS (fig. 8): First eight body segments with rows of spinules laterally and dorsally; ventrally, first four welts consist of spinules only; remaining six segments with two ventral rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 29–40 spines, median spines distinctly smaller than lateral ones; second row with 15–29 spines; 2–4 anteromedian spines forming short anterior row. Australian specimens had fewer spines (first rows 18–23, second row 27–30 spines). Tips of spines not very pointed, but rather rounded. Except for last abdominal segment, integument not pubescent.

LAST ABDOMINAL SEGMENT (fig. 5, ventral view; fig. 7, lateral view fig. 9, dorsal view; fig. 466, subanal tubercle; fig. 468, lateral tubercle): Distinctly bulbous, dorsally very pubescent; anal plate wing-shaped, inner and outer lobes somewhat flat, not very well separated; outer lobe rounded laterally; postanal protuberance weakly developed, mainly consisting of a number of spines; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles, subanal sensory organ posterior to each tubercle; pair of ventral tubercles with a ventral sensory organ at each base; distinct depression be-

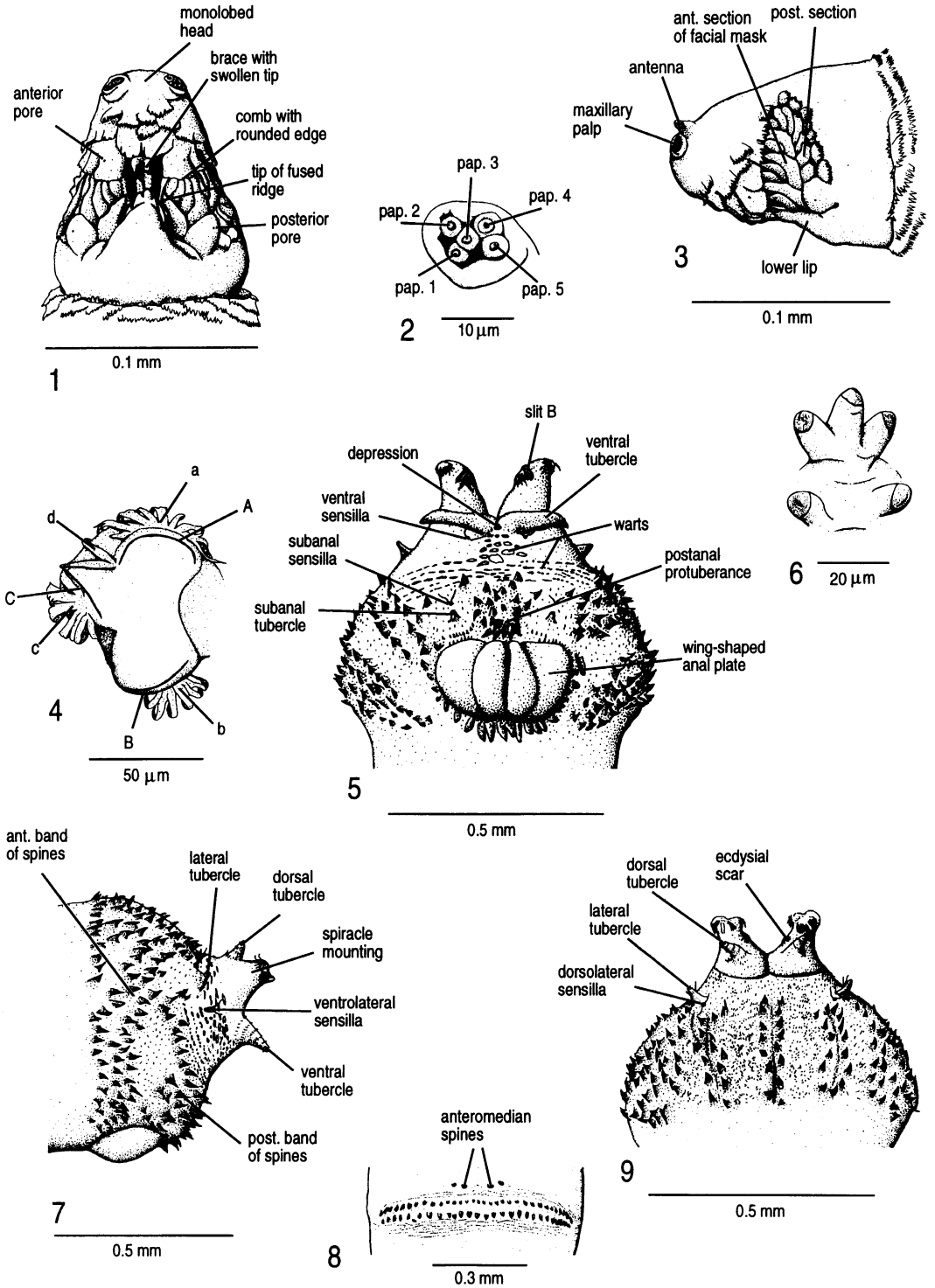


Fig. 1–9. *Australosepsis niveipennis*. **Cephalic region:** 1: ventral; 3: lateral; **maxillary palp:** 2; **posterior spiracle:** 4; **last segment:** 5: ventral, 7: lateral, 9: dorsal; **anterior spiracle:** 6; **creeping welt:** 8.

tween bases; hairs posterior to postanal protuberance transformed into small number of warts, warts anterior to depression in Zimbabwen specimens considerably larger than on remainder of segment; in Australian specimens, warts barely or not larger; laterally, spines arranged into an anterior and a posterior band; area between bands sparsely pubescent; pair of lateral tubercles with both ventro- and dorsolateral sensory organs; spiracle mountings short, moderately large dorsal tubercle; dorsal side of last segment with three longitudinal grooves, each bordered by a row of irregularly spaced spines on either side; integument between rows densely hirsute; hairs of all sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 4): Consists of flat spiracular plate with three openings and four processes of spiracular hairs, each associated with openings ("a–c") and composed of 6–9 hairs; unassociated process ("d") always of two long, narrow hairs; opening below two-hair process straight ("C"), barely extending beyond spiracular plate; opening "B" very long, visible on ventromedian surface of spiracle mounting (fig. 5), opening "A" arched at one end toward root of process "d"; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 9).

BIOLOGY: *Australosepsis niveipennis* has been collected mainly from cow dung (Iwasa, 1984; Zuska, 1968). In Australia where it has probably been introduced, it dominates the cow dung communities in arid areas (Colless, 1980). It generally favors open pastures and is exceptionally heat- and drought-tolerant. Snowball (1944) reared specimens from cow dung (in Australia; see also Ferrar, 1987) but also reported that it has been associated with carrion. Hafez (1947; 1948) collected and reared *A. niveipennis* from buffalo and cow dung. In this substrate the larval development took four days at a temperature of 26–28° (at 20°C: 6–7 days). I observed this species depositing eggs readily in fresh cow dung, and the total development time from egg to the imago can be as short as six days. Despite its abundance on fresh cow pats (Australia and Zimbabwe), I have never observed any pre- or postcopulatory guarding. Large males tend to be yellow-red whereas small males are dark brown-to-black like the females. Whether different behavior is associated with the color morphs (as in other species, see *Sepsis punctum*) is unknown.

DISTRIBUTION: *Australosepsis niveipennis* is widespread in the Old World tropics and subtropics (see Iwasa, 1987; 1989). Colless (1980) provides the exact distribution for Australia (see also Zuska, 1889). In the Palearctic the species is restricted to North Africa [Egypt, Israel, and Palestine; (Hennig, 1949)].

2. GENUS *DECACHAETOPHORA* DUDA, 1926

Decachaetophora aeneipes (De Meijere, 1913)

Locality: Primorskiy kray, 40 km SE Ussuriysk, (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 2
Length: 9.85–10.57 mm (n = 2)
Largest width of body segments: 1.16–1.22 mm (n = 2)
Width of last segment: 1.26–1.33 mm (n = 2)

CEPHALIC REGION (fig. 10, ventral view; fig. 12, lateral view): About as wide as long, bilobed with rather small lower lip; distinct posterior pores on lower lobe and anterior pores on comb to either side of brace; brace simple, tips not enlarged; combs not restricted to anterior section of cephalic lobes, but also present on facial mask; combs wider than long with long pointed teeth; combs absent from inner side of cephalic lobes and around maxillae; facial mask with numerous serrate ridges converging onto anteromedian corner of lower lobe; only two ridges along mouth cavity with smooth edge.

MAXILLA (fig. 11): Five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four compound papillae consisting of two superimposed lobes (pap. 1–3, 5), one (pap. 4) composed of three superimposed lobes; distinct gap between groups of two and three separated by an incomplete fleshy lobe.

ANTERIOR SPIRACLE (fig. 15): 12–14 lobes arranged along a very broad central axis which widens toward tip; tip formed by multiple lobes.

CREEPING WELTS (fig. 17): First five welts with rows of spinules around entire segment:

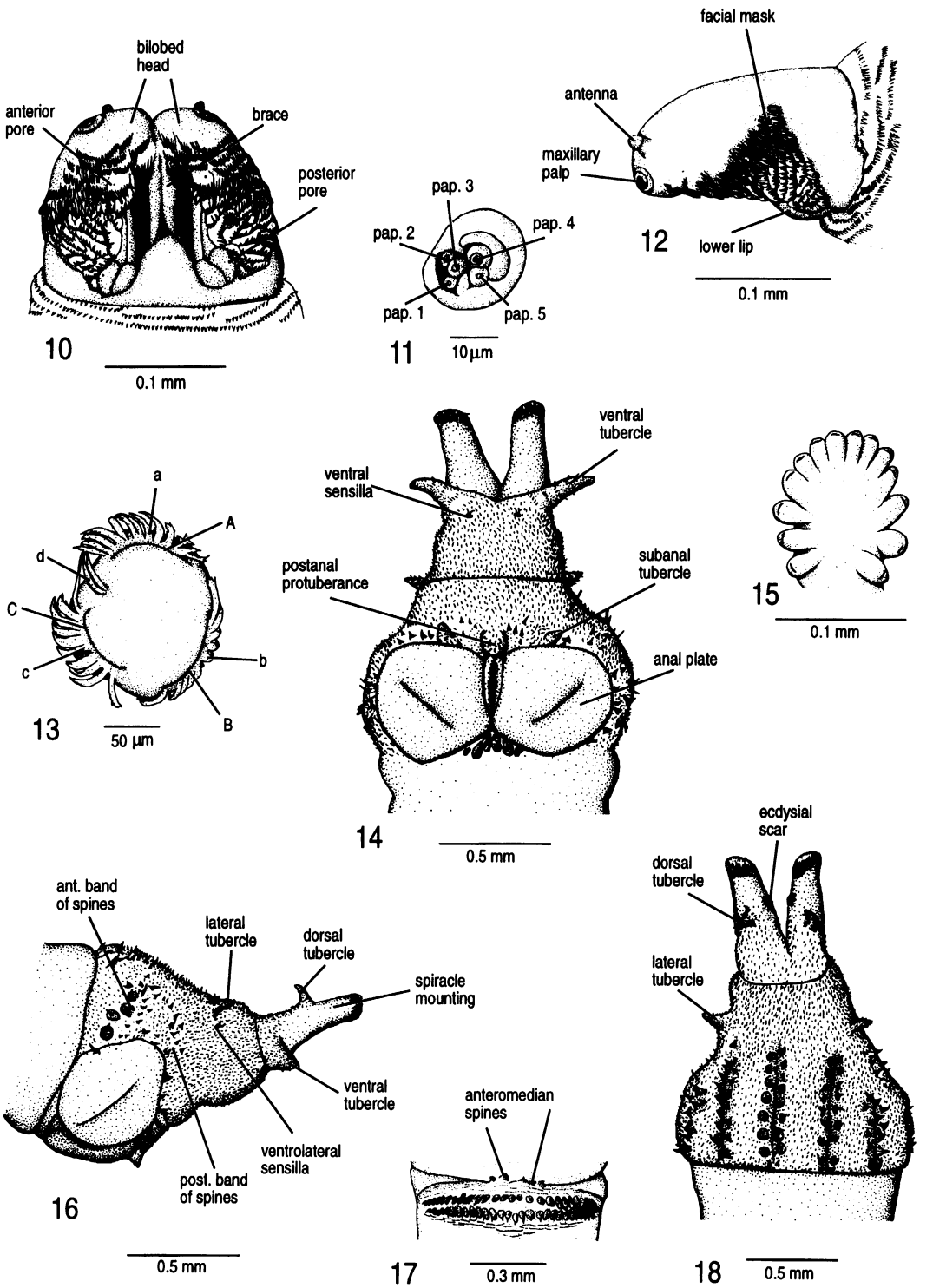


Fig. 10–18. *Decachaetophora aeneipes*. **Cephalic region:** 10: ventral, lateral: 12; **maxillary palp:** 11; **posterior spiracle:** 13; **last segment:** 14: ventral, 16: lateral, 18: dorsal; **anterior spiracle:** 15: **creeping welt:** 17.

from 6th welt on without spinules dorsally; from 7th welt on also without spinules laterally; ventrally first four welts consisting of spinules only; remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior; first row of spines with 18–26 spines, median spines slightly smaller than lateral ones, second row with 22–28 spines; 5–6 anteromedian spines forming an anterior short row; all spines large with unusually broad base and sharp point. Except for last abdominal segment, integument not pubescent.

LAST ABDOMINAL SEGMENT (fig. 14, ventral view; fig. 16, lateral view; fig. 18, dorsal view): Bulbous, posterior half elongated; dense, short pubescence; anal plate large with diagonal fold, about as wide as last segment, rounded laterally; postanal protuberance rather small, hairy to spiny; preanal protuberance absent, but short crescent-shaped preanal row of spines present; pair of weakly developed, bare subanal tubercles; subanal sensory organ immediately posterior to tip of each tubercle; pair of well-developed ventral tubercles with ventral sensory organ at each base; laterally, bands composed of few spines; only anterior band with strong spines ventrolaterally like those of creeping welt, posterior band with few, much smaller, spines; moderately large lateral tubercle associated with dorso- and ventrolateral sensory organs; spiracle mountings moderately long, with long and slender dorsal tubercle; dorsal surface of last segment with three longitudinal grooves, each bordered by a row of regularly spaced strong spines on either side, integument between rows densely hirsute; sensory organs with short hairs.

POSTERIOR SPIRACULAR DISC (fig. 13): Flat spiracular plate with three openings and four processes of spiracular hairs, those associated with openings ("a–c") composed of 8–10 hairs more or less arranged along the rim of spiracular plate; unassociated process ("d") with two long hairs; openings weakly curved and arranged along the rim of spiracular disc; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 18).

BIOLOGY: Little is known about the biology of *D. aeneipes*. Iwasa (1984) reported that in Japan, the adults are commonly found in the vicinity of cattle breeding pastures in mountainous areas. He stated that "The larvae mainly seem to breed in the compost of cow and pig dung, and human excrement." Ozerov (1989) confirmed that larvae develop in human excrement and that adults can be collected from other animal dung as well as in "filthy refuse pits." Coffey (1966) collected the species from chicken dung.

DISTRIBUTION: *Decachaetophora* occurs throughout the Oriental region but is also known from the fringes of the Palearctic (Hennig, 1949; Japan: Iwasa, 1987; 1989). Apparently it has been introduced to western North America (Steyskal, 1943).

3. GENUS *DICRANOSEPSIS* DUDA, 1926

Dicranosepsis bicolor (Wiedemann, 1830)

Locality: 30 mi west of Cairns (Queensland, Australia), coll. R. Meier
Specimens examined: 5
Length: 5.41–5.92 mm ($\bar{x}$ = 5.70 0.18; n = 5)
Largest width of body segments: 0.62–0.80 mm ($\bar{x}$ = 0.71 0.06; n = 5)
Width of last segment: 0.64–0.81 mm ($\bar{x}$ = 0.70 0.06; n = 5)

CEPHALIC REGION (fig. 19, ventral view; fig. 21, lateral view): Much longer than wide, weakly bilobed, large lower lip; posterior pores on lower lobe and anterior pores on comb to either side of brace; brace with tips distinctly enlarged into hooklike projections; 5–6 combs restricted to anterior section of cephalic lobes, mostly in horizontal rows, usually much wider than long with multiple teeth; combs absent around maxillae; facial mask composed entirely of few fringed ridges/combs in no apparent order, the two ridges next to either side of mouth opening with straight edges and fused to each other at tip.

MAXILLA (fig. 20): Composed of five compound papillae; four out of five consisting of two superimposed lobes (pap. 1–3, 5), only one with three superimposed lobes (pap. 4); no gap between the papillae.

ANTERIOR SPIRACLE (fig. 24): Consists of 4–5 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 26): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of

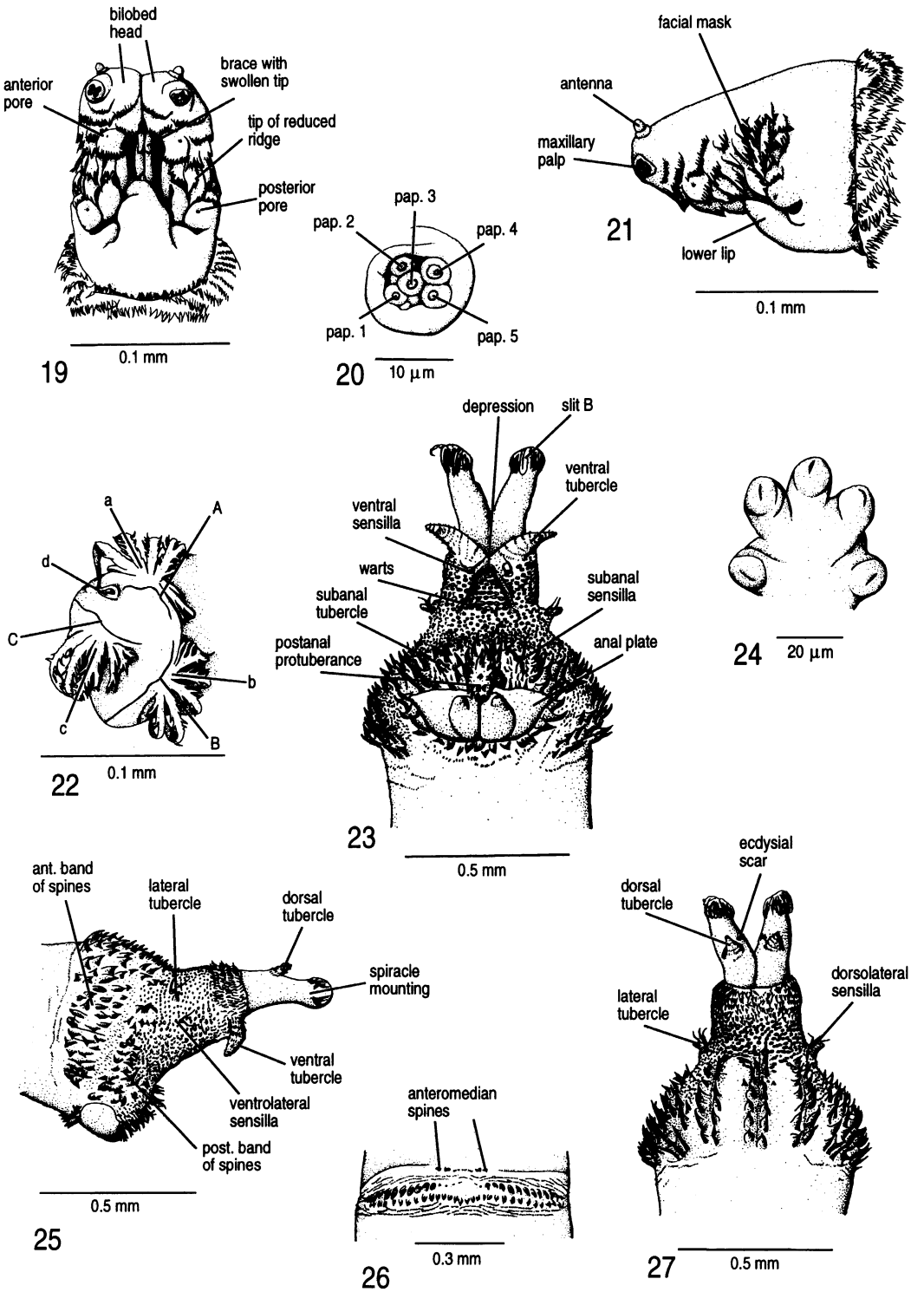


Fig. 19–27. *Dicranosepsis bicolor.* **Cephalic region:** 19: ventral, 21: lateral; **maxillary palp:** 20; **posterior spiracle:** 22; **last segment:** 25: lateral, 27: dorsal, 24: ventral; **anterior spiracle:** 24; **creeping welt:** 26.

spinules, remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior to rows; first row of spines with 18–26 spines, median ones missing or reduced in size; second row with 18–26 spines; four anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 23, ventral view; fig. 25, lateral view; fig. 27, dorsal view): Anterior section distinctly bulbous, with numerous small warts laterally and dorsally as well as in area between depression and two bare diagonal lines; hairs between the two bands of spines; anal plate large, wing-shaped, posterior tip of inner lobe projecting, outer lobe pointed laterally; anal plate with row of spines around anterior edge; postanal protuberance very well developed; weakly developed, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with ventral sensory organ at each base; with an anterior and a posterior band of spines; anterior band incomplete ventrally; spines large with sharp drawn-out points; small lateral tubercle associated with dorso- and ventrolateral sensory organs; spiracle mountings long, with dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of regularly spaced spines on either side; area between spines bare; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 22): Three openings and four processes of spiracular hairs: processes ("a–c") associated with openings with 5–7 hairs, unassociated process ("d") with two unbranched narrow hairs; opening "B" extending well beyond spiracular plate onto ventromedian surface of spiracle mounting (fig. 23), opening "A" arched at one end toward the root of process "d"; opening "C" barely extending beyond spiracular plate; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 27).

BIOLOGY: This is a very widespread and common species in the Old World tropics. Due to its exceptionally variable morphology it has spawned many synonyms. Nevertheless, no rearing record or description of behavior appears to be in the literature. In Australia, I caught the species on cow dung as well as human excrement. It is one of the first sepsids to arrive at fresh substrate. It deposits eggs readily in cattle feces from which it has also been bred (development time very short, about a week). I did not observed pre- or postcopulatory guarding.

DISTRIBUTION: *Dicranosepsis bicolor* is widespread throughout the Oriental region, including some islands of the Philippines and Sri Lanka (Hennig, 1949; Iwasa, 1987; 1989). It is also found in the Palearctic (Hennig, 1949: Shanghai) and Australian regions (Zuska, 1989; Colless, 1980: Queensland; Hennig, 1949: New Guinea). Colless (1980) speculated that it may have been introduced to Australia.

4. GENUS *LASIONEMOPODA* DUDA, 1926

Lasionemopoda hirsuta (Meijere, 1906)

Locality: 5 mi west of Moruya (New South Wales, Australia), coll. R. Meier
Specimens examined: 9
Length: 12.04–15.24 mm (n = 4)
Largest width of body segments: 1.06–1.43 mm (n = 4)
Width of last segment: 0.80–1.03 mm (n = 4)

CEPHALIC REGION (fig. 28, ventral view; fig. 30, lateral view): Much longer than wide, bilobed, small lower lip; posterior pores on lower lobe and anterior pores on comb to either side of brace; brace with tips distinctly enlarged into hooklike projections; numerous combs on anterior section of cephalic lobes including the inner sides and area around maxillary palp; facial mask composed entirely of combs and few fringed ridges in no apparent order; the two ridges lining the mouth opening on either side are straight-edged but not fused to each other at tip.

MAXILLA (fig. 29): Composed of five compound papillae; four out of five consisting of two superimposed lobes (pap. 1–3, 5), only one with three superimposed lobes (pap. 5); without gap between papillae but remnant of a fleshy lobe present.

ANTERIOR SPIRACLE (fig. 33): Consisting of 4–5 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 35): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules, remaining six welts ventrally with

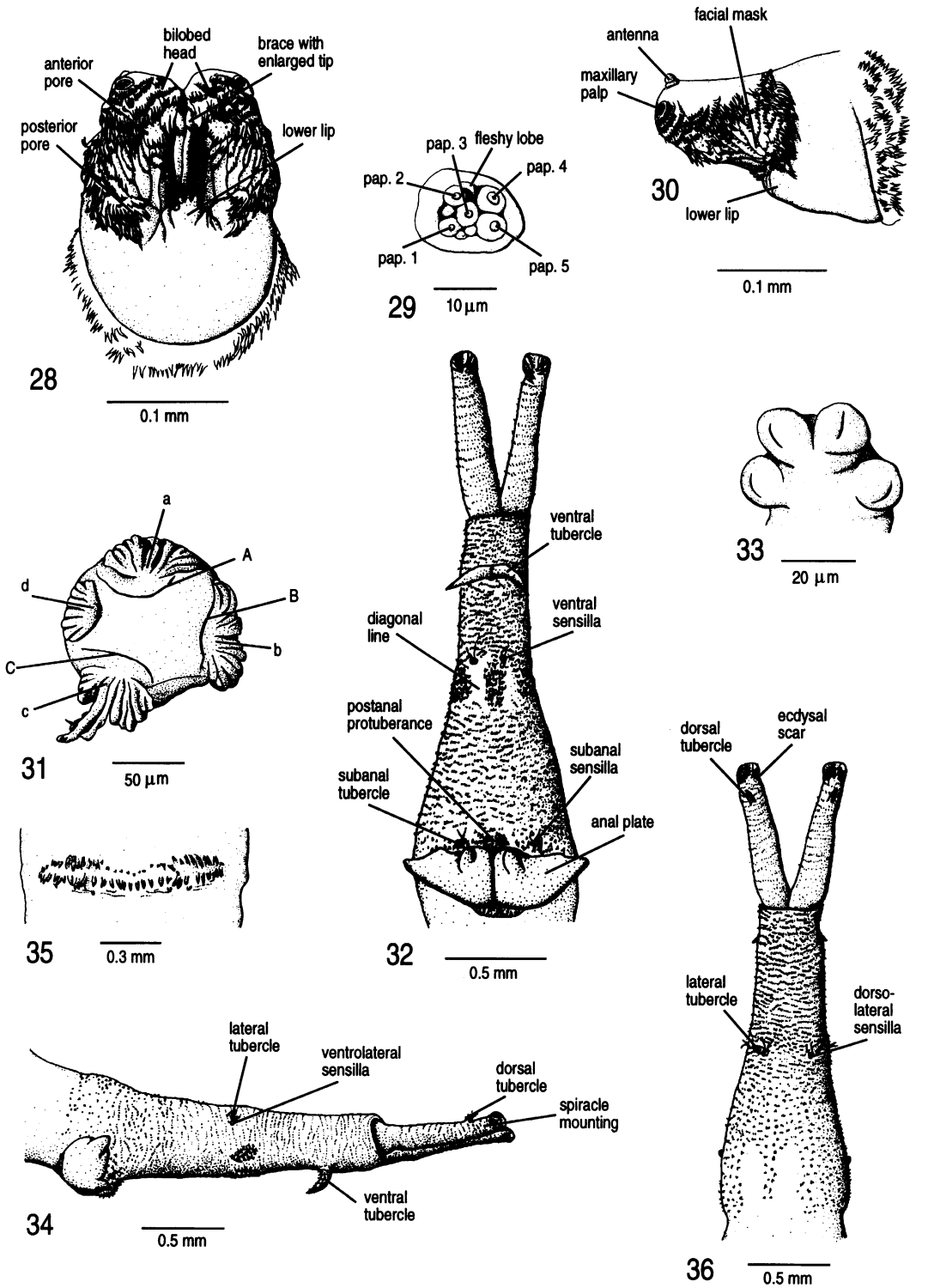


Fig. 28–36. *Lasionemopoda hirsuta.* **Cephalic region:** 28: ventral; 30: lateral; **maxillary palp:** 29; **posterior spiracle:** 31; **last segment:** ventral: 32, lateral: 34, dorsal: 36; **anterior spiracle:** 33; **creeping welt:** 35.

two rows of reclinate spines and additional rows of spinules anterior and posterior to the rows; first row of spines with 26–31 spines, median ones missing or reduced in size; second row with 21–30 spines; at least some creeping welts with anteromedian spines; spines in irregular order and sometimes pointing craniad. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 32, ventral view; fig. 34, lateral view; fig. 36, dorsal view): Anterior section slightly swollen, with numerous short rows of short, spinulelike hairs laterally and dorsally as well as in area to either side of two bare diagonal lines where spinules are thicker; anal plate large, wing-shaped, posterior tip of inner lobe projecting, outer lobe pointed laterally; anal plate with a few spines at anterior edge; postanal protuberance weakly developed; small hairy subanal tubercle; subanal sensory organ posterior to each tubercle; pair of small ventral tubercles which are not at base of spiracle mounting but considerably more anterior; each tubercle associated with a ventral sensory organ in an even more anterior position; without distinct bands of spines, but with enlarged spinulelike hairs in area where these bands are found in most other sepsids; small lateral tubercle associated with a dorso- and ventrolateral sensory organ; spiracle mountings very long and hairy with very small dorsal tubercle; dorsal side of segment with two bare stripes, enlarged spines on either side constituting remnants of the three double rows of spines in most other sepsids; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 31): Rounded surface with three openings and four processes of spiracular hairs, all processes with 6–7 hairs ("a–c"); weakly curved openings in rectangular arrangement; ecdysial scar in dorsomedian position well below spiracular plate (fig. 36).

BIOLOGY: *Lasionemopoda hirsuta* is quite common in temperate and subtropical Australia where I was able to breed it from cow dung (see Ferrar, 1987; Snowball, 1944). I also collected imagines from human excrement. This species favors shaded pastures where it is found on fresh dung, usually close to a water source. I did not observe any pre- or postcopulatory behavior. Males were defending small territories along the shores bodies of water.

DISTRIBUTION: This may very well be the only endemic Australian sepsid (Colless, 1980; see also Zuska, 1989, for seasonal and spatial distribution). Apparently, it has been introduced into New Zealand where the first records are from the 1950s, although this species is conspicuous enough to have been collected earlier if it had been present (Colless, 1980).

5. GENUS *MEROPLIUS* RONDANI, 1874

Key to these species modified after Ozerov (1991a). The validity of this key is questionable since the intraspecific variability of the characters could not be adequately studied. However, because *M. vittatus* has a much more restricted range than *M. minutus* most specimens can be identified based on locality information.

1. Dorsal tubercle originating at distal third of spiracle mounting (fig. 52); usually with six lobes on anterior spiracle, sometimes 7 (fig. 51) ..... *M. vittatus*
– Dorsal tubercle originating in the middle of spiracle mounting (fig. 43); usually with eight lobes on anterior spiracles, sometimes 7 (fig. 42) ..... *M. minutus*

Meroplius minutus (Wiedemann, 1830)

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 3
Length: 4.96–5.65 mm (n = 2)
Largest width of body segments: 0.64–0.70 mm (n = 3)
Width of last segment: 0.70–0.85 mm (n = 3)

First descriptions of the larvae of this species are provided by Hennig (1949) and later Mangan (1977).

CEPHALIC REGION (fig. 37, ventral view; fig. fig. 39, lateral view): Slightly longer than wide, distinctly bilobed, moderately large lower lip; posterior pores on lower lobes and anterior pores on comb to either side of brace; Hennig (1949) depicted two round lobes at the position of the pore-bearing combs which I believe to be identical to these combs; tips of brace not distinctly enlarged into hooklike

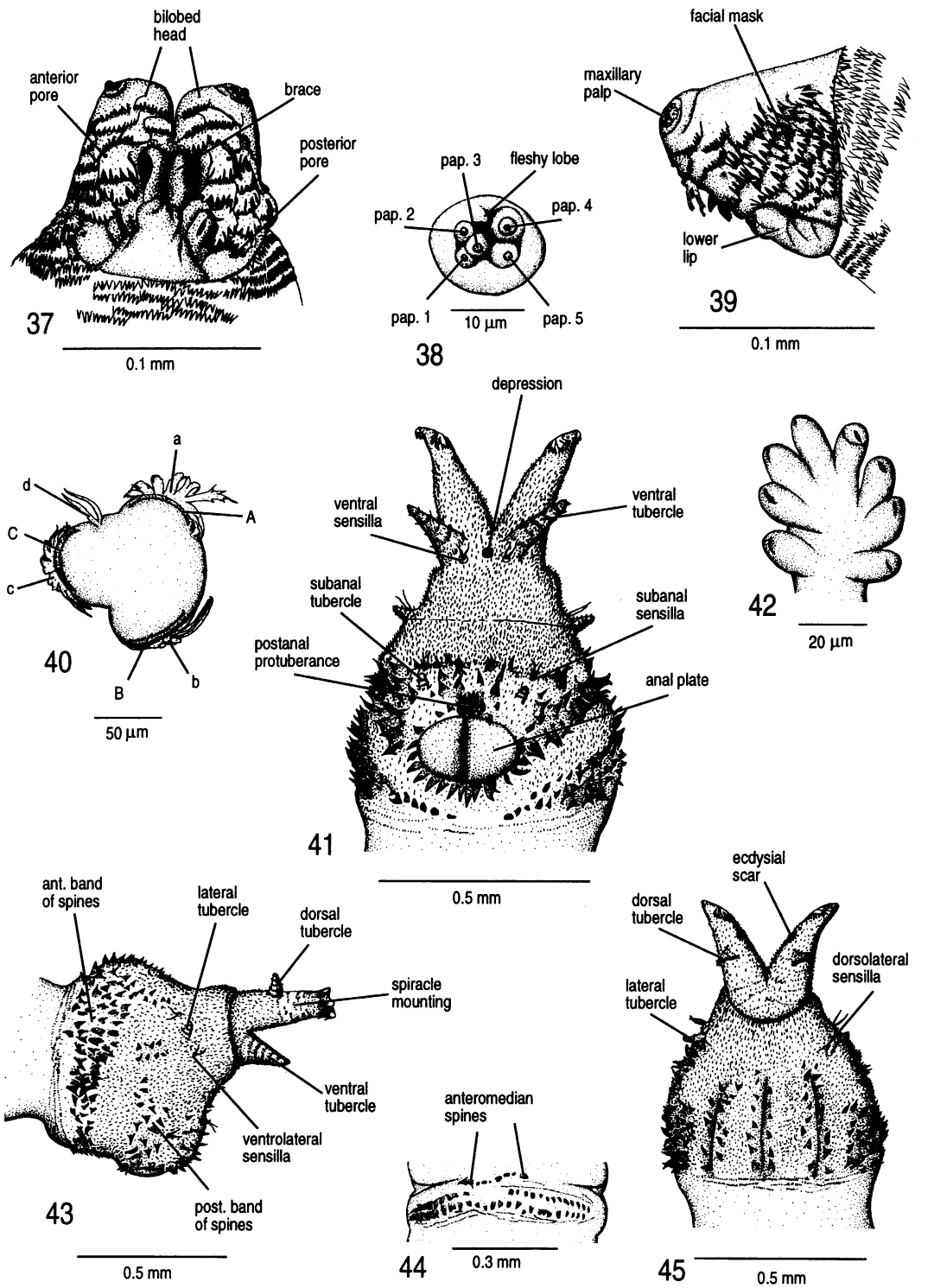


Fig. 37–45. *Meroplius minutus*. **Cephalic region:** 37: ventral, 39: lateral; **maxillary palp:** 38; **posterior spiracle:** 40; **last segment:** 41: ventral, 43: lateral, 45: dorsal; **anterior spiracle:** 42; **creeping welt:** 44.

projections, but brace gaping along full length; entire facial mask covered with combs which are wider than long with multiple moderately large teeth; combs absent from inner side of cephalic lobes and around maxillae; facial combs coarsely fringed, fringes often bifurcated; facial mask small compared to the close relative *Xenosepsis fukuharai*. Ventral view of cephalic region and cephalopharyngeal skeleton is depicted in Hennig (1949).

MAXILLAE (fig. 38): Composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four compound papillae consisting of two superimposed lobes (pap. 1–3, 5), one with three superimposed lobes (pap. 4); remnant of a fleshy lobe separates the two groups.

ANTERIOR SPIRACLE (fig. 42): Has 7–8 lobes arranged along a central axis, which does not narrow toward tip (text fig. 34 in Hennig, 1949: 8 lobes; fig. 6 in Mangan, 1977: 8 lobes).

CREEPING WELTS (fig. 44): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining welts ventrally with two rows of reclinate spines and few additional rows of spinules anterior and posterior to spines; first row of spines with 22–29 spines, median ones missing or reduced in size; second row with 23–27 spines; 7–9 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument not pubescent.

LAST ABDOMINAL SEGMENT (fig. 41, ventral view; fig. 43, lateral view; fig. 45, dorsal view): Moderately bulbous, posterior half elongated, very hairy, warts absent; anal plate simple, not wing-shaped or enlarged, rounded laterally; postanal protuberance small; complete row of preanal spines along anal plate; weakly developed, hairy subanal tubercle; subanal sensory organ posterior to each tubercle; pair of ventral tubercles and a ventral sensory organ at each base; distinct depression between bases of ventral tubercles; anterior band of spines well defined, more or less complete ventrally; posterior band of spines broken up into a dorsolateral group of spines and a ventrolateral band; spines large with pointed tip; lateral tubercle associated with one dorso- and one ventrolateral sensory organ; spiracle mountings moderately long, with moderately large dorsal tubercle halfway on spiracle mounting; dorsal surface of last segment with three longitudinal grooves, each bordered by a row of more or less irregularly spaced spines on either side; area between rows pubescent; anterior border of last segment with continuous rows of spinules all around; hairs of sensory organs long. A lateral view of the last segment is depicted in Hennig (1949) and a ventral view in Mangan (1977). Both drawings agree with the description furnished here.

POSTERIOR SPIRACULAR DISC (fig. 40): Flat, trifoliate plate with three openings and four processes of spiracular hairs; processes ("a–c") associated with openings composed of 6–8 hairs, unassociated process ("d") of two hairs; other than in *Xenosepsis*, hairs generally not branched; weakly curved openings in triangular arrangement (see also text fig. 44 in Hennig, 1949); ecdysial scar in dorsomedian position just above dorsal tubercle (fig. 45). In his ventral view of the last segment, Mangan (1977) indicated that one spiracular slit extends onto the spiracle mounting. I consider this an erroneous observation.

Hennig's (1949) descriptions deviated in two points from the one provided here. He stated that the creeping welts surround the entire body segments (see fig. in Hennig, 1949). This is only the case for the spinules of the welts on anterior segments. On more posterior segments, the spinules are missing laterally and dorsally. Hennig also described two strong bristles or fleshy tubercles on the lateral aspect of the body segments. Neither Ozerov (1991a) nor I was able to confirm this observation. Hennig studied puparia which were only associated with adults of *M. minutus* and the specimens may have belonged to a different species.

BIOLOGY: *Meroplius minutus* is a generalist with a preference for exceptionally filthy habitats. Apparently, it is particularly attracted to human excrement (Howards 1900 in Hennig, 1949; Iwasa, 1984) and favors the more liquid variety ("Ich fand sie massenhaft an Abortjauchepfützen": Duda, 1925; van der Goot, 1985, 1987b). Larvae have also been collected in a rabbit cage (Hennig, 1949) and on carcasses of rodents (Ozerov, 1991a). Adults occur in cattle feeding pens (Mangan, 1977) and can be collected from carrion (Mangan, 1977), dog carcasses (Reed, 1958),

rotting vegetation (Mangan, 1977), rotting cabbage (Minder, 1963), rotting fungi (Ozerov, 1991a), and pig dung (Iwasa, 1984). Cow dung is conspicuously avoided (Iwasa, 1984). Interestingly, *M. minutus* used to be common in the Netherlands and Belgium but has not been collected there for the past 50 years. Due to improved sanitary conditions, it may have been extirpated in these countries (van der Goot, 1987b). Ozerov (1991a) observed that large, old quantities of human feces are the preferred substrate and that fresh dung and smaller patches are avoided. Development from egg to imagines takes 12–14 days.

DISTRIBUTION: *Meroplius minutus* has an exceptionally wide distribution. It occurs throughout the Holarctic region as far north as Alberta in the New World and Finland in Europe (see Hennig, 1949; Iwasa, 1987; Mangan, 1977). It is also found in the Oriental region (Taiwan).

Meroplius vittatus Ozerov, 1985

Locality: Primorskiy kray, Glazkovka, 20 km SW Valentin (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 7
Length: 4.61–5.05 mm ($\bar{x}$ = 4.89 0.15; n = 5)
Largest width of body segments: 0.59–0.73 mm ($\bar{x}$ = 0.64 0.05; n = 6)
Width of last segment: 0.59–0.71 mm ($\bar{x}$ = 0.64 0.04; n = 6)

CEPHALIC REGION (fig. 46, ventral view; fig. fig. 48, lateral view): longer than wide, distinctly bilobed; small lower lip; posterior pores on lower lobe and anterior pores on comb to either side of brace; brace gaping along full length, tips not enlarged into hooklike projections; combs not only on cephalic lobes but covering entire facial mask, wider than long with multiple coarse often bifurcated teeth; combs absent from inner side of cephalic lobes and around maxillae; similar combs, but facial mask reduced in size compared to close relative *Xenosepsis fukuharai*.

MAXILLAE (fig. 47): composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four compound papillae consisting of two superimposed lobes (pap. 1–3, 5), one with three superimposed lobes (pap. 4); distinct gap between groups, with remnant of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 51): 6–7 lobes arranged along a short central axis.

CREEPING WELTS (fig. 53): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining welts with two rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 23–28 spines, median spines reduced in size; second row with 20–28 spines; 4–7 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument not pubescent.

LAST ABDOMINAL SEGMENT (fig. 50, ventral view; fig. 52, lateral view; fig. 54, dorsal view): Moderately bulbous and short; very hairy, warts absent; anal plate simple, not wing-shaped or enlarged; rounded laterally; postanal protuberance moderately large; preanal row of spines along anal plate; weakly developed, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of ventral tubercles with a ventral sensory organ at each base; depression between bases; anterior row of spines well defined, meeting ventrally at midline; posterior row of spines divided into a dorsolateral group of spines and a ventrolateral row; spines large with pointed tip; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, dorsal tubercle originating at distal third; dorsal surface of last segment with three longitudinal grooves, each bordered by a row of irregularly spaced spines on either side; area between grooves pubescent; anterior border of last segment with more or less continuous row of spinules all around; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 49): Flat trifoliate plate with three openings and four processes of spiracular hairs; processes ("a–c") associated with openings with 6–9 branched hairs, unassociated process ("d") with two hairs; openings weakly curved in a triangular arrangement; spiracular plate with numerous porelike depressions; ecdysial scar in dorsomedian position halfway between plate and dorsal tubercle (fig. 54).

BIOLOGY: The biology of *M. vittatus* and *M. minutus* is similar. Imagines are found on fresh dung, carcasses, stable manure, and close

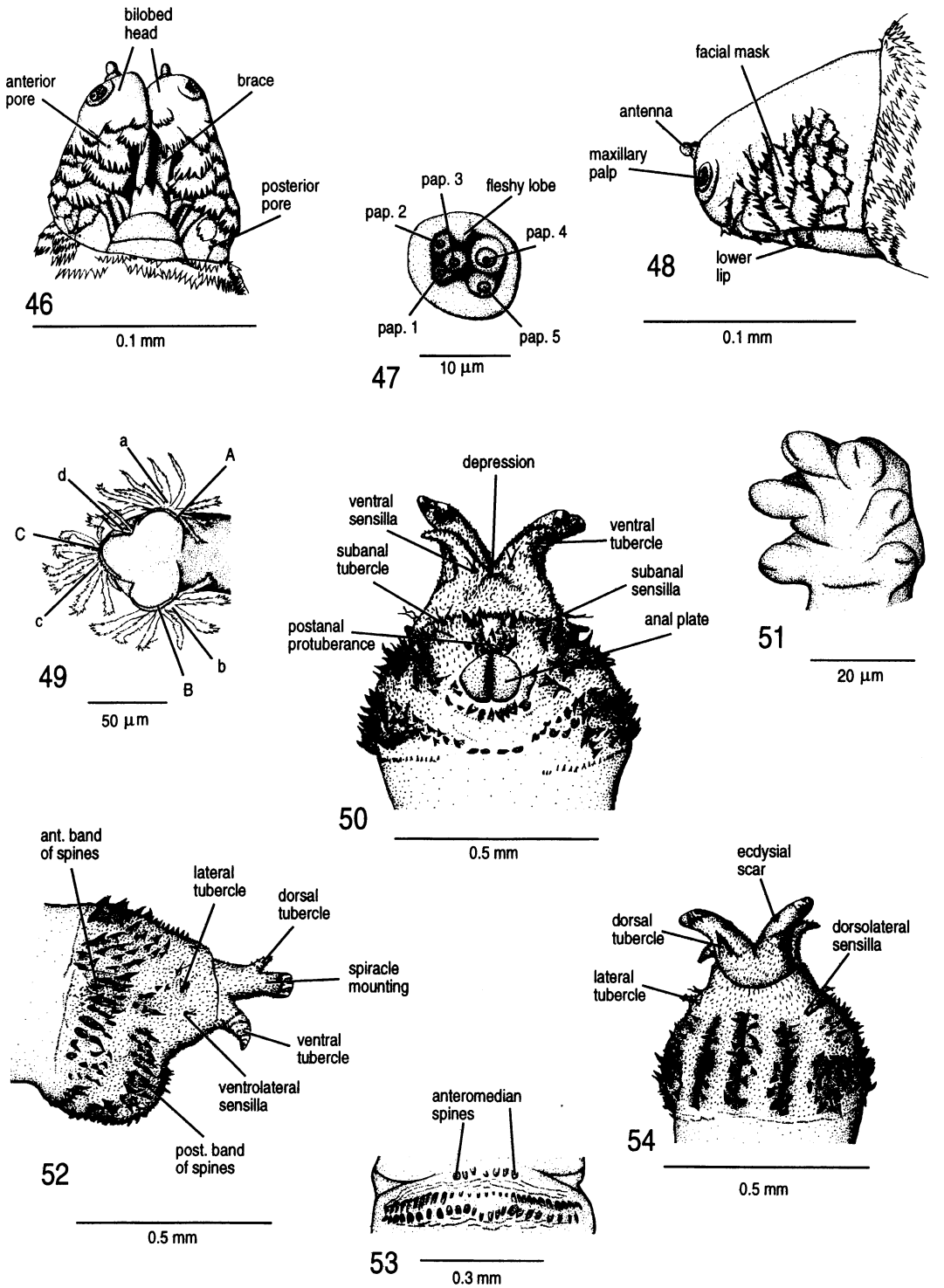


Fig. 46–54. *Meroplius vittatus.* **Cephalic region:** 46: ventral, 48: lateral; **maxillary palp:** 47; **posterior spiracle:** 49; **last segment:** 50, ventral, 52: lateral, 54: dorsal; **anterior spiracle:** 51; **creeping welt:** 53.

to refuse pits. Small patches of dung are avoided (Ozerov, 1991a).

DISTRIBUTION: Far East of the USSR (Ozerov, 1991b).

6. GENUS *NEMOPODA* ROBINEAU-DESVOIDY, 1830

Key to these species modified after Ozerov (1987). This key is not satisfactory since the number of spiracle lobes used to separate *pectinulata* and *speiseri* is overlapping.

1. Preanal row of spines along entire anterior margin of anal plate with at least ten spines; subanal tubercles large (fig. 59) ..... *N. nitidula*
– Preanal row of spines with at most six spines and restricted to center of the anal plate (figs. 66, 73) 2
2. Anterior spiracle with 14–17 lobes (fig. 72) .. *N. speiseri*
– Anterior spiracle with at most 12–14 lobes (fig. 65) ..... *N. pectinulata*

Nemopoda nitidula (Falln, 1820)

Locality: Berlin (Germany) and Ithaca (New York, USA), coll. R. Meier
Specimens examined: 12
Length: 3.8–7.12 mm ($\bar{x}$ = 5.16 1.16; n = 10); 6–8 mm (Ozerov, 1987)
Largest width of body segments: 0.73–1.17 mm ($\bar{x}$ = 0.90 0.12; n = 10); 0.9–1.mm (Ozerov, 1987)
Width of last segment: 0.62–0.93 mm ($\bar{x}$ = 0.74 0.09; n = 10)

Larvae of *Nemopoda nitidula* have also been described by Hennig (1949: 18; see also his illustration of cephalopharyngeal skeleton) and Ozerov (1987). Their descriptions agree with the results of my study. Ozerov (1987) claims that Hennig's descriptions were based on a mixture of specimens of *N. nitidula* and *N. pectinulata*.

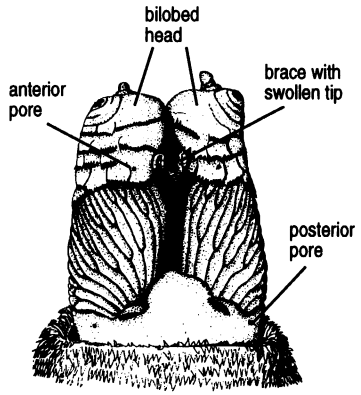
CEPHALIC REGION (fig. 55, ventral view; fig. 57, lateral view): Considerably longer than wide; weakly bilobed, rather short lower lip; one anterior pore each on comb on either side of brace; posterior pores not on lobe, but behind posterior margin of facial mask; brace slender and long, tips distinctly enlarged into hooklike projections; combs restricted to anterior section of cephalic lobes, wider than long with multiple small teeth; combs absent from inner side of cephalic lobes and around maxillae; facial mask with numerous narrow smooth-edged ridges; primary ridges spanning across entire facial mask; shorter intercalary ridges that are half or one quarter the length of primary ridges; combs absent behind posterior margin of facial mask.

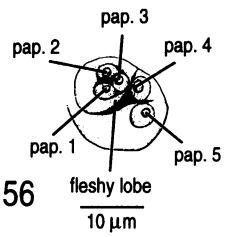
MAXILLA (fig. 56): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one of three superimposed lobes (pap. 4); gap between groups distinct with a very narrow fleshy lobe separating them; fold is either complete or nearly so.

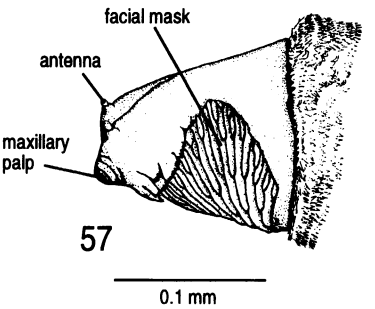
ANTERIOR SPIRACLE (fig. 60): 11–16 lobes arranged along a wide central axis (text fig. 37 in Hennig, 1949: 13 lobes; Brindle, 1965: 16 lobes; Ozerov, 1987: 10–12 lobes).

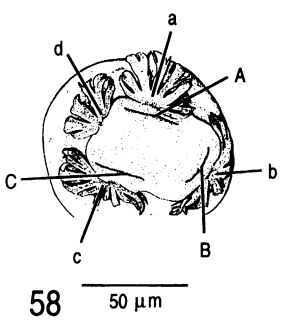
CREEPING WELTS (fig. 62): Except for first four segments which have some bare spots, all body segments densely pubescent (see also Hennig, 1949:18); first four segments with rows of spinules all around segmental borders; starting with 5th segment, following six welts ventrally with two rows of reclinate spines; first row of spines with 23–30, median spines distinctly smaller than lateral ones; second row with 25–28 spines; about seven anteromedian spines forming a short anterior row; last body segments with secondary annulations.

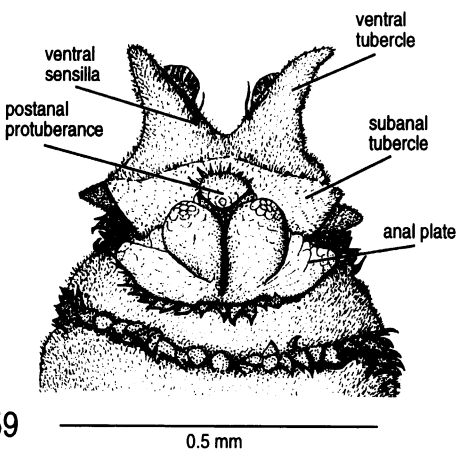
LAST ABDOMINAL SEGMENT (fig. 59, ventral view; fig. 61, lateral view; fig. 63, dorsal view): Not bulbous, narrower than middle segments, very hairy; anal plate wing-shaped, inner lobe very bulbous; postanal protuberance fairly large, spiny; preanal row of spines along entire length of anal plate; pair of very large, hairy subanal tubercles present; subanal sensory organ posterior to tips of each tubercle; pair of large ventral tubercles, about as long or longer than spiracle mounting, each with a ventral sensory organ at base; peculiar arrangement of spines: anterior band divided into lower row meeting ventrally and two lateral bands; posterior band with few spines; ventral spines especially large, hooklike with sharp points and wide bases; pair of lateral tubercles associated with a dorso- and a ventrolateral sensory organ each; spiracle mountings short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, usually each bordered by an irreg-

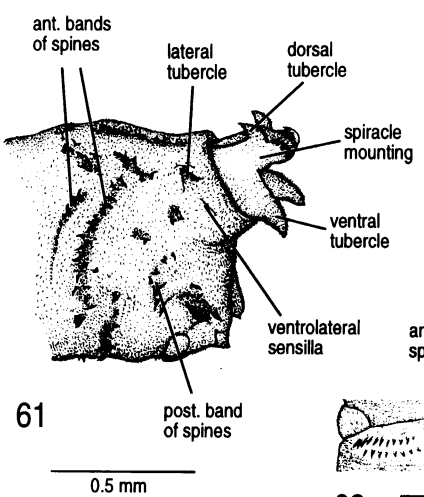


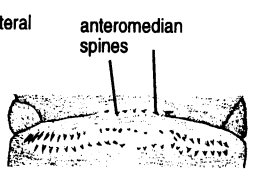












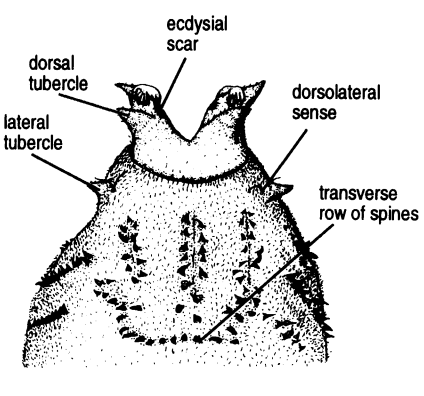


Fig. 55–63. *Nemopoda nitidula.* **Cephalic region:** 55: ventral, 57: lateral; **maxillary palp:** 56; **posterior spiracle:** 58; **last segment:** 59: ventral, 61: lateral, 63: dorsal; **anterior spiracle:** 60; **creeping welt:** 62.

ularly spaced row of spines on either side; sometimes with only one row on outer sides of lateral grooves; additional anterior transverse row of spines; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 58): Consisting of slightly bulging strongly sclerotized (dark brown; see Hennig, 1949) spiracular plate with three openings and four processes of spiracular hairs; processes ("a–c") associated with openings with 8–10 wide hairs, unassociated process ("d") with 4–5 hairs; almost straight openings in rectangular arrangement; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 63).

BIOLOGY: *Nemopoda nitidula* is a very common Holarctic sepsid. It is particularly abundant in the spring and apparently restricted to cooler, moister habitats during the summer. It has been reared from rotting fungus (probably *Boletus*, Brindle, 1965), a plasmodium of an undetermined myxomycete (Buxton, 1954), a rotting log (Smith, 1957), rodent carcasses (Ozerov, 1989), a dead fox (Smith, 1975), dead snails (Keilin, 1919), slime molds (Buxton, 1954), human excrement (Hennig, 1949; Ozerov, 1989) and cow dung (personal obs.). In a laboratory experiment, females favor rotting flesh over cow dung (personal obs.). In both substrates the larvae are able to complete development (development times: 21 days at 20°C, 14 days at 24°C personal obs.). Adults have also been collected from liquid human excrement (Duda, 1925) and various carcasses (Reed, 1958; van der Goot, 1986a). Hennig (1952: 233) speculated that sepsids on carcasses may visit the gut contents of the dead animal. This is certainly not the case for *N. nitidula* which definitely breeds on decaying flesh.

DISTRIBUTION: *Nemopoda nitidula* is one of the most common sepsids in the Holarctic region. In the New World, Mangan (1977) describes it from Quebec and Alberta south to Virginia, Ohio, Indiana, and I have frequently caught specimens in New York. The southern end of its distribution is unknown. In the Old World the northern border is Finland (Hennig, 1949), but the species is also known from Zaire (Zuska, 1977) and may have a continuous distribution across Russia to Japan (Iwasa, 1984; Far East of Russia: Ozerov, 1987).

Nemopoda pectinulata Loew, 1873

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 4
Length: 5.54–8.20 mm (n = 4); 6–8 mm (Ozerov, 1987)
Largest width of body segments: 0.79–1.23 mm (n = 4); 0.9–1 mm (Ozerov, 1987)
Width of last segment: 0.78–0.93 mm (n = 4)

The specimens available for study had completely or, in one specimen, partly retracted cephalic regions. Thus, only a few characters of this region could be studied. *Nemopoda pectinulata* larvae have been described by Ozerov (1987).

CEPHALIC REGION: Bilobed, one pore each on combs to either side of brace; brace with tips distinctly enlarged into hooklike projections; combs restricted to anterior section of cephalic lobes, wider than long with multiple small teeth; combs absent from inner side of cephalic lobes and around maxillae; facial mask composed of smooth-edged ridges; visible ridges in parallel arrangement similar to *N. nitidula*.

ANTERIOR SPIRACLE (fig. 65): 12–14 lobes (Ozerov, 1987: 14 lobes) arranged along a central axis.

CREEPING WELTS (fig. 64): Except for first four segments which have some bare spots, all body segments densely pubescent (see also Hennig, 1949: 18); first four segments with rows of spinules all around segmental borders; starting with 5th segment, the following six welts consist of two ventral rows of reclinate spines; first row of spines with 23–30 spines, median ones slightly smaller than lateral ones; second row with 16–25 spines; 4–7 anteromedian spines forming a short row. Last body segments sometimes with secondary annulations; occasionally middorsal spines on various segments.

LAST ABDOMINAL SEGMENT (fig. 66, ventral view; fig. 68, lateral view; fig. 69, dorsal view): Slightly bulbous, but narrower than middle segments, very hairy; anal plate wing-shaped, inner and outer lobe very bulbous; postanal protuberance small and spiny; short preanal row of spines along anterior margin of anal plate (fewer spines than in *N. nitidula* which, according to Ozerov [1987] has at least 10 spines); pair of fairly large, hairy subanal tu-

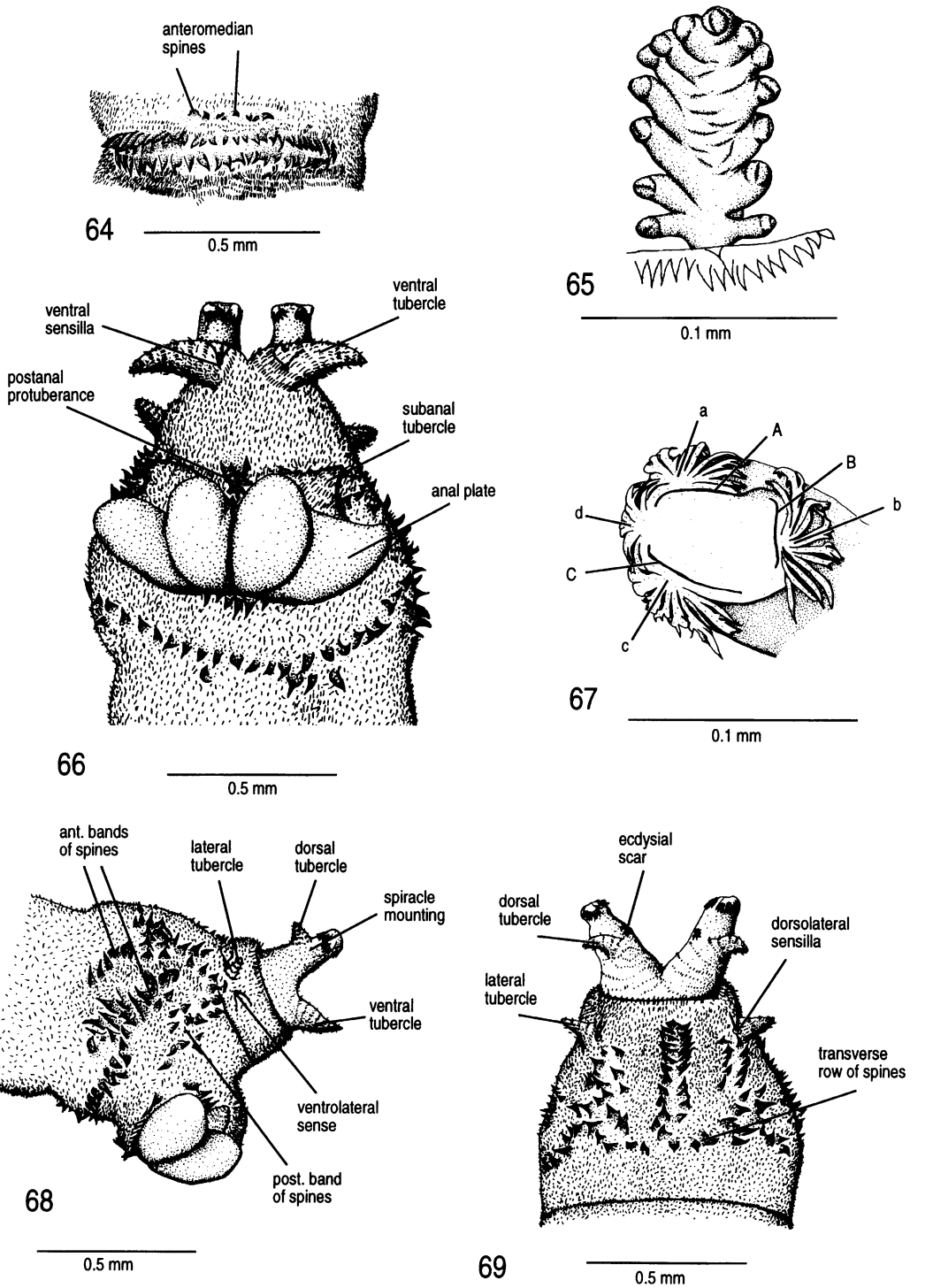


Fig. 64–69. *Nemopoda pectinulata.* **Creeping welt:** 64; **anterior spiracle:** 65; **posterior spiracle:** 67; **last segment:** 66: ventral, 68: lateral, 69: dorsal.

bercles (smaller than in *N. nitidula*); subanal sensory organ immediately lateroposterior to tip of each tubercle; pair of large ventral tubercles, about as long or even longer than spiracle mounting, with a ventral sensory organ at each base; peculiar arrangement of spines: anterior row divided into a lower row meeting ventrally and two lateral rows; posterior row of spines; spines large and almost hooklike with sharp points and wide bases; pair of lateral tubercles associated with a dorso- and a ventrolateral sensory organ each; spiracle mountings short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by rows of spines on either side; additionally with anterior transverse row of spines; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 67): Has three slits and four processes of spiracular hairs, processes ("a–c") associated with slits with 8–11 wide hairs, unassociated process ("d") with 4–5 hairs; slits almost straight in rectangular arrangement; position of ecdysial scar was difficult to determine but appeared to be in a dorsomedian position halfway between dorsal tubercle and spiracular plate.

BIOLOGY: *Nemopoda pectinulata* is largely sympatric with *N. nitidula* and morphologically very similar. However, it is considerably rarer and appears to prefer moister habitats (*an schlammigen Bächen*, Duda 1925). Iwasa (1984) reported that "this species is found in mountainous areas in Japan, but not common. The adult flies . . . gather on human excrement."

DISTRIBUTION: *Nemopoda pectinulata* is restricted to the Palearctic and Oriental regions (Iwasa, 1989: Pakistan; Iwasa, 1987: Nepal and Taiwan; Far East of Russia). According to Hennig (1949), it can be found in all of the Palearctic region, but in the Oriental region, it appears restricted to the northern parts.

Nemopoda (Pseudonemopoda) speiseri (Duda, 1926)

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 2
Length: 6.04–6.31 mm (n = 2); 7–9 mm (Ozerov, 1987)
Largest width of body segments: 0.83–1.03 mm (n = 2); 1.0–1.1 mm (Ozerov, 1987)
Width of last segment: 0.82–0.86 mm (n = 2)

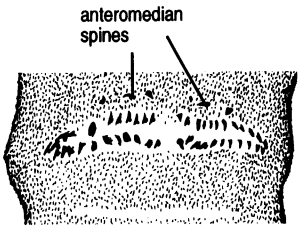
On both available specimens the cephalic region was almost entirely retracted and only the maxilla could be seen. The larvae of this species were previously described by Ozerov (1987).

MAXILLA (fig. 71): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four compound papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); gap between groups partly formed by very narrow almost complete fleshy lobe.

ANTERIOR SPIRACLE (fig. 72): On both available specimens 14 lobes arranged along a central axis (according to Ozerov [1987] 16–17 lobes).

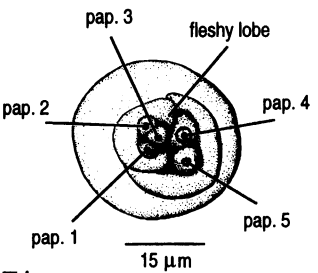
CREEPING WELTS (fig. 70): Except for first four segments which have some bare spots, all body segments densely pubescent (see also Hennig, 1949:18); first four segments with rows of spinules all around segmental borders; starting with 5th segment, welts consist of two ventral rows of reclinate spines; first row of spines with 23–25 spines, median spines hardly smaller than lateral ones; second row with 22–23 spines; six anteromedian spines forming a short anterior row; some welts with spines pointing craniad.

LAST ABDOMINAL SEGMENT (fig. 73, ventral view; fig. 75, lateral view; fig. 76, dorsal view): Not bulbous, narrower than middle segments, very hairy; anal plate wing-shaped, inner and outer lobes very bulbous (however, according to Ozerov [1987] anal plate simple); postanal protuberance spiny; short preanal row of spines along anterior margin of anal plate; pair of large hairy subanal tubercles; subanal sensory organ posterior to tip of each tubercle; pair of moderately large ventral tubercles, shorter than spiracle mounting, with a ventral sensory organ at each base; no depression at base of ventral tubercles; peculiar arrangement of spines: anterior row divided into one ventrolateral row meeting ventrally and two lateral rows; posterior band of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings comparatively short, with small dorsal tubercle; dorsal side of segment



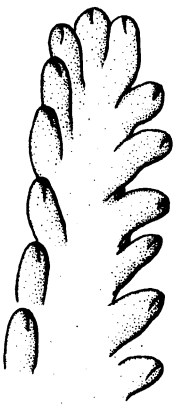
70

0.5 mm



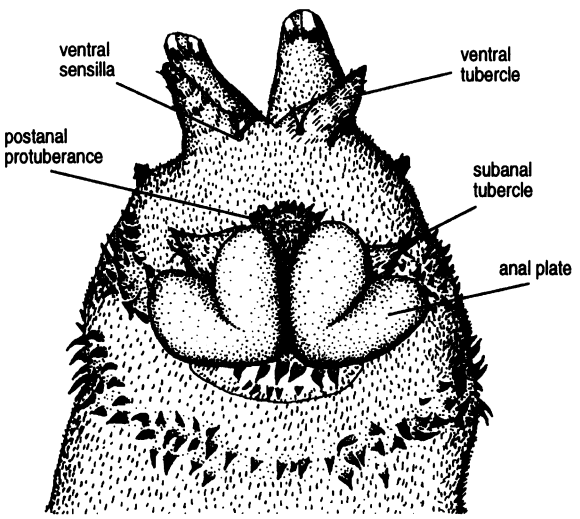
15 µm

71



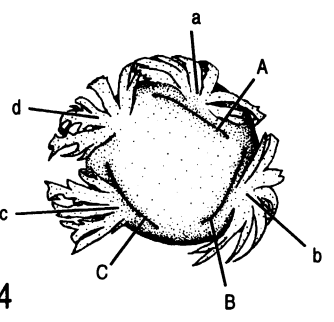
72

0.1 mm



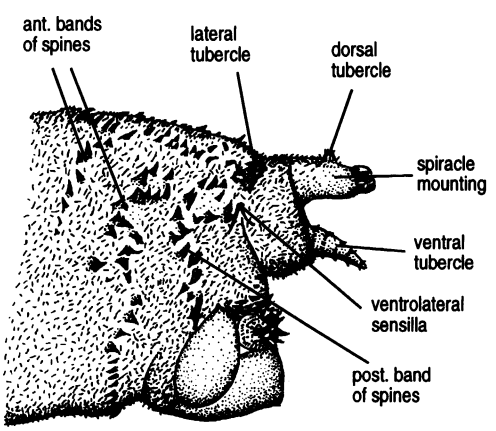
73

0.5 mm



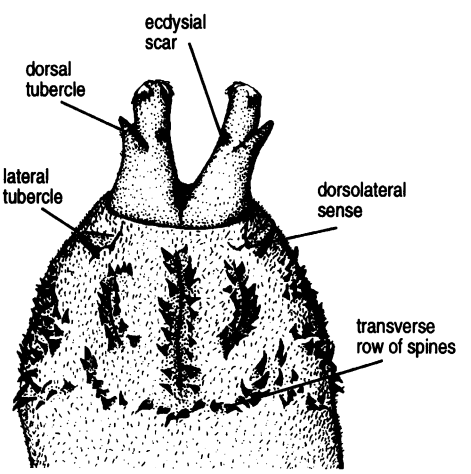
74

0.1 mm



75

0.5 mm



76

0.5 mm

Fig. 70–76. *Nemopoda speiseri*. **Creeping welt:** 70; **maxillary palp:** 71; **anterior spiracle:** 72; **posterior spiracle:** 74; **last segment:** 73: ventral, 75: lateral, 76: dorsal.

with three longitudinal grooves, each bordered by a row of spines on either side; additionally with anterior transverse row of spines; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 74): Has three openings and four processes of spiracular hairs, processes ("a–c") associated with openings with 5–6 wide hairs, unassociated process ("d") with four hairs; nearly straight openings in rectangular arrangement (however, according to Ozerov [1987] slits are in an almost parallel arrangement); ecdysial scar in dorsomedian position immediately above dorsal tubercle (fig. 76).

As already pointed out in the description, there are some differences between Ozerov's (1987) and my findings. Since I received my specimens from Ozerov, I have no explanation for the discrepancies.

BIOLOGY: The only information on the biology of *N. speiseri* comes from Ozerov (1989) who describes this species as common in the Far East and very rare in Europe. He collected larvae from carcasses of small vertebrates.

DISTRIBUTION: Due to the rarity of the species its distribution is incompletely known. In the Palearctic region it is known from European localities (Sweden, Germany, Poland, Czechoslovakia), Mongolia (Soos, 1972) and the Amur-region around Chabarowsk (Ozerov, 1987).

7. GENUS *ORTALISCHEMA* FREY, 1925

Ortalischema albitarse Frey, 1925

Locality: Caucasus, North Ossetia, 10 km SE Alagir, near 1600 m (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 11
Length: 7.55–8.92 mm ($\bar{x}$ = 8.30 0.44; n = 10)
Largest width of body segments: 0.85–1.08 mm ($\bar{x}$ = 0.95 0.07; n = 10)
Width of last segment: 0.75–0.95 mm ($\bar{x}$ = 0.88 0.06; n = 10)

CEPHALIC REGION (fig. 77, ventral view; fig. 79, lateral view): Longer than wide and pointed in a lateral view; distinctly bilobed, moderately large lower lip; anterior papilliform sensory organ not positioned on a comb; posterior pore and lower lobe absent; brace slender and long, gaping, tips forming narrow hooklike projections; combs on facial mask, around maxillae, and inner side of cephalic lobes, about as wide as long with numerous very fine teeth; facial mask with finely serrate ridges; primary ridges spanning across facial mask; intercalary secondary and tertiary ridges are shorter than primary ridges; no combs posterior to facial mask; facial mask enlarged, covering entire posterior part of cephalic region and reaching dorsal side (fig. 79). Spinules of posteriorly adjacent segment in numerous dense rows, hammer-shaped; prothoracic segment narrowing at mid-segment.

MAXILLA (fig. 78): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one with three superimposed lobes (pap. 4), distinct gap between groups which are separated from each other by a fleshy lobe.

ANTERIOR SPIRACLE (fig. 82): 7–8 lobes in fanlike arrangement.

CREEPING WELTS (fig. 84): First five and last two segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior of spines; first row of spines with 21–28 spines, median spines not reduced in size, second row with 20–30 spines, median spines smaller; spines bean-shaped with rounded tips, not pointed. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 81, ventral view; fig. 83, lateral view; fig. 85, dorsal view): Not bulbous, but almost rectangular in lateral view, not hairy; anal plate enlarged with weakly expressed diagonal fold; postanal protuberance absent; short preanal row of spines along anal plate; large, bare subanal tubercles, not associated with a sensory organ; ventral tubercles and depression missing; double row of spines ventrally which probably constitutes creeping welt of last abdominal segment, this row continues halfway up laterally forming homolog of anterior band of spines in most sepsids; a row of spines posterior to anal plate is missing; spines medium-sized with round tips; lateral tubercles absent; spiracle mountings very short, dorsal tubercle absent; dorsal side of segment with three longitudinal lines, inner one raised, lateral ones as narrow furrows; dorsally with fleshy scales

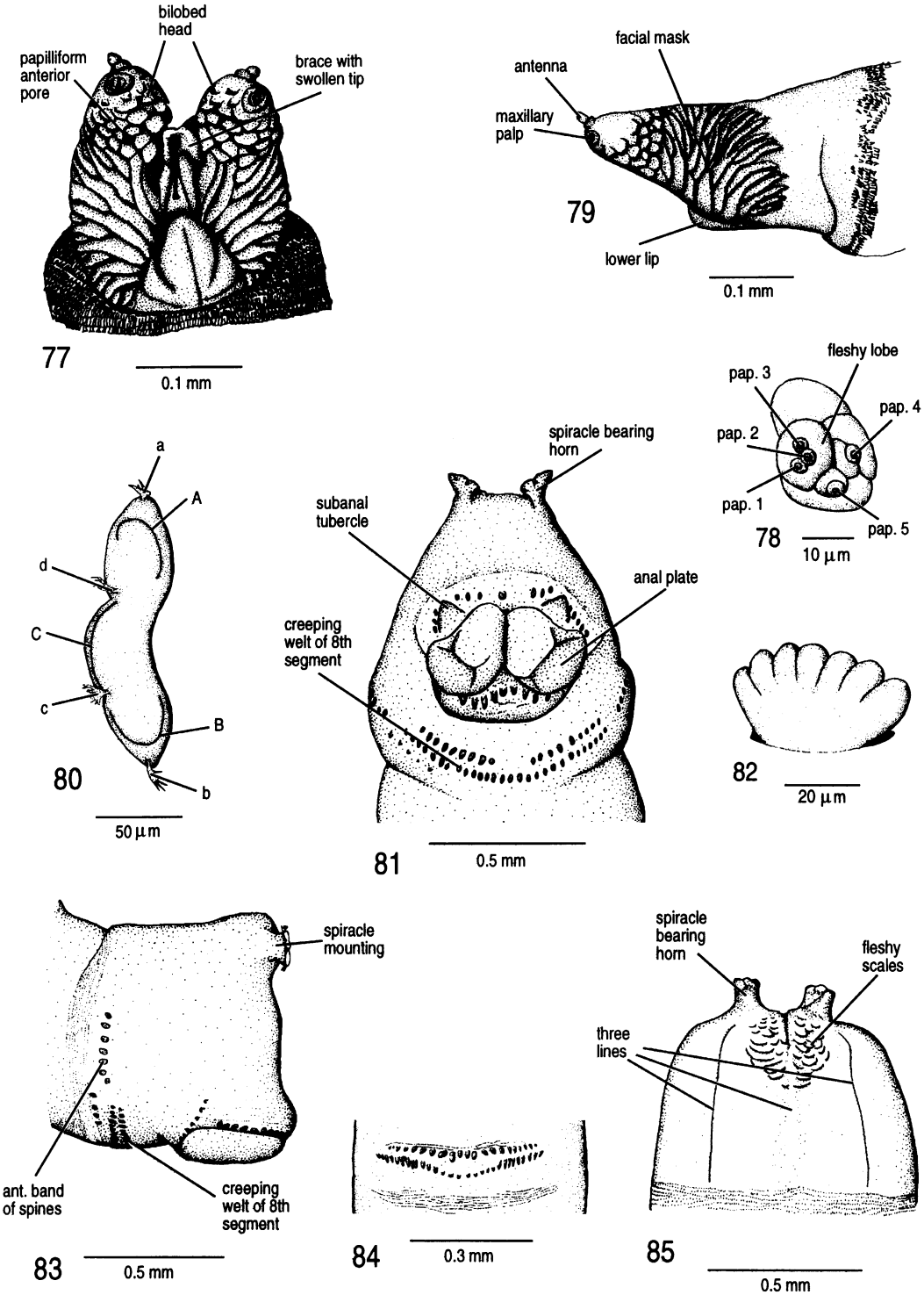


Fig. 77–85. *Ortalischema albitarse.* **Cephalic region:** 77: ventral, 79: lateral; **maxillary palp:** 78; **posterior spiracle:** 80; **last segment:** 81: ventral, 83: lateral, 85: dorsal; **anterior spiracle:** 82; **creeping welt:** 84.

on last segment; laterally and dorsally with numerous rows of spinules anterior to last segment.

POSTERIOR SPIRACULAR DISC (fig. 80): Has three openings and four processes of spiracular hairs; processes small, with few short hairs; curved openings in rectangular arrangement; spiracular plate and spiracle mountings laterally compressed, longoval in cross-section; position of ecdysial scar unclear in all specimens.

BIOLOGY: Little is known about the biology of *O. albitarse*. Pont (1987a) reported a simultaneous catch of *Zuskamira* and *Ortalischema* on horse dung. Iwasa also collected this species on horse droppings.

DISTRIBUTION: This species has a strange Palearctic distribution with numerous records from Scandinavia, Hungary and Italy but none from Central Europe (Hennig, 1949). Zuska and Pont (1984) report specimens from Russia and the Ukraine, Iwasa (1985) from Japan and Mongolia.

8. GENUS *ORYGMA* MEIGEN, 1830

Orygma luctuosum Meigen, 1830

Locality: Acadia National Park (Maine, USA), coll. R. Meier

Specimens examined: 16

Length: 11.06–16.13 mm ($\bar{x}$ = 12.99 1.33; n = 10); 12 mm (Kiefer in Hennig, 1949); 6–16 mm (Egglishaw, 1960)

Largest width of body segments: 2.01–2.51 mm ($\bar{x}$ = 2.23 0.16; n = 10); 1.8–2 mm (Egglishaw, 1960)

Width of last segment: 1.47–1.87 mm ($\bar{x}$ = 1.63 0.13; n = 10)

The larvae have been described previously by Egglishaw (1960; for earlier references, see Hennig, 1949). A summary of the first three papers can be found in Hennig (1937). Egglishaw (1960) furnishes a very detailed descriptions of all three instars as well as the egg. The descriptions are in good agreement with my results.

CEPHALIC REGION (fig. 86, ventral view; fig. 88, lateral view; fig. 463, detail): About as long as wide, weakly bilobed, with rather small lower lip; anterior sensory organ papilliform and not fused to a comb; posterior pore and lower lobe absent; brace slender and long, gaping, anterior ends not fused; numerous combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to anterior sensory organ, much wider than long with numerous rounded teeth, numerous combs on inner side of cephalic lobes or around maxillae; facial mask with ridges in parallel arrangement, some of which span entire facial mask, others are narrower and fuse to form main ridges (fig. 88); facial mask large; no combs posterior to facial mask (see also Egglishaw [1960] for excellent figures).

MAXILLA (fig. 87): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), with wide gap between groups formed by a fleshy lobe.

ANTERIOR SPIRACLE (fig. 91): 12–15 lobes in fanlike arrangement (Roubaud in Hennig, 1937: 13 lobes; Egglishaw, 1960: about 15 lobes).

CREEPING WELTS (fig. 93): First eight segments with rows of spinules laterally; first seven with spinules dorsally; ventrally, first four welts consisting of spinules; remaining welts ventrally with three long rows of reclinate spines; first row of spines with 22–32 spines, median ones reduced in size; second row with 21–31, third with 15–28 spines; spines of third row very small and in interspaces of second row's spines. Egglishaw (1960) reports up to 33 spines per row on anterior creeping welts and as few as 19 on the posterior creeping welts; all body segments without hairs.

LAST ABDOMINAL SEGMENT (fig. 90, ventral view; fig. 92, lateral view; fig. 94, dorsal view): Not bulbous or hairy; anal plate very narrow, hardly visible, what appears to be the anal plate are subanal tubercles; postanal protuberance absent; preanal row of spines along posterior margin of subanal tubercle, row continues upward to form homolog of posterior band of spines in other sepsid larvae, but in *Orygma* it remains restricted to ventral side of body; very large subanal tubercles covered with spinules, not associated with any sensory organ; pair of ventral tubercles; no depression between their bases; double row of spines anteroventral to anal plate (homolog of creeping welt of last abdominal segment); bands of spines absent in lateral view of last segment; spiracle mountings rather short, wide, with small dorsal tubercle; dorsal surface of last segment with three weakly ex-

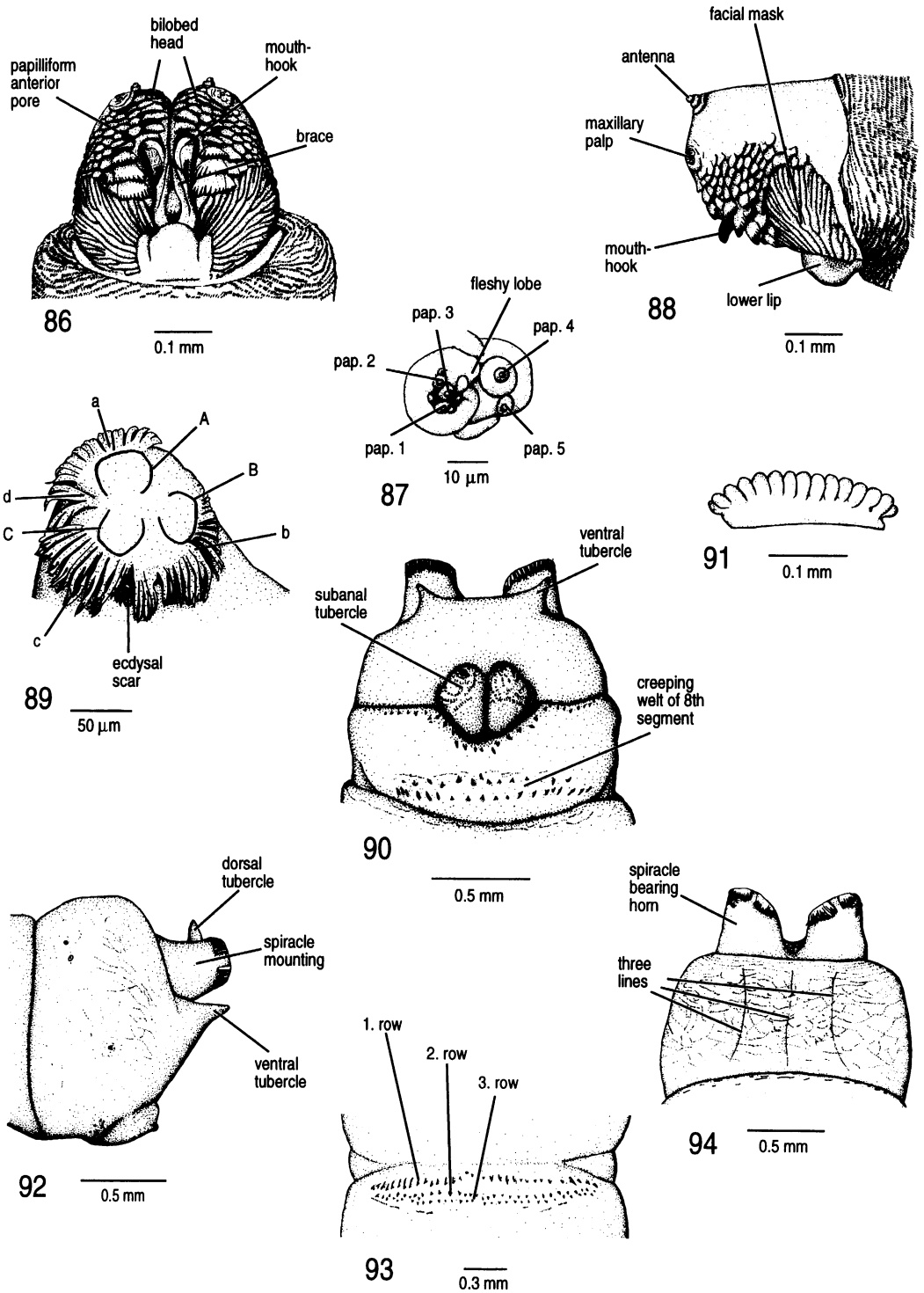


Fig. 86–94. *Orygma luctuosum.* **Cephalic region:** 86: ventral, 88: lateral; **maxillary palp:** 87; **posterior spiracle:** 89; **last segment:** 90: ventral, 92: lateral, 94: dorsal; **anterior spiracle:** 91; **creeping welt:** 93.

pressed longitudinal grooves, with numerous denticles forming a reticulate pattern.

POSTERIOR SPIRACULAR DISC (fig. 89): Has three crescent-shaped openings and four processes of spiracular hairs; processes ("a–c") associated with openings with 7–10 hairs that are arranged along rim of spiracular disc and do not arise from a distinct single root (see also Egglishaw, 1960), unassociated process ("d") with 2–3 hairs that are branched; ecdysial scar not on spiracular plate, but immediately below plate.

BIOLOGY: *Orygma luctuosum* is exceptional for a sepsid in that it is found exclusively on seashores where it breeds on rotting brown algae, mainly *Laminaria* and *Fucus* (van der Goot, 1986a; Pont, 1979). It is reported to prefer small, dry and well-compressed beds of decomposing wrack but in Maine (USA), I have collected this species in larger and rather moist accumulations of brown algae. *Orygma* is a reluctant flier and rarely covers more than a meter at a time. It can be easily shaken from sea wrack. Courtship is essentially missing and copulations often occur immediately after capture in an aspirator vial. *Orygma* copulates frequently (Egglishaw, 1960), and eggs are laid very rapidly after eclosion (1–4 days after eclosion; 40–180 in 12 h). Under laboratory conditions, eggs were not only deposited into sea weed but also rotting nettle (*Urtica*) that had been soaked in salt water. The larvae pupate in tightly-packed wrack and eclose after 8–13 days in May or up to 19 weeks in November (Egglishaw, 1960); i.e., this species hibernates as a pupa. There are two population peaks in England; one in late spring (April—May) and one in September. In the laboratory, adults live for two to four weeks. *Orygma* is less abundant on most shores than the dominant coelopid species.

DISTRIBUTION: *Orygma* is restricted to the northern Holarctic. Specimens are known from England, Ireland, Iceland, France, Belgium, Germany, and the United States where it is restricted to the eastern coast north of Massachusett.

9. GENUS *PALAEOSEPSIS* DUDA, 1925

Key to species.

1. Cephalic region elongated behind facial mask, forming neck .... *P. pusio, P. polychaeta*
- Cephalic region short not elongated behind facial mask 2
2. Facial mask consisting of few ridges with long fringes ..... *P. mitis*
- Facial mask consisting of considerably more ridges, most anterior ridge only with fringed edge ..... *P. diversiformis*

Palaeosepsis diversiformis Ozerov, 1993

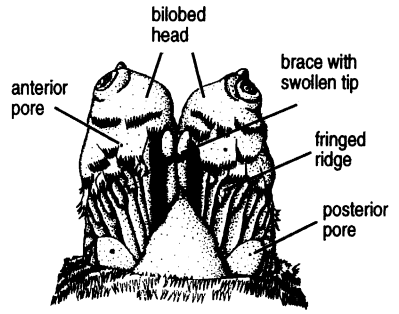
Locality: Las Alturas (Provincia Puntarenas, Costa Rica), coll. R. Meier
Specimens examined: 4
Length: 3.73–4.59 mm (n = 4)
Largest width of body segments: 0.54–1.06 mm (n = 4)
Width of last segment: 0.57–1.07 mm (n = 4)

CEPHALIC REGION (fig. 95, ventral view; fig. 97, lateral view): Longer than wide, distinctly bilobed, large lower lip; large posterior pores on lower lobe and anterior pores on comb to either side of brace; brace long and narrow, fused, with anterior tips distinctly enlarged into hooklike projections; 6–10 combs restricted to anterior section of cephalic lobes; combs usually much wider than long with multiple long pointed teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask mainly composed of smooth-edged ridges; pattern of ridges not well organized into blocks like in *Sepsis*, but with long primary ridges spanning across entire facial mask and usually one shorter intercalary ridge that is fringed; no combs posterior to facial mask.

MAXILLA (fig. 96): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); no distinct gap between groups of two (pap. 4, 5) and three (pap. 1–3); no remnant of a separating fleshy lobe.

ANTERIOR SPIRACLE (fig. 100): 5–6 short and stout lobes arranged along a central axis.

CREEPING WELTS (fig. 102): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 27–34 spines, median spines distinctly smaller than lateral ones, second row with 21–28 spines; 7–9 anteromedian spines forming a short anterior



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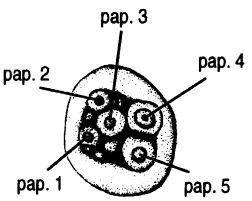
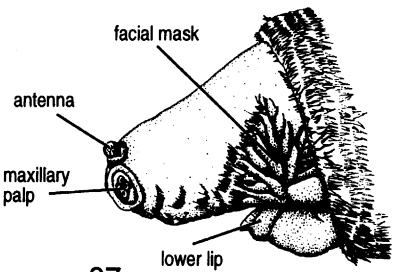


96 10 µm



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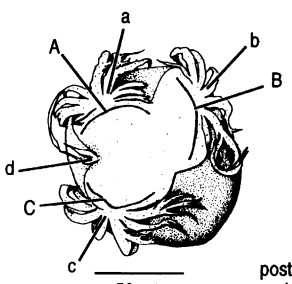

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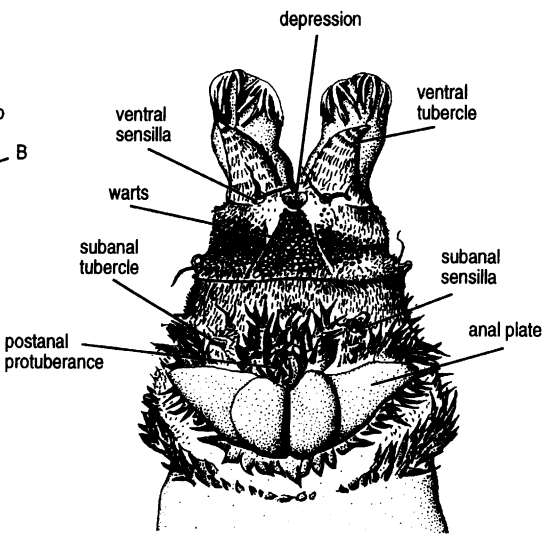

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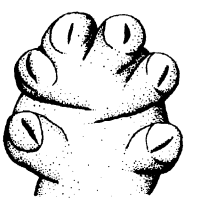

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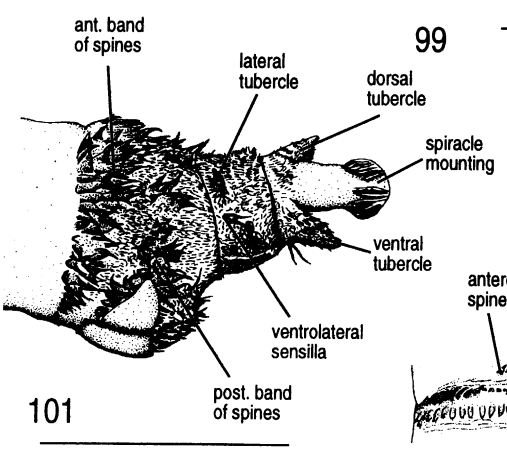

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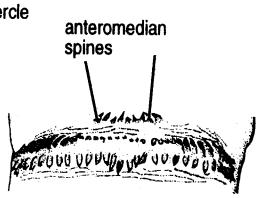

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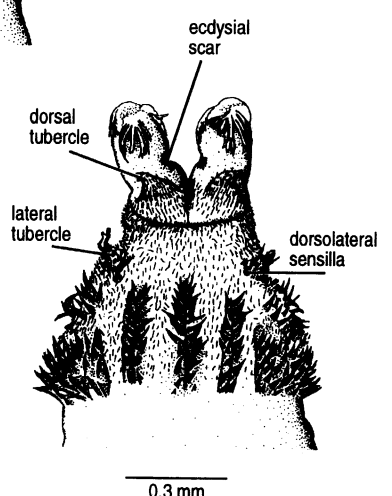

103

row; sometimes these spines point craniad. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 99, ventral view; fig. 101, lateral view; fig. 103, dorsal view): Anterior section slightly bulbous, numerous warts in posterior half; two bare diagonal lines stretching from bases of ventral tubercles craniad; deep depression between bases of tubercles; remaining segment covered by dense, long hairs; anal plate large, wing-shaped, pointed laterally with row of strong spines around anterior edge; postanal protuberance very well developed, spiny; weakly developed, bare subanal tubercle; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with ventral sensory organ at each base; with an anterior and a posterior bands of spines; anterior band is complete ventrally; posterior row is divided into dorsolateral group of spines and ventrolateral row; spines large with sharp drawn-out point; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, very wide even at tip; moderately large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a dense row of spines on either side; area between lines hairy; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 98): Has three openings and four processes of spiracular hairs on trifoliate plate, processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") with two unbranched narrow hairs; openings in triangular arrangement; ecdysial scar in dorsomedian position above dorsal tubercle (fig. 103).

BIOLOGY: Little is known about this recently described species. I collected it in Las Alturas (Costa Rica) on a fresh cow pats in a shady pasture close to a small creek and used cow dung as breeding substrate. Eberhard (personal commun.) observed precopulatory guarding. However, the behavior deviates from the precopulatory guarding of other sepsids in several regards, i.e., copulations usually take place on the cow pat and not in the surrounding grass.

DISTRIBUTION: Specimens are known from Costa Rica and Argentina.

Palaeosepsis mitis (Curran, 1927)

Locality: Las Alturas (Provincia Puntarenas, Costa Rica), coll. R. Meier
Specimens examined: 6
Length: 3.30–3.72 mm ($\bar{x}$ = 3.43 0.15; n = 6)
Largest width of body segments: 0.48–0.52 mm ($\bar{x}$ = 0.52 0.04; n = 6)
Width of last segment: 0.49–0.59 mm ($\bar{x}$ = 0.54 0.04; n = 6)

CEPHALIC REGION (fig. 104, ventral view; fig. 106, lateral view): Considerably longer than wide, distinctly bilobed with large lower lip; distinct posterior pores on lower lobe and anterior pores on one comb to either side of brace; brace rather short and stout, anterior tips distinctly enlarged into hooklike projections; large number of combs on cephalic lobes as well as on facial mask where ridges are replaced/transformed into combs; only one very wide ridge remains which runs along mouth opening; combs with multiple long, drawn out teeth; combs absent from inner side of cephalic lobes and around maxillae.

MAXILLA (fig. 105): Composed of five compound papillae; four consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 109): 4–5 lobes arranged along a very short central axis.

CREEPING WELTS (fig. 111): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 20–26 spines, median spines distinctly smaller or missing, second row with 16–24 spines; 3–4 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

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Fig. 95–103. *Palaeosepsis diversiformis*. **Cephalic region:** 95: ventral, 97: lateral; **maxillary palp:** 96; **posterior spiracle:** 98; **last segment:** 99: ventral, 101: lateral, 103: dorsal; **anterior spiracle:** 100; **creeping welt:** 102.

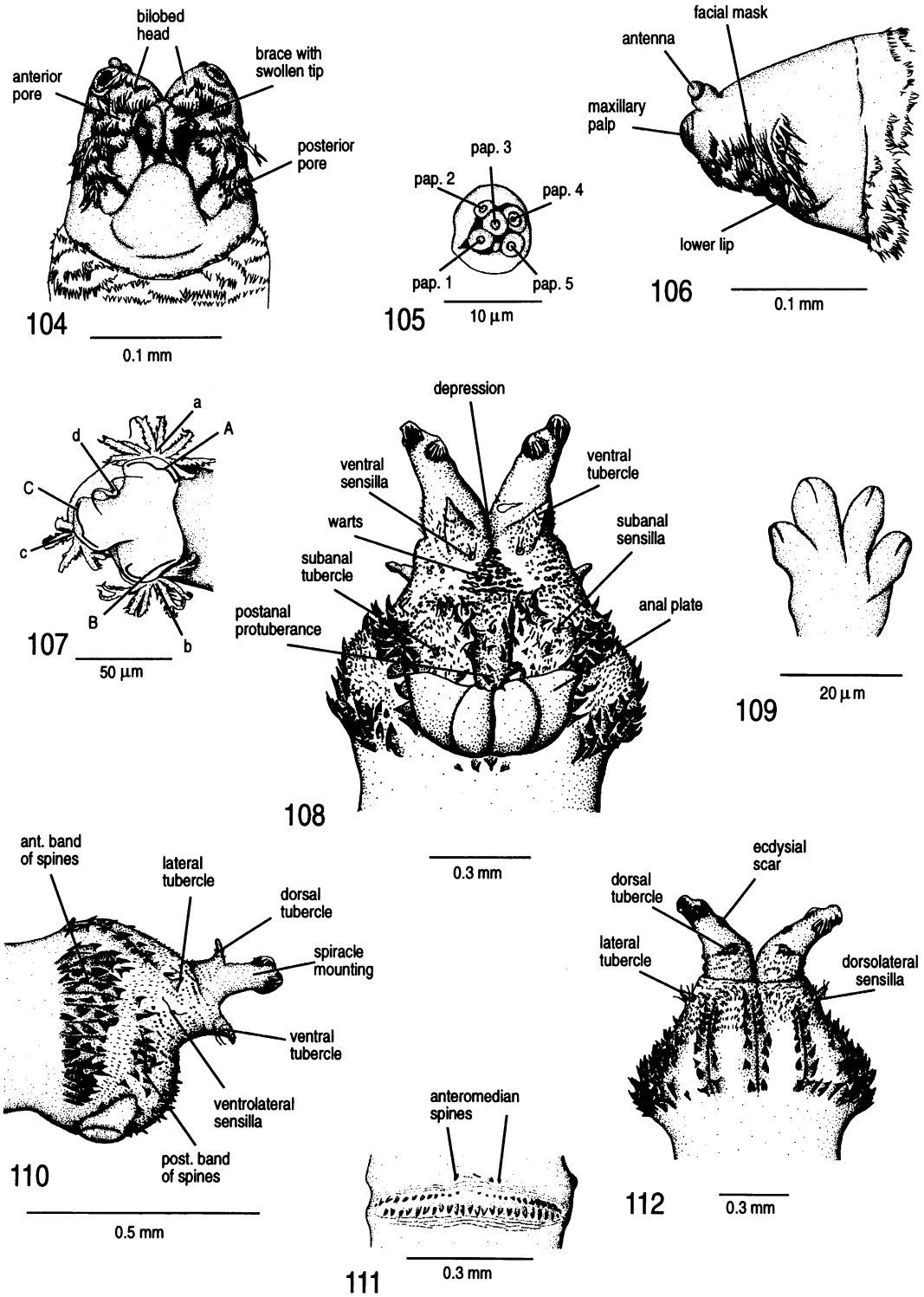


Fig. 104–112. *Palaeosepsis mitis.* **Cephalic region:** 104: ventral, 106: lateral; **maxillary palp:** 105; **posterior spiracle:** 107; **last segment:** 108: ventral, 110: lateral, 112: dorsal; **anterior spiracle:** 109; **creeping welt:** 111.

LAST ABDOMINAL SEGMENT (fig. 108, ventral view; fig. 110, lateral view; fig. 112, dorsal view): Distinctly bulbous, numerous warts posterior to area with spines; warts distinctly larger in area between depression and two bare diagonal lines running from depression craniad; remaining segment with sparse pubescence; anal plate large, wing-shaped, pointed laterally with few spines at anterior edge; postanal protuberance very well developed, spiny; very small, bare subanal tubercles; with a subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; with an anterior and a posterior band of spines; anterior band is incomplete ventrally; posterior band indistinctly divided into dorsolateral group of spines and ventrolateral band; spines large, with sharp drawn-out point; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, not wide, somewhat narrowing toward tip, with moderately long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; spines regularly spaced; only posterior part of area between lines sparsely pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 107): Has three openings and four processes of spiracular hairs on trifoliate plate, processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") with two unbranched narrow hairs; openings in triangular arrangement; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 112).

BIOLOGY: I collected *P. mitis* in Costa Rica at mid-elevation on a cow pasture together with numerous specimens of *P. pusio*. Both species were very common at a site where larger quantities of moist cow dung had accumulated. *P. mitis* shows precopulatory guarding.

DISTRIBUTION: This species has been described from Columbia (Steyskal, 1968), but also occurs in Costa Rica.

Palaeosepsis polychaeta Ozerov, 1993

Locality: Las Alturas (Provincia Puntarenas, Costa Rica), coll. R. Meier
Specimens examined: 9
Length: 5.72–6.38 mm ($\bar{x}$ = 5.99 0.23; n = 9)
Largest width of body segments: 0.53–0.66 mm ($\bar{x}$ = 0.58 0.05; n = 9)
Width of last segment: 0.50–0.72 mm ($\bar{x}$ = 0.61 0.07; n = 9)

CEPHALIC REGION (fig. 113, ventral view; fig. 115, lateral view): Much longer than wide, with comparatively long and narrow necklike base, distinctly bilobed with moderately large lower lip; posterior pores on lower lobe and anterior pores on one comb to either side of brace; brace long and narrow, fused with anterior tips being distinctly enlarged into hooklike projections; 11–16 combs restricted to anterior section of cephalic lobes; combs in horizontal arrangement; combs usually wider than long with multiple rather long and pointed teeth; combs absent from facial mask and around maxillae, few combs on inner side of cephalic lobes; facial mask mostly composed of smooth-edged ridges, pattern of ridges not well organized as in *Sepsis*, but with long primary ridges reaching furrow alternating with short intercalary, sometimes serrate ridges; combs absent along posterior margin of facial mask.

MAXILLA (fig. 114): Composed of five compound papillae; four consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 118): 6–8 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 120): First six segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 24–32 spines, median spines distinctly smaller than lateral ones, second row with 22–28 spines; 6–7 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 117, ventral view; fig. 119, lateral view; fig. 121, dorsal view): Anterior section bulbous, with numerous warts in posterior half (posterior to a fold); remaining segment with dense, long hairs; anal plate large, wing-shaped, outer lobe pointed laterally; anal plate with row of spines around anterior edge; postanal protuberance very well developed, spiny; weakly devel-

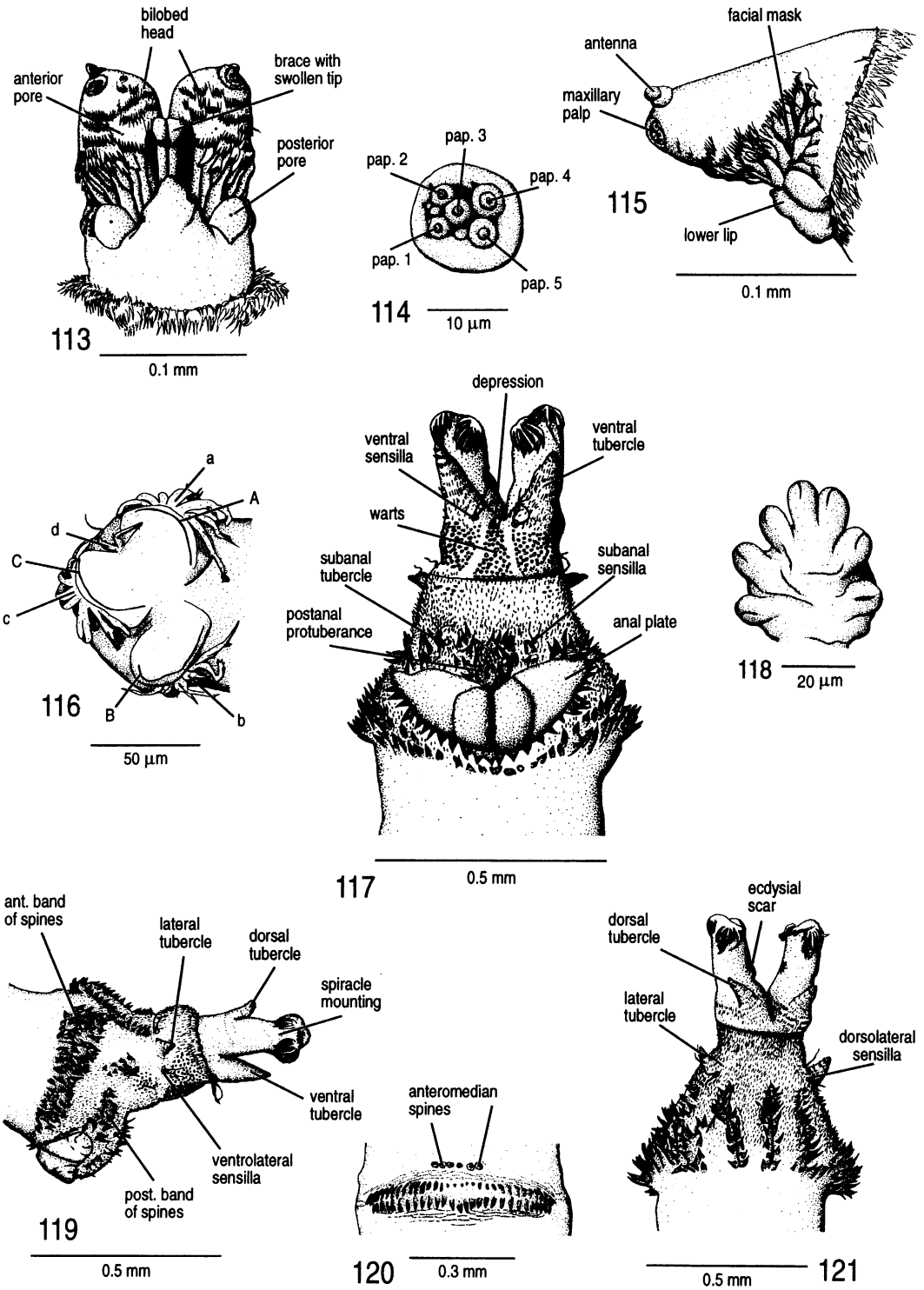


Fig. 113–121. *Palaeosepsis polychaeta.* **Cephalic region:** 113: ventral, 115: lateral; **maxillary palp:** 114; **posterior spiracle:** 116; **last segment:** 117: ventral, 119: lateral, 121: dorsal; **anterior spiracle:** 118; **creeping welt:** 120.

oped, bare subanal tubercles; with a subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; diagonal line bare of warts between a depression at bases of ventral tubercles and fold; with an anterior and a posterior band of spines; anterior band is complete ventrally; posterior band is divided into dorsolateral group of spines and a ventrolateral band; spines large, with large base and sharp, drawn-out point; large lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings long, but very wide even at tip, with moderately long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; spines regularly spaced; area between grooves densely hirsute except for anteriormost area; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 116): Has three openings and four processes of spiracular hairs on trifoliate plate, processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") with two unbranched narrow hairs; openings arranged in triangular fashion; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 121).

BIOLOGY: This recently described species was collected in Las Alturas (Costa Rica) at midelevation on a shady pasture where it was visiting fresh cow pats. The larvae were reared in the laboratory on cow dung. I did not observe any precopulatory guarding but the species was quite rare and I may have overlooked such behavior.

DISTRIBUTION: Costa Rica, Panama, Honduras, and Venezuela.

Palaeosepsis pusio (Schiner, 1868)

Locality: Las Alturas (Provincia Puntarenas, Costa Rica), coll. R. Meier
Specimens examined: 10
Length: 3.56–4.12 mm ($\bar{x}$ = 3.86 0.24; n = 9)
Largest width of body segments: 0.31–0.56 mm ($\bar{x}$ = 0.46 0.07; n = 10)
Width of last segment: 0.40–0.58 mm ($\bar{x}$ = 0.53 0.07; n = 10)

CEPHALIC REGION (fig. 122, ventral view; fig. 124, lateral view): Much longer than wide, with comparatively long and narrow necklike base, distinctly bilobed; large lower lip; posterior pore on lower lobe and anterior pore on one comb to either side of brace; apical third of brace fused and tips distinctly enlarged into hooklike projections; 10–12 combs restricted to anterior section of cephalic lobes, mostly in horizontal rows; combs usually much wider than long with multiple rather large teeth; combs absent on facial mask, inner side of cephalic lobes, and around maxillae; facial mask composed of smooth-edged ridges, pattern of ridges not well organized like in *Sepsis*, with long primary ridges reaching a midfurrow alternating with short intercalary secondary, sometimes serrate, ridges.

MAXILLA (fig. 123): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 127): 5–7 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 129): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules, remaining six welts ventrally with two rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 25–34 spines, median spines distinctly smaller than lateral ones or missing, second row with 21–31 spines; 7–8 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 126, ventral view; fig. 128, lateral view; fig. 130, dorsal view): Anterior section distinctly bulbous, with few small warts laterally and in area between two bare diagonal lines; remaining segment densely pubescent; anal plate large, wing-shaped, outer lobe pointed laterally; anal plate with row of spines around anterior edge; postanal protuberance very well developed; weakly developed, bare subanal tubercles; with a subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; with an anterior and a posterior band of spines; anterior band is complete ventrally, posterior band somewhat divided into dorsolateral group of spines and a ventrolateral band; spines large with sharp drawn-out point; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mount-

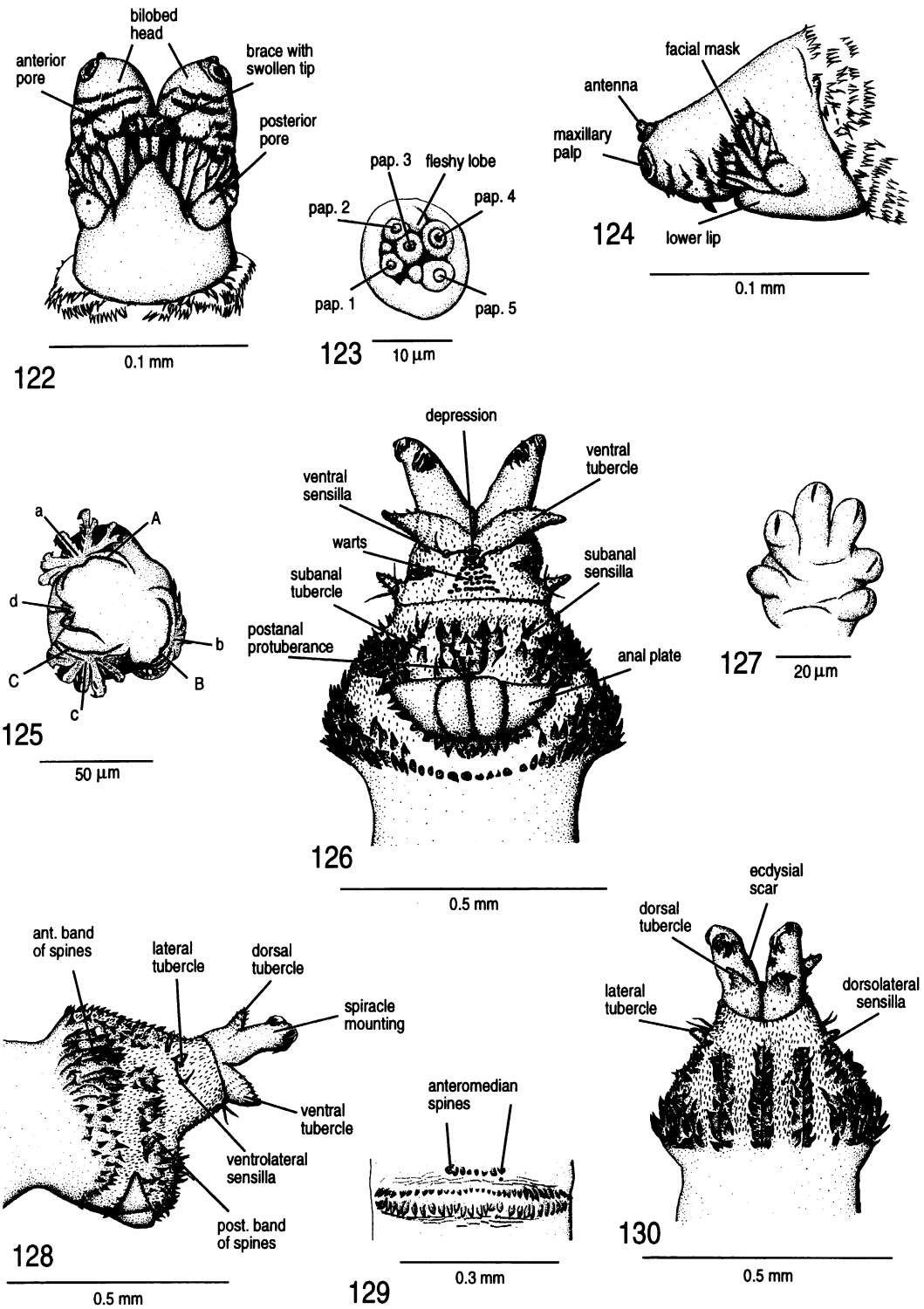


Fig. 122–130. *Palaeosepsis pusio.* **Cephalic region:** 122: ventral, 124: lateral; **maxillary palp:** 123; **posterior spiracle:** 125; **last segment:** 126: ventral, 128: lateral, 130: dorsal; **anterior spiracle:** 127; **creeping welt:** 129.

ings moderately long, with moderately long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of regularly spaced spines on either side; area between grooves densely pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 125): Has three openings and four processes of spiracular hairs on trifoliate plate, processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") with two unbranched narrow hairs; openings in triangular arrangement; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 130).

BIOLOGY: This species was extremely common in Costa Rica (Las Alturas) at a site with a large accumulation of moist cow dung. It was bred in the laboratory from cow dung and displays precopulatory guarding.

DISTRIBUTION: *Palaeosepsis pusio* is known from the West Indies, Florida, Texas and all of South America including Argentina (but see Steyskal [1968] for comment on potential misidentifications).

10. GENUS *PARAPALAEOSEPSIS* DUDA, 1926

Parapalaeosepsis compressa Zuska, 1970

Locality: 30 mi west of Cairns (Queensland, Australia), coll. R. Meier
Specimens examined: 6
Length: 5.67–6.25 mm ($\bar{x}$ = 6.01 0.19; n = 6)
Largest width of body segments: 0.66–0.83 mm ($\bar{x}$ = 0.78 0.06; n = 6)
Width of last segment: 0.76–0.91 mm ($\bar{x}$ = 0.86 0.05; n = 6)

CEPHALIC REGION (fig. 131, ventral view; fig. 133, lateral view; fig. 464: detail): Longer than wide, bilobed, small lower lip; posterior pore on lower lobe and anterior pores on one comb to either side of brace; brace with tips that are distinctly enlarged into hooklike projections; 5–7 combs restricted to anterior section of cephalic lobes; combs mostly in horizontal rows, much wider than long with multiple teeth; with some combs on inner side of cephalic lobes; facial mask composed entirely of a moderate number of mostly fringed ridges in no apparent order; two ridges next to either side of mouth opening with straight edges but not fused to each other.

MAXILLA (fig. 132): Composed of five compound papillae; four out of five consisting of two superimposed lobes (pap. 1–3, 5), only one with three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 136): 7 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 138): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules, remaining six welts with two long rows of reclinate spines and additional short rows of spinules anterior and posterior to spines; first row of spines with 25—27, median spines distinctly smaller than lateral ones, second row with 20–28 spines; 3–6 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 135, ventral view; fig. 137, lateral view; fig. 139, dorsal view): Anterior section distinctly bulbous, with numerous small warts laterally including area between bands of spines (see below) and dorsally between three double rows of spines; warts also in area between a depression and two bare diagonal lines running craniad; anal plate large, wing-shaped, outer lobe rounded laterally; anal plate with row of spines around anterior edge; postanal protuberance well developed; weakly developed bare subanal tubercle; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with ventral sensory organ at each base; with an anterior and a posterior band of spines; anterior band incomplete ventrally, spines large with sharp drawn-out points; small lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of regularly spaced spines on either side; posteriorly, area between grooves bare, anteriorly with a few warts; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 134): Has three openings and four processes of spiracular hairs, processes ("a–c") associated with openings with 6–7 hairs, unassociated process ("d") with two unbranched narrow hairs; opening below two-hair process straight ("C") extending just beyond spiracular plate, the one above ("A") arched at one end toward root of process "d"; opening "B" extending far onto ventromedian side of spiracle

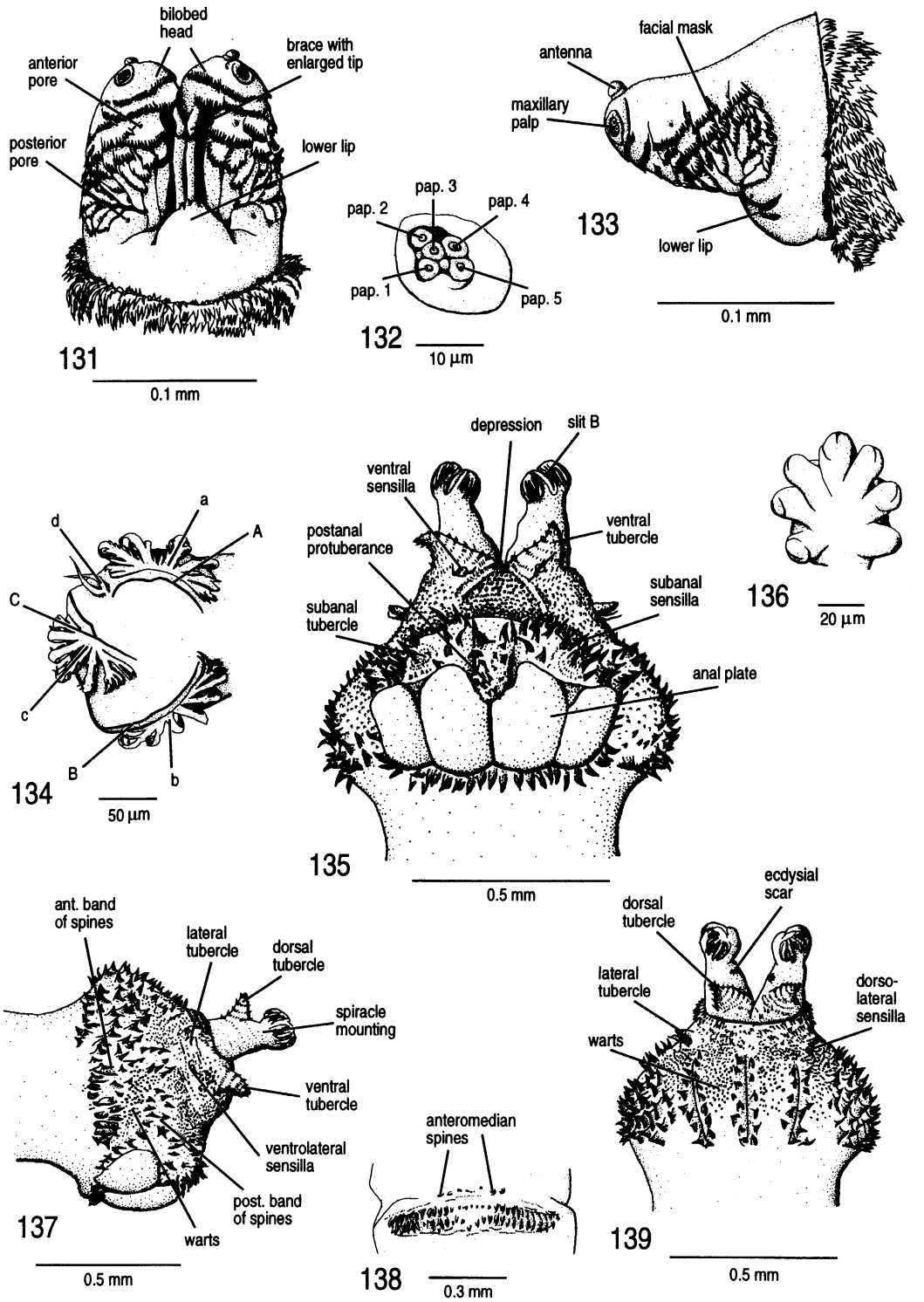


Fig. 131–139. *Parapalaeosepsis compressa.* **Cephalic region:** 131: ventral, 133: lateral; **maxillary palp:** 132; **posterior spiracle:** 134; **last segment:** 135: ventral, 137: lateral, 139: dorsal; **anterior spiracle:** 136; **creeping welt:** 138.

mounting (fig. 135); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 139).

BIOLOGY: This species is common in Queensland (Australia) where I collected it on cow and human excrement in pastures as well as on the edge of a rain forest. Under laboratory conditions it bred in cow dung. There was no evidence of any pre- or postcopulatory guarding.

DISTRIBUTION: *Parapalaeosepsis compressa* is known only from the Australian region (Bismarck Archipelago, New Guinea and Australia; Zuska, 1970; 1989). Colless (1980) provided maps for its spatial and seasonal distribution in Australia.

Parapalaeosepsis plebeia (Meijere, 1906)

Locality: 5 mi west of Moruya (New South Wales, Australia), coll. R. Meier
Specimens examined: 6
Length: 5.28–6.16 mm ($\bar{x}$ = 5.71 0.31; n = 6)
Largest width of body segments: 0.61–0.77 mm ($\bar{x}$ = 0.68 0.05; n = 6)
Width of last segment: 0.59–0.80 mm ($\bar{x}$ = 0.71 0.06; n = 6)

CEPHALIC REGION (fig. 140, ventral view; fig. 142, lateral view): Longer than wide, distinctly bilobed, small lower lip; posterior pores on lower lobe and anterior pore on one comb to either side of brace; brace with tips that are distinctly enlarged into hooklike projections; 5–7 combs restricted to anterior section of cephalic lobes; combs mostly in horizontal rows, usually much wider than long with multiple teeth; combs absent from inner side of cephalic lobes and around maxillae; facial mask composed entirely of moderate number of fringed ridges in no apparent order, the two ridges next to either side of mouth opening with straight edges, but not fused to each other.

MAXILLA (fig. 141): Composed of five compound papillae; four out of five consisting of two superimposed lobes (pap. 1–3, 5), only one with three superimposed lobes (pap. 4); no gap between papillae, but with remnant of a separating fleshy lobe between a group of two and three.

ANTERIOR SPIRACLE (fig. 145): 5–6 short and stout lobes arranged along a wide central axis.

CREEPING WELTS (fig. 147): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules, remaining six welts with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 26—36, median spines distinctly smaller than lateral ones, second row with 16–24 spines; 4–8 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 144, ventral view; fig. 146, lateral view; fig. 148, dorsal view): Anterior section distinctly bulbous, with numerous small warts laterally including area between bands of spines (see below) and dorsal aspect of last segment, but also area between a depression and two bare diagonal lines running craniad; anal plate large, wing-shaped, posterior tip of inner lobe projecting, outer lobe pointed laterally; row of spines around anterior edge; postanal protuberance well developed; weakly developed, bare subanal tubercle; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; with an anterior and a posterior band of spines; anterior band is incomplete ventrally, spines large with sharp drawn-out points; small lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of regularly spaced spines on either side; anteriorly, area between grooves bare, posterior with a few warts; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 143): Has three openings and four processes of spiracular hairs, processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") with two unbranched narrow hairs; opening below two-hair process straight ("C") extending just beyond spiracular plate, the one above ("A") arched at one end toward root of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 144); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 148).

BIOLOGY: Little is known about the biology of *P. plebeia*, although it is one of the most common sepsids in Australia. Snowball

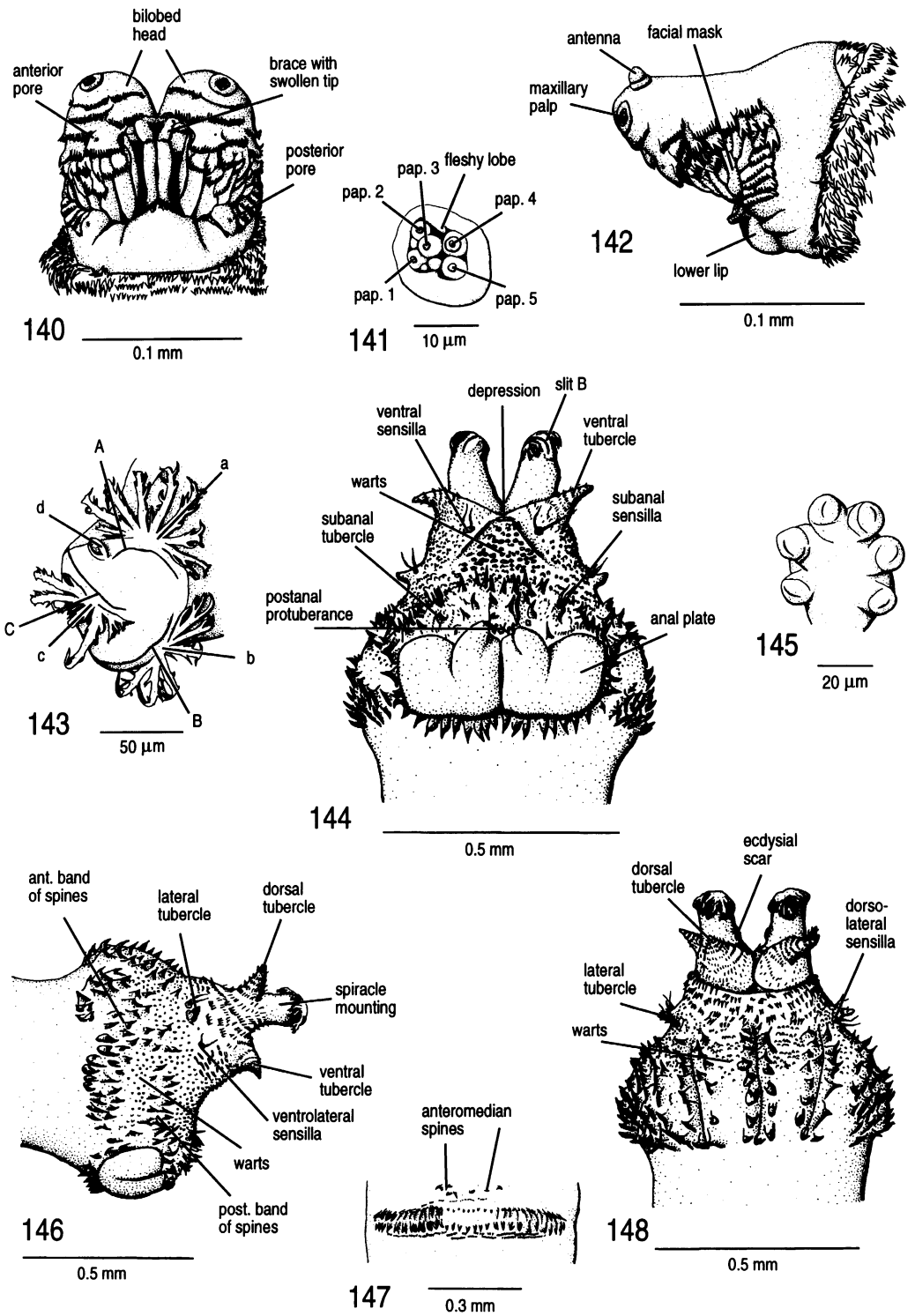


Fig. 140–148. *Parapalaeosepsis plebeia.* **Cephalic region:** 140: ventral, 142: lateral; **maxillary palp:** 141; **posterior spiracle:** 143; **last segment:** 144: ventral, 146: lateral, 148: dorsal; **anterior spiracle:** 145; **creeping welt:** 147.

(1944) bred it from cow dung and also reported it as associated with carrion (see also Ferrar, 1987). I collected and reared it in large numbers on cow dung and human feces. Together with *Australosepsis niveipennis*, it is one of the first sepsids to arrive at the substrate. Within minutes of deposition the first flies arrive in large numbers. However, there was no evidence of pre- or postcopulatory guarding (despite indications in Snowball, 1944). In contrast to *Australosepsis niveipennis*, it is most common on shady and moist pastures. I never collected this species on open pastures.

DISTRIBUTION: *Parapalaeosepsis plebeia* is known from New Guinea, the Solomon Islands, the Bismarck Archipelago, and Australia (including Tasmania: Zuska, 1970; 1989). Colless (1980) provided maps for its spatial and seasonal distribution in Australia. He argues that this species may have originated in Australia and subsequently spread to New Guinea. The species is unusual for its genus in that it is most abundant in temperate climates.

11. GENUS *PARATOXOPODA* DUDA, 1926

Paratoxopoda amonane Vanschuytbroeck, 1961

Locality: Honde-Valley (Eastern Highlands, Zimbabwe), coll. R. Meier
Specimens examined: 11
Length: 6.62–8.43 mm ($\bar{x}$ = 7.61 0.75; n = 10)
Largest width of body segments: 1.04–1.44 mm ($\bar{x}$ = 1.22 0.11; n = 10)
Width of last segment: 0.98–1.45 mm ($\bar{x}$ = 1.22 0.11; n = 10)

CEPHALIC REGION (fig. 149, ventral view; fig. 151, lateral view): Much wider than long; cephalic region distinctly bilobed, with moderately sized lower lip, eight long fingerlike projections at anterior end of lip; one comb on either side of mouthhooks with sensory organ consisting of a little papilla and a pore on a comb; posterior pores on lower lobes; brace distinctly divided longitudinally, each half with three projections, combs not restricted to anterior section of cephalic lobes, but also on facial mask, wider than long with numerous fine teeth; numerous combs on inner side of cephalic lobes and around maxillae; facial mask with serrate ridges, leading to last segment of mouth opening.

MAXILLA (fig. 150): Composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups rather narrow, no fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 154): 8–9 lobes in fanlike arrangement.

CREEPING WELTS (fig. 156): All segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; most remaining welts with two long rows of very small reclinate spines and short additional rows of spinules anterior and multiple rows posterior to spines; first row of spines with 39–40 spines, discounting median ones that are the size of denticles; second row with 35–39 spines; last creeping welts with spines in no clear order. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 153, ventral view; fig. 155, lateral view; fig. 157, dorsal view): Slightly bulbous, in lateral view very short, covered with dense, short pubescence; anal plate very large with diagonal fold; postanal protuberance consisting of a few spines; otherwise without spines on last segment; very small, hairy subanal tubercles; subanal sensory organ immediately lateral to each tubercle; ventral tubercles rather small without a depression between their bases but with a ventral sensory organ at each base; lateral tubercles very small, with a dorso- and a ventrolateral sensory organ; extremely short spiracle mountings; three spiracle openings with associated processes of hair on separate elevations (fig. 152); spiracle mounting with small dorsal tubercle; dorsal side of segment with additional grooves besides the usual three longitudinal ones; in lateral view, numerous rows of spinules anteriorly in a reticulate pattern, sensory organs with short hairs, sometimes with three instead of two sensory hairs.

POSTERIOR SPIRACULAR DISC (fig. 152): Very unusual with three spiracle openings on separate elevations; openings are long and S-shaped, all openings are associated with a process of 3–4 spiracular hairs, no unassociated process of spiracular hairs was found;

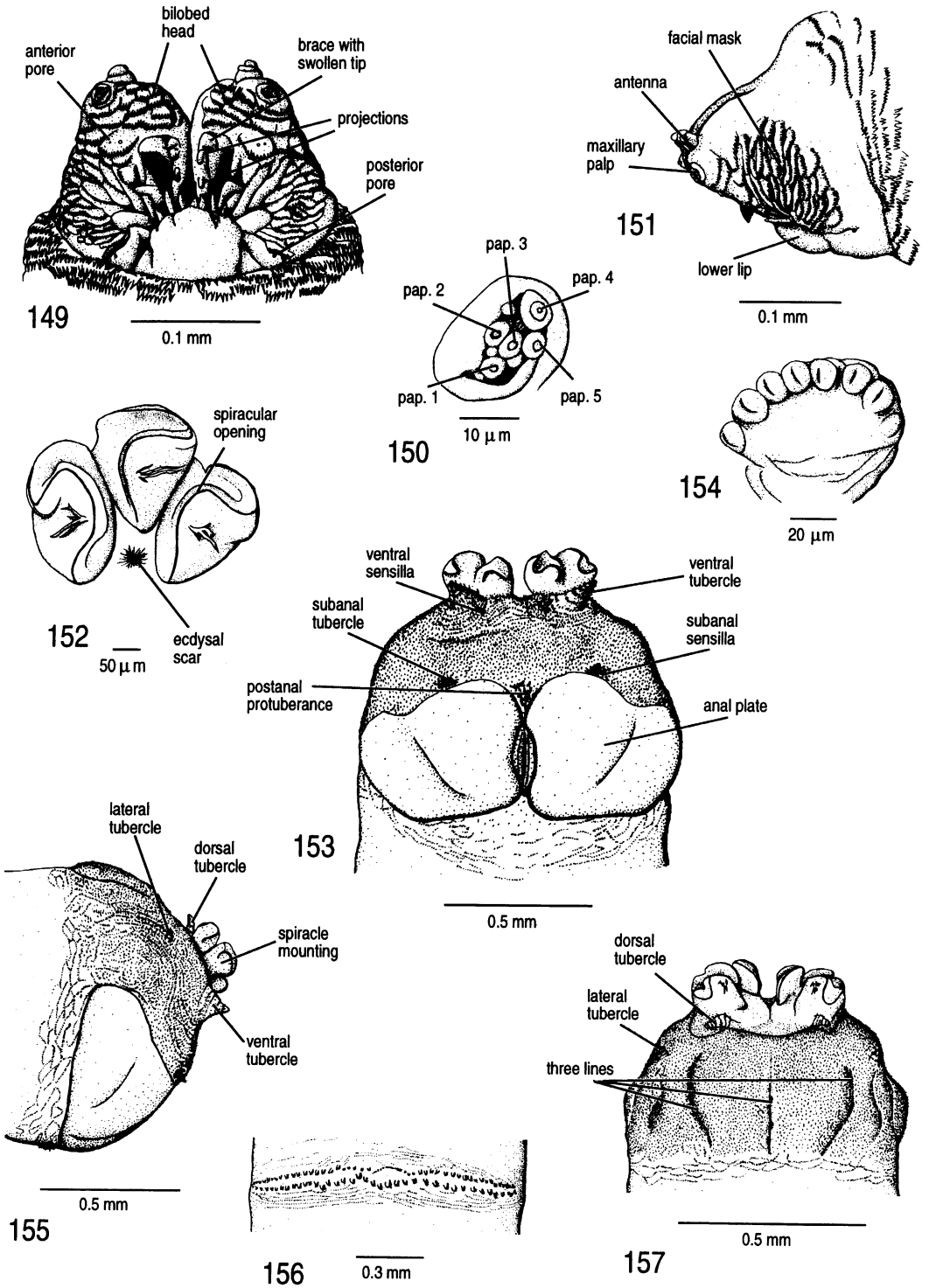


Fig. 149–157. *Paratoxopoda amonane.* **Cephalic region:** 149: ventral, 151: lateral; **maxillary palp:** 150; **posterior spiracle:** 152; **last segment:** 153: ventral, 155: lateral, 157: dorsal; **anterior spiracle:** 154; **creeping welt:** 156.

ecdysial scar is positioned between elevated spiracle openings outside of spiracular "plate," but on spiracle mounting.

BIOLOGY: The biology of the species in the *Toxopoda* group is largely unknown. I am hereby summarizing all available information. I collected *P. amonane* on cow dung, where it can be locally common. About 30 minutes after deposition the first males arrive which are followed by the larger females. Under laboratory condition, *P. amonane* deposited eggs readily in cow dung in which this species also completed its development. Dung in shaded spots is preferred over breeding substrate that is exposed to direct sunlight. The species was exceedingly rare at 1500 m but common in a valley at about 400 m. Intriguing is its courtship behavior. The males confront the females head-on and slowly wave their very long front legs which have some white tarsi. The females may respond with the same signal. This courtship may go on for more than an hour. I never actually observed copulation. A detailed behavioral study would certainly be very rewarding. I also collected an unidentified species of *Toxopoda* in Australia. A similar kind of courtship behavior was observed, but here copulations took place readily in small plastic containers. All attempts to breed this species in the laboratory with various kinds of dung were unsuccessful. Since most sepsids readily breed in captivity, dung may not have been the right substrate, although the flies were collected from human excrement.

Cuthbertson (1937) reported that the breeding site of *Paratoxopoda depilis* is fresh, isolated deposits of cattle dung (around Harare, Zimbabwe; Cuthbertson 1937). Braack (1981) described regular visits of an unidentified species of *Paratoxopoda* to carrion of antelopes. Ozerov (1991b) collected imagines of *Toxopoda mordax* from "a dung heap of cattle." Iwasa (1984) collected some specimens of *Toxopoda viduata* "at wild field between paddy field and sugar cane field." At least one species of *Paratoxopoda* may be ovoviviparous since eggs with fully developed first instar larvae were found in the uterus of several females. In the same species sperm appears to be transmitted in a spermatophore (Kotrba, personal commun.).

DISTRIBUTION: This species is known from the locus typicus in Zaire, Uganda, Nigeria, Kenya, South Africa and Zimbabwe. I established a breeding culture from specimens originally caught in the Honde Valley in Zimbabwe.

12. GENUS *SALTELLA* ROBINEAU-DESVOIDY, 1830

Key to the species (translation of Ozerov 1986a).

1. Last abdominal segment elongated (fig. 173), spines on this segment same color as cuticle (white) ..... *S. sphondylii*
– Last abdominal segment not elongated (fig. 164), spines on this segment black 2
2. Ring of very small black spinules between ventral and lateral tubercle; anterior spiracle short, with 10–12 fingerlike lobes (fig. 163) ..... *S. nigripes*
– Without ring of black spinules between lateral and ventral tubercles; anterior spiracle with 14–16 fingerlike lobes ..... *S. orientalis*

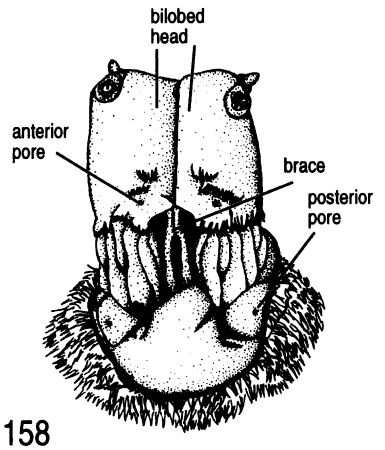
Saltella nigripes Robineau-Desvoidy, 1830

Locality: Caucasus, North Ossetia, near Alagir (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 6
Length: 5.43–5.84 mm ($\bar{x}$ = 5.65 0.14; n = 6)
Largest width of body segments: 0.61–0.74 mm ($\bar{x}$ = 0.67 0.05; n = 6)
Width of last segment: 0.73–0.85 mm ($\bar{x}$ = 0.79 0.04; n = 6)

The larvae of this species were previously described by Ozerov (1986a).

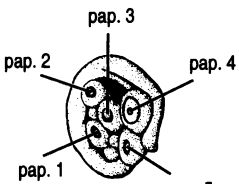
CEPHALIC REGION (fig. 158, ventral view; fig. 160, lateral view): Much longer than wide (especially section anterior to facial mask), cephalic lobes largely adjacent, almost fused, thus cephalic region only weakly bilobed; moderately large lower lip; posterior pores on lower lobe and anterior pore on one comb to either side of brace; brace fused only at apical tip; few small combs (5–8) restricted to anterior section of cephalic lobes, wider than long with multiple long teeth; combs absent on inner side of cephalic lobes and around maxillae; facial mask with few smooth-edged ridges (9–11; fig. 160); lower lobe not elongated; combs absent behind posterior margin of facial mask.

MAXILLA (fig. 159): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae



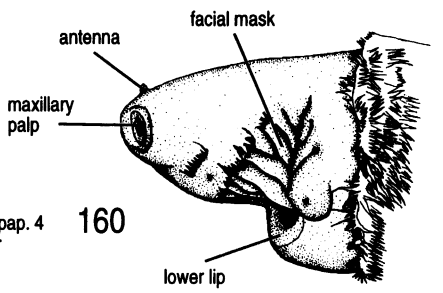
158

0.1 mm



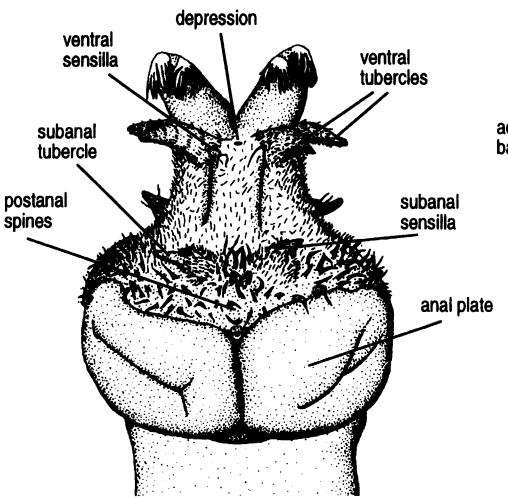
159

10 µm



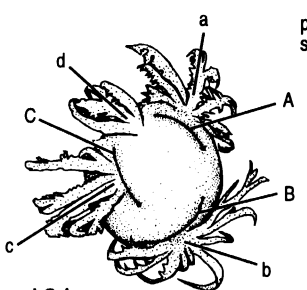
160

0.1 mm



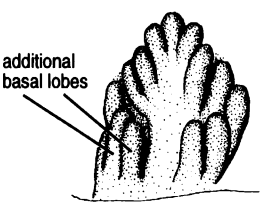
162

0.5 mm



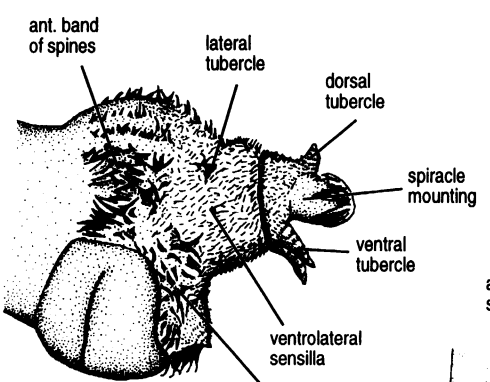
161

50 µm



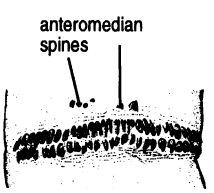
163

20 µm



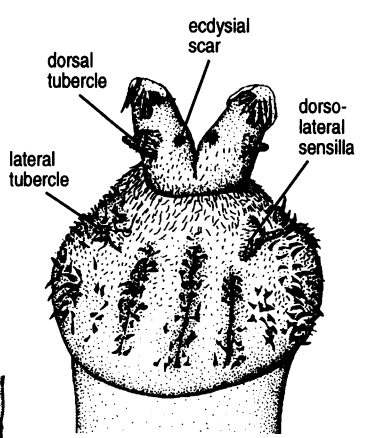
164

0.5 mm



165

0.3 mm



0.5 mm

166

consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 163): About 8–12 lobes arranged along a wide central axis which narrows toward tip, with 2–4 additional papillae at base of central axis.

CREEPING WELTS (fig. 165): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts with two long rows of reclinate spines and additional short rows of spinules anterior and posterior to spines; first row of spines with 28—31 spines, median ones sometimes reduced in size; second row with 21–28 spines; 3–7 anteromedian spines in two groups forming a short anterior row; spines with rather blunt tip. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 162, ventral view; fig. 164, lateral view; fig. 166, dorsal view): Very bulbous, with dense, short hairs; anal plate very large, as wide as last segment, with diagonal fold, rounded laterally; postanal protuberance missing, but corresponding area with numerous spines; preanal protuberance or spines absent; pair of well developed, bare subanal tubercles on pubescent elevations; subanal sensory organ immediately posterior to each tip; two pairs of well developed long ventral tubercles, pair of ventral sensory organs at their base; very shallow indistinct depression between bases of ventral tubercles; bare line stretching from bases of ventral tubercles craniad; with a posterior and an anterior band of spines, the latter not meeting ventrally; spines small, with long, narrow, drawn-out tips; large lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with moderately long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of irregularly spaced spines on either side; pubescence between rows restricted to posterior section; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 161): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") with 3–4 hairs; weakly curved openings in rectangular arrangement; opening "B" closer to "C" than "A"; ecdysial scar dorsomedially of dorsal tubercle (fig. 166).

BIOLOGY: Papp (1971) collected *S. nigripes* from cattle dung where the females deposit eggs when dung is about 12 hours old. Schweiger (1988) confirmed that this species oviposits eggs in cow dung. However, his record of *S. nigripes* in Berlin is unusual. This species had not previously been reported from Germany.

DISTRIBUTION: According to Hennig (1949) and Zuska and Pont (1984) this species is known from southern Europe, Israel, Turkmenistan, southern Russia, and Turkey.

Saltella orientalis

Author's Note: I was able to study material from all other previously described sepsid larvae, except for this species. Since the original description is in Russian, I decided to provide a translation of Ozerov (1986a): body cylindrical, tapering toward the anterior end, with a bulbous end and some paired protuberances. The cuticle is white, firm, shiny and smooth.

The cephalic region is conical with a tapering end. The antennae are not large and consist of two segments. The basal antennal segment is cylindrical, wider and lower than the second antennal segment. The latter is egg-shaped, height about twice the width. There are spinules below the antennae on a low conical tubercle. On the ventral side of the cephalic region, in front of the protruding ends of the mouthhooks, are 3–4 "premouthteeth." Each row consists of 3–10 teeth.

The mouth apparatus has a weakly curved mouthhook which points downward. The toothed sclerites are small and bar-shaped. Additional sclerites are missing. The hypo-

←

Fig. 158–166. *Saltella nigripes*. **Cephalic region:** 158: ventral, 160: lateral; **maxillary palp:** 159; **posterior spiracle:** 161; **last segment:** 162: ventral, 164: lateral, 166: dorsal; **anterior spiracle:** 163; **creeping welt:** 165.

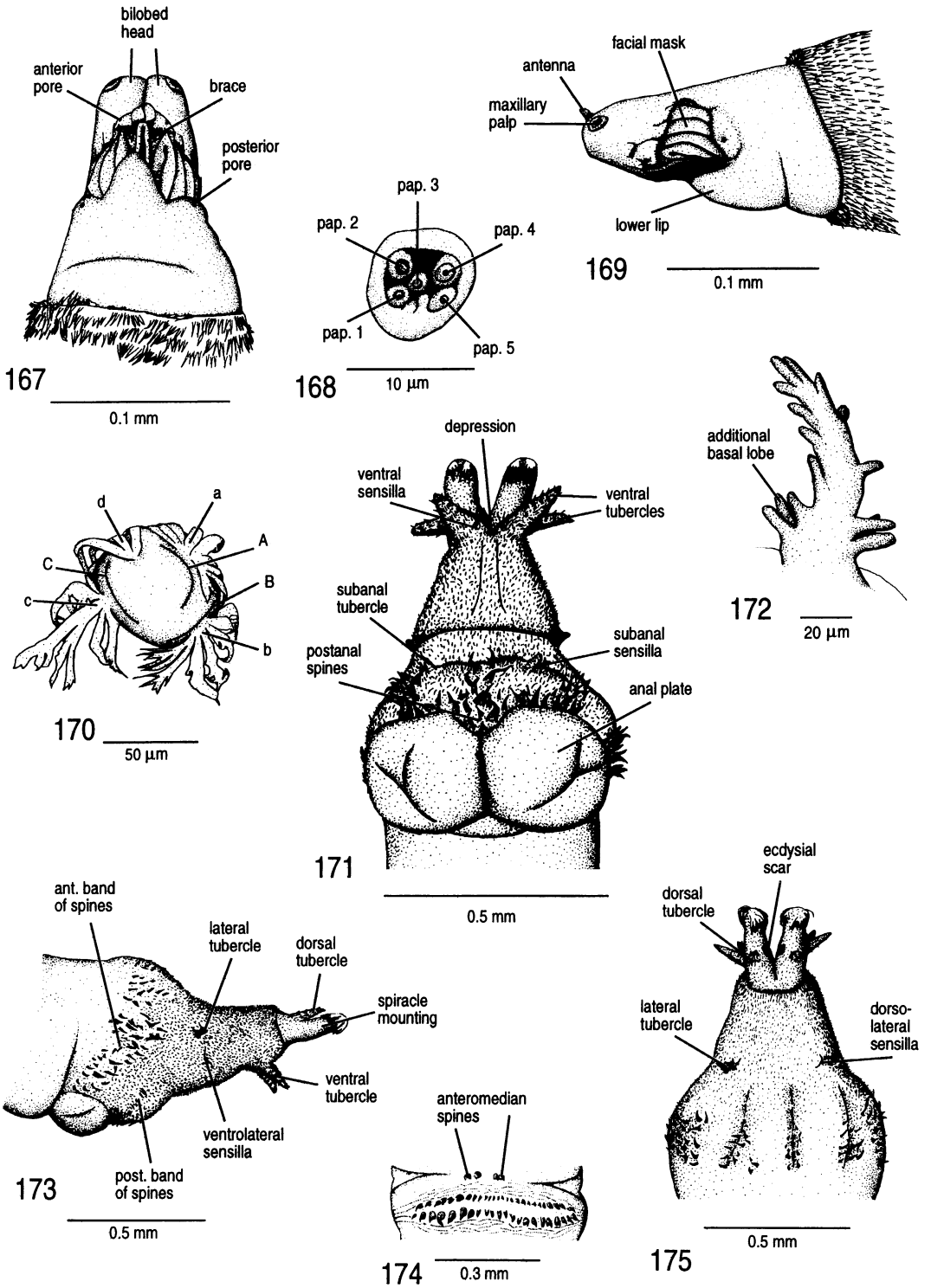


Fig. 167–175. *Saltella sphondylii.* **Cephalic region:** 167: ventral, 169: lateral; **maxillary palp:** 168; **posterior spiracle:** 170; **last segment:** 171: ventral, 173: lateral, 175: dorsal; **anterior spiracle:** 172; **creeping welt:** 174.

stomal sclerites are, when viewed laterally, of an irregular trapezoid shape with one opening in the middle. The parastomal sclerites are long and thin, not reaching the tip of the hypostomal sclerite. The dorsal extensions of the pharyngeal sclerite, which are strongly narrowed and completely pigmented toward the tip, are slightly shorter, or as long as the ventral ones. They are also half to one third as wide as the ventral extensions. The lower margin and the tips of the ventral extension are weakly pigmented, longer and about four times as wide as the dorsal ones.

The first and the second thorax segments taper toward anterior. They are 1.5 to 2 times as long as wide at the posterior end of the segments. The width of the anterior and posterior ends of the third thoracic segment and the first seven abdominal segments are approximately equal. All thoracic- and the first seven abdominal segments have 10–18 rows of small spinules which form rings. Also, the abdominal segments 2–7 bear ventrally two rows consisting of 28–32 spines which are arranged on the creeping welts. Toward the end of each segment, there are an additional 4–6 spines in two groups.

There are black or light-colored spines as well as four groups of protuberances on the anterior end of the 8th abdominal segment: two lateral, two dorsal which bear the posterior spiracles ["spiracle mountings"in remaining descriptions], two ventral, and two behind the anal plate. The lateral protuberances and the ones behind the anal plate are small conical tubercles. The dorsal tubercles have small conical extensions on the dorsal side ["dorsal tubercles" in remaining descriptions]. The ventral tubercles are bifurcated, which is typical only for the larvae in the genus *Saltella*.

The area of the preanal protuberance is almost completely reduced and forms a very narrow and weakly differentiated area between the seventh abdominal segment and the anal plate. It does not bear any black spines.

The anal plate is paired. Each half consist of two fused anal "hills." The anal opening is between these two halves.

The anal plate is positioned on the ventral side between the seventh and the last abdominal segment. Although the borders are not very distinct, it can always be recognized. The surface is smooth and somewhat protruding which makes it stand out from the surrounding segments, in particular from the eighth, whose anterior margin is covered by black spines.

The anterior spiracle has 15–16 lobes, some positioned at the base. The fingerlike lobes are longer at the base than toward tip. The posterior spiracle bears weakly arched slits. The spiracular plate is 1.5–2 times as long as it is wide. Two of the slits are parallel and the third is transverse to the first two and displaced toward one side.

BIOLOGY: Females deposit eggs in relatively fresh cow dung that has already formed a crust. Such substrate is mainly found on warm, open pastures. Larvae develop at temperatures as high as 30°C (Ozerov, 1986a). Like larvae of all other species of *Saltella*, the immatures die if the substrate is too moist.

DISTRIBUTION: This species is only known from southern Kansu (China) and the Far East of Russia (southern region of Chabarowsk and southern Primorje [Ozerov, 1986a]).

Saltella sphondylii (Schrank, 1803)

Locality: Caucasus, North Ossetia (Georgia), near Alagir, coll. Dr. A. L. Ozerov, Lomonosov University Moscow and Berlin (Germany), coll. R. Meier

Specimens examined: 9

Length: 3.84–7.02 mm ($\bar{x}$ = 5.36 1.04; n = 9); 6 mm (Schumann, 1962)

Largest width of body segments: 0.41–0.85 mm ($\bar{x}$ = 0.61 0.17; n = 9)

Width of last segment: 0.48–0.78 mm ($\bar{x}$ = 0.60 0.11; n = 8)

A description of larvae and puparia is provided by Hennig (1949), Schumann (1962) and Ozerov (1986a). Mangan (1977) included this species in his key but did not provide a description. Schumann (1962) described all three instars.

CEPHALIC REGION (fig. 167, ventral view; fig. 169, lateral view): Much longer than wide (especially section posterior of facial mask), lobes largely adjacent, thus cephalic region only weakly bilobed, large lower lip; posterior pore on both lower lobes and anterior pore on one comb to either side of brace; brace fused only at apical tip; very few small combs (4–5), restricted to anterior section of cephalic lobes, about as wide as long with mul-

tiple short teeth, no combs on inner side of cephalic lobes or around maxillae; facial mask with very few smooth-edged ridges (4–5) which are all anterior to an elongated lower lobe; all ridges span across entire facial mask (see also Schumann, 1962); no combs posterior to facial mask. The cephalopharyngeal skeleton is depicted in Hennig (1949).

MAXILLA (fig. 168): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); gap between groups of two (pap. 4, 5) and three (pap. 1–3) absent, but with remnant of separating fleshy lobe.

ANTERIOR SPIRACLE (fig. 172): 15–17 lobes arranged along a long central axis which narrows toward tip (text fig. 31 in Hennig, 1949: 13; fig. 59 in Schumann, 1962: 14–15 lobes); with a few basal lobes (see fig. in Schumann, 1962). Mangan (1977) confirmed the presence of basal lobes which he reports to be longer than lobes along central axis.

CREEPING WELTS (fig. 174): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 21–26 spines, median ones reduced in size, second row with 17–24 spines; 4–7 anteromedian spines in two groups forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 171, ventral view; fig. 173, lateral view; fig. 175, dorsal view): Moderately bulbous, with dense, short hairs; area posterior to subanal tubercle greatly elongated; anal plate large, as wide as last segment, swollen with diagonal fold, rounded laterally; postanal protuberance present as a group of spines; preanal protuberance or spines absent; weakly developed, subanal tubercles; subanal sensory organ posterior to each tubercle; two pairs of well developed long ventral tubercles (see description in Hennig, 1949; Mangan, 1977) and one pair of ventral sensory organs; shallow depression between bases of tubercles; diagonal bare line running from bases of ventral tubercles craniad; bands of spines weakly developed; only spines on ventral side moderately large; anterior band not meeting ventrally; short posterior band of much smaller spines; small lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings long, with rather long dorsal tubercle; dorsal side of segment with three longitudinal grooves, anterior halves of each bordered by a row of irregularly spaced spines on either side; anteriorly, no hairs between the rows of spines; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 170): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 4–8 hairs, unassociated process ("d") with 3–4 hairs; weakly curved openings in rectangular arrangement; ecdysial scar in dorsomedian position immediately above dorsal tubercle (fig. 175). Hennig (1949) noted that the spiracle mountings are strongly sclerotized down to the base and depicts the spiracular plate.

BIOLOGY: Duda (1925) reported that *S. sphondylii* is very common in Europe and North America. It is found on liquid manure, stable manure (Hennig, 1949, from Italy) and wet pastures. The species is also commonly collected on cattle dung (in Japan: Iwasa, 1984; Mangan, 1977; Valiela, 1969; van der Goot, 1986a) and yak dung (Papp, 1976). Rearing records and reports on egg deposition in cow dung are common (Coffey, 1966; Foster, 1967; Hinton, 1960; Hammer, 1941; Laurence, 1954; Ozerov, 1989; Papp, 1976; Pont, 1979; Schumann, 1962; Schweiger, 1988; Valiela, 1974; Wharton and Moon, 1979). Ozerov (1989) also reported rearings from pig dung. Eggs are usually deposited on crusted pats that are normally about 24 hours old (Hammer, 1941: fresher ones in midsummer; Papp, 1971; Pont, 1979; Schumann, 1962; Schweiger, 1988). Usually 10–20 eggs are placed at the base of open crevices on the pat (0.5–1.5 cm away from entrance), often in beetle tunnels (Hammer, 1941). In midsummer, development takes 29–35 days (Hammer, 1941). However, Schumann (1962) reported a much more rapid development (6 days for the development from egg to pupa). The larvae pupate in or below the cow pat (Hammer, 1941). Foster (1967) reports that males protect the females during oviposition.

Schumann (1962) also observed that paired imagines deposit the eggs. More detailed studies by Schulz (personal commun.) revealed that the males engage in postcopulatory guarding, and females with mature eggs in their ovaries copulate. In all other sepsids that Schulz studied, only females without mature ovas were found in copula.

Many sepsids feed on flower nectar. There are an unusually large number of records for *S. sphondylii* on umbellifers and composites (Macquart in Duda, 1925 on *Daucus*; Minder, 1963: wild carrot; Ozerov, 1989; van der Goot, 1986a: *Ranunculus*, *Hieracium*, *Achillea*, *Heracleum*; personal obs.). Visits to flowers may also be important for finding mates. Katja Schulz and I observed several copulating pairs of *S. sphondylii* on umbellifer flowers.

DISTRIBUTION: This species has a Holarctic distribution and can be found everywhere from France to Japan and most of the USA (Mangan, 1977; Zuska and Pont, 1984). Melander and Spuler (1917) speculated that *sphondylii* was introduced to the Nearctic region as early collectors never mention it and it is today quite common. However, Pont (in litt.) rightfully pointed out that the species is easily overlooked, because it occurs mainly on old cow pats.

13. GENUS *SEPSIS* FALLÉN

Key to species.

Many species in the genus *Sepsis* cannot be distinguished as larvae. Except for the first couplet, the following key requires SEM work or microscopical preparations.

1. Last segment strongly constricted and elongated behind the anal plate (e.g., figs. 180, 260); under SEM: cephalic lobes fused (e.g., figs. 176, 256) ..... *S. biflexuosa*, *S. kaszabi*
- Last segment somewhat constricted but not elongated (e.g., fig. 189) or if elongated then not constricted behind anal plate (e.g., fig. 224) 2
2. Last segment elongated behind anal plate, but not constricted (e.g., figs. 215, 224, 232) ..... *S. flavimana*, *S.* (*Sepsidimorpha*) *secunda* and *S.* (*Sepsidimorpha*) *duplicata*.
- Last segment not elongated (e.g., figs. 189, 197) 3
3. Last segment with hairs between anal plate and ventral tubercles (e.g., figs. 269, 350) ... 4
- Last segment with warts between anal plate and ventral tubercles (e.g., figs. 189, 197) ... 5
4. Process "d" of the posterior spiracle consisting of more than two hairs, hairs branched (fig. 349); facial mask with numerous very narrow ridges (figs. 346, 348) ..... *S. violacea*
- Process "d" of the posterior spiracle consisting of two unbranched narrow hairs (fig. 268); facial mask with fewer ridges (e.g., figs. 265, 267) ..... *S. lateralis*
5. Cephalic lobes fused (e.g., fig. 202) ..... *S. dissimilis*
- Two separate cephalic lobes forming a bilobed cephalic region (e.g., figs. 185, 194) 6

6. The remaining species of *Sepsis* are extremely difficult to identify as immatures. Table 2 summarizes the most important differences which are, unfortunately, largely continuous when studied across all species. Some species can nevertheless be identified while others can be ruled out based on the combination of subtle morphological variation and geographic distribution.

Sepsis biflexuosa Strobl, 1893

Locality: Ithaca (New York, USA), coll. R. Meier
Specimens examined: 17.
Length: 4.53–5.57 mm ($\bar{x}$ = 5.05 0.30; n = 9)
Largest width of body segments: 0.51–0.66 mm ($\bar{x}$ = 0.61 0.05; n = 9)
Width of last segment: 0.61–0.73 mm ($\bar{x}$ = 0.66 0.04; n = 9)

Hennig (1949) provided a description of the larvae. He noted the elongated last segment and spiracle mountings (see his figures). He recognized that one of the spiracle openings extends beyond the spiracular plate, and that there are three double rows of spines on the dorsum of the last segment. Schumann (1962) noticed that the morphology of the larvae is essentially identical to that of *S. duplicata*. Mangan (1977) described the spiracular plate of the posterior spiracle.

CEPHALIC REGION (fig. 176, ventral view; fig. 178, lateral view): Very long, much longer than wide; cephalic region monolobed, with long lower lip; anterior pore on one large comb to either side of brace; posterior pore on elongated lower lobe; brace with tips distinctly enlarged into bulbous hooklike projections; 10–11 combs restricted to anterior section of cephalic lobes; combs arranged in horizontal rows, usually wider than long, with multiple

TABLE 2
Differences Between the *Sepsis* that May Help in Identifying Very Similar Species

	number of ridges on the blocks forming the anterior section of facial mask	number of ridges on posterior section	no. of lobes on anterior spiracle	size of the anal plate	pubescence on the dorsal side of the hind end
S. cynipsea	4:4-5/2-3/2-3/2-3	6-7	6-8	large	post. 2/3
S. defensa	4:4/3/2/2	4-7	5-7	large	post. half
S. fulgens	4:3-4/2-3/2-3/2	2-5	6-7	medium	post. half
S. helvetica	4:4/3/2-3/2	4-5	6-7	large	post. half
S. latiforceps	3:4/3-4/3-4	10	7-8	large	post. half
S. monostigma	3:4-6/3-4/3-4	8-10	6-7	large	post. half
S. neglecta	4:4-5/3-5/3-5/3	5-7	5-6	very small	entire
S. neocynipsea	6:4-5/3-5/3-5/3-5/2/2	10	7-8	large	entire
S. orthocnemis	4:3-4/3/2-3/2-3	3-4	3-6	medium	post. half
S. punctum	4:5-6/3-5/3-4/3-4	9-13	5-7	large	entire
S. thoracica	5:4-5/2/2/2/2	5-6	5-7	small	post. 2/3

rather long teeth; combs absent from facial mask and around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges on either side of mouth opening large and fused to each other at anterior end; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into three blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary ridges; block next to mouth opening with 3–4 ridges, the two remaining blocks with 2–3 ridges, posterior section with three short ridges dorsal to lower lobe; several combs around entire facial mask including posterior margin. The cephalopharyngeal skeleton is depicted in Hennig (1949).

MAXILLA (fig. 177): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 181): Consisting of 5–6 lobes along a narrow central axis (fig. in Hennig, 1949: 5 lobes).

CREEPING WELTS (fig. 183): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts with two long ventral rows of reclinate spines and multiple additional rows of spinules anterior and posterior to rows of spines; first row of spines with 19–21 spines, median ones missing or reduced in size; second row with about 18–26 spines; 3–5 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 180, ventral view; fig. 182, lateral view; fig. 184, dorsal view): Distinctly bulbous at anterior end, with many hairs and/or warts; anal plate wing-shaped, inner and outer lobes rather flat; lateral lobe not very pointed; postanal protuberance very well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles; subanal sensory organ poste-

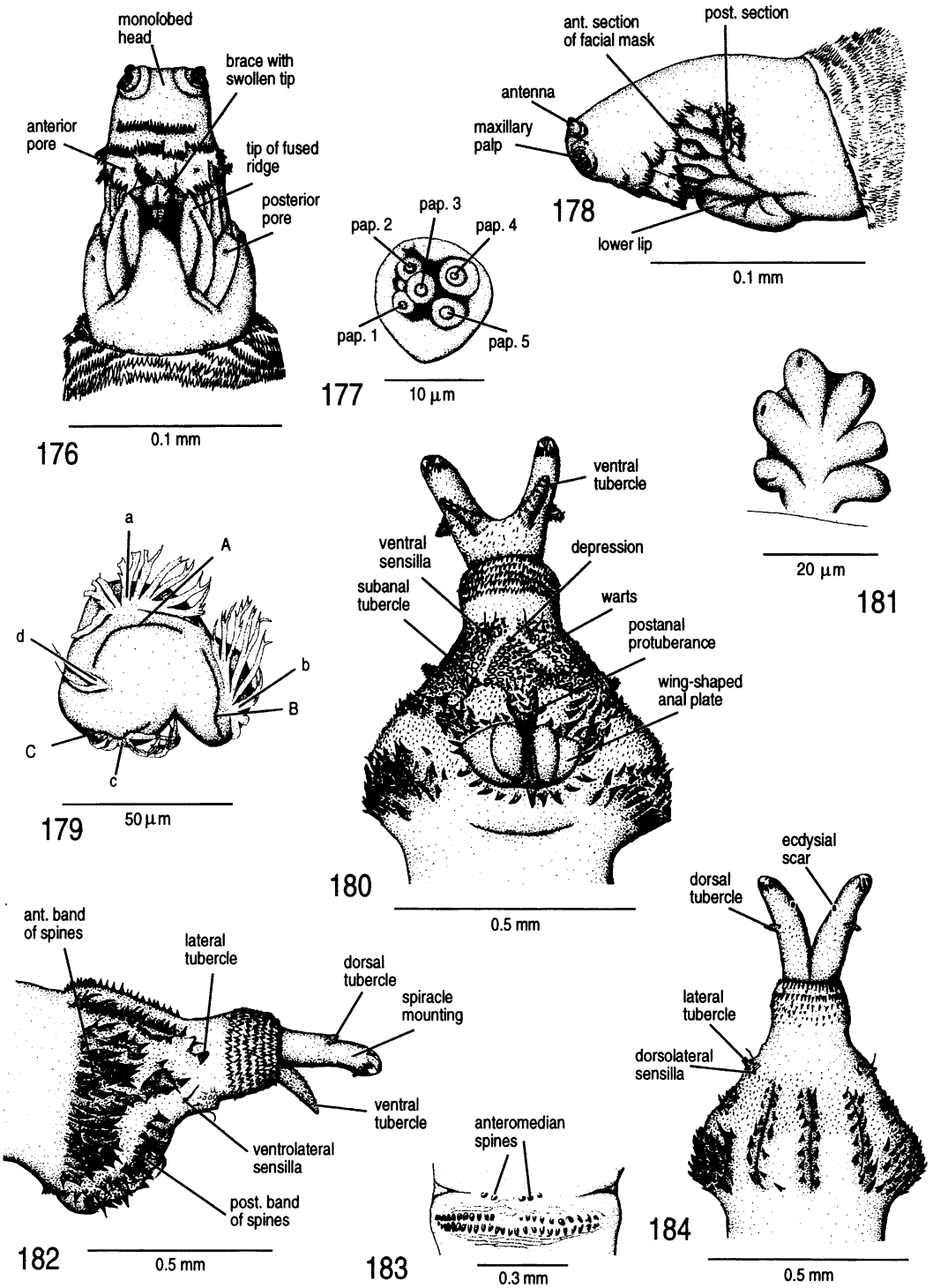


Fig. 176–184. *Sepsis biflexuosa.* **Cephalic region:** 176: ventral, 178: lateral; **maxillary palp:** 177; **posterior spiracle:** 179; **last segment:** 180: ventral, 182: lateral, 184: dorsal; **anterior spiracle:** 181; **creeping welt:** 183.

rior to each tubercle; pair of small ventral tubercles at base of spiracle mountings; area between bases of ventral tubercles and depression, that in other sepsids is found at base of ventral tubercles, greatly expanded, so that depression and ventral sensory organ are not associated with ventral tubercles but are in a more anterior position; hairs posterior to postanal protuberance transformed into warts; warts in a field circumscribed by two diagonal, bare lines strongly enlarged; behind this field, last segment strongly constricted; spines arranged into an anterior and a posterior band; area between bands pubescent; lateral tubercle with a dorso- and a ventrolateral sensory organ; spiracle mountings long, with small dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; posterior end, with few hairs between grooves; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 179): Bulging, with three openings and four processes of spiracular hairs, processes ("a–c") associated with openings with 5–7 hairs, unassociated process ("d") always with only two unbranched hairs; opening "C" straight, extending just beyond spiracular plate, slit A arched toward root of process "d"; slit "B" extending onto ventral side of spiracle mounting; ecdysial scar in dorsomedian position closer to dorsal tubercle than to spiracular plate (fig. 184). The arrangement of the spiracle opening is also depicted in Hennig (1949). Mangan (1977) correctly noted that one spiracular slit extends beyond the spiracular plate and runs along the spiracular mountings.

BIOLOGY: *Sepsis biflexuosa* appears to be specialized on cow dung from which it has been reared repeatedly (Coffey, 1966; Hammer, 1941; Laurence, 1954; Papp, 1976; Schweiger, 1988; Wharton and Moon, 1979). Imagines have been collected from cow feces in open pastures (Mangan, 1977; Papp, 1971; Valiela, 1969), small mammal feces (Mangan, 1977), sewage leaks and overflows (Mangan, 1977), horse dung (Coffey, 1966; Papp, 1976) pig dung (Coffey, 1966), stable manure (references in Schulz, 1989) and in cattlesheds (Minder, 1963). Development time from egg to imagines is 25–32 days (Hammer, 1941; Laurence, 1954). Van der Goot (1986a) found the flies visiting flowers of *Heracleum*. *Sepsis biflexuosa* belongs to a group of sepsid species that specialize on older cow pats and has a long development time. It is very common in the eastern United States and rather rare in Germany where it is largely replaced by *S. flavimana* which appears to have a similar natural history.

DISTRIBUTION: *Sepsis biflexuosa* has a Holarctic distribution. It is known from Mongolia and more or less all of Europe as well as most of North America (Mangan, 1977: southernmost locality: New Mexico; Hennig, 1949; Zuska and Pont, 1984). It is apparently particularly successful in colonizing islands since it is known from the Canary (Baez, 1982) and the Hawaii islands (Zuska, 1960).

Sepsis cynipsea (Linnaeus, 1758)

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 9
Length: 4.54–5.77 mm ($\bar{x}$ = 5.26 0.43; n = 5)
Largest width of body segments: 0.59–0.87 mm ($\bar{x}$ = 0.72 0.10; n = 5)
Width of last segment: 0.62–0.98 mm ($\bar{x}$ = 0.79 0.12; n = 5)

Hennig (1949) previously described larvae that were associated with imagines of this species. He found the facial mask to be similar to that of *Nemopoda nitidula* and the morphology of the last segment and the anterior spiracle to be more similar to that of *Meroplius minutus*. Both results are confirmed by this study. Schumann (1962) gave a detailed description of all three instars. My results agree with his description.

CEPHALIC REGION (fig. 185, ventral view; fig. 187, lateral view): Longer than wide; cephalic region distinctly bilobed; posterior pore on lower lobes and anterior pore on one large comb to either side of mouthhooks; tips of brace distinctly enlarged into hooklike projections; 5–6 combs restricted to anterior section of each cephalic lobe, wider than long with multiple small teeth; no combs on facial mask, the inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip, ridges organized into anterior and posterior sections separated by midfurrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto the most

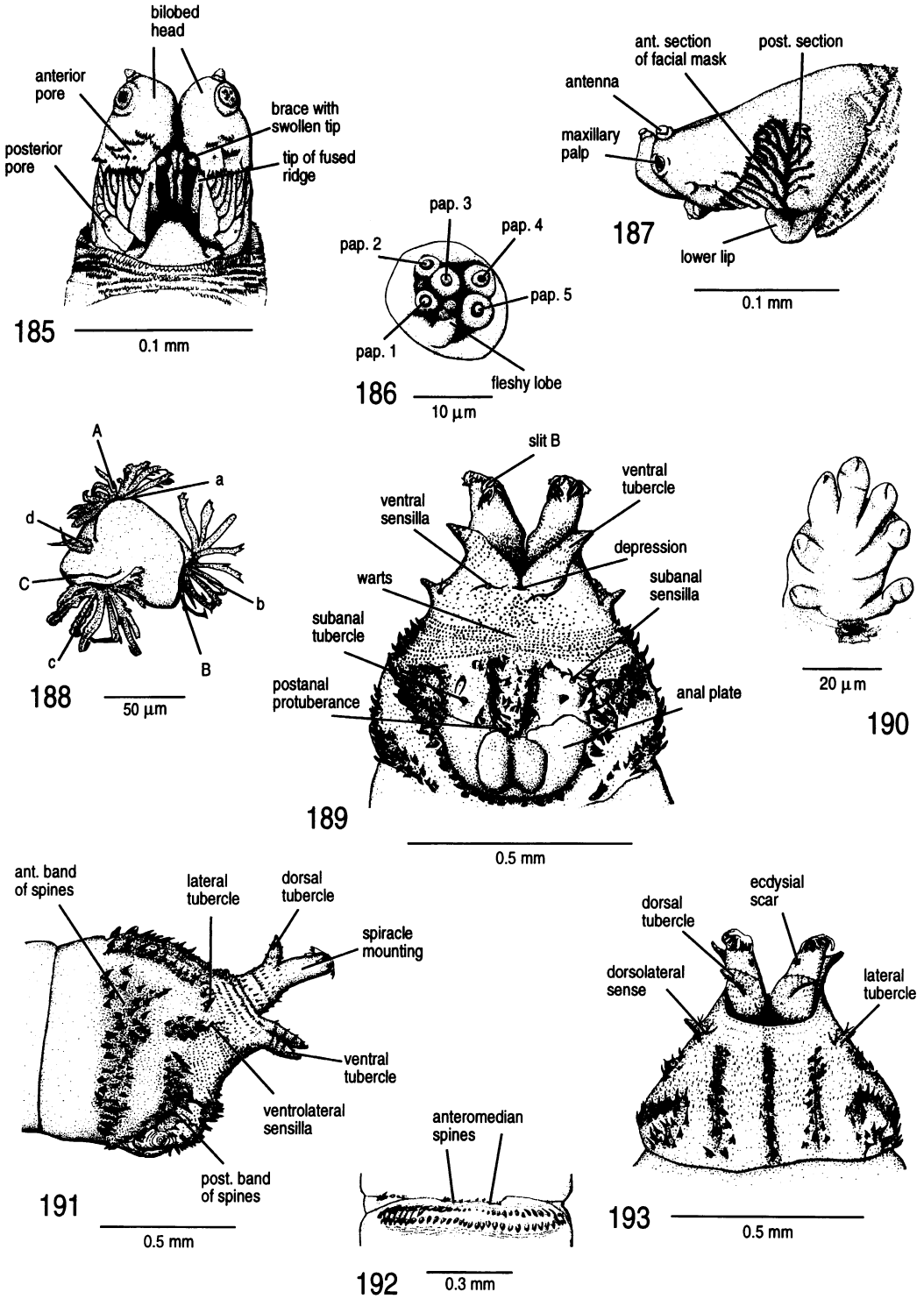


Fig. 185–193. *Sepsis cynipsea.* **Cephalic region:** 185: ventral, 187: lateral; **maxillary palp:** 186; **posterior spiracle:** 188; **last segment:** 189: ventral, 191: lateral, 193: dorsal; **anterior spiracle:** 190; **creeping welt:** 192.

dorsal ridge of preceding block, and shorter, intercalary ridges; block next to mouth opening with 4–5 ridges, the remaining blocks with 2–3 ridges; no combs behind posterior margin of facial mask; posterior section with 6–7 short ridges dorsal to lower lobe. A ventral view of the cephalopharyngeal skeleton and the cephalic region is depicted in Hennig (1949; as text fig. 52! and not text fig. 51 as indicated in the legend). The blocklike arrangement of the ridges can be inferred from Hennig's drawing.

MAXILLA (fig. 186): Composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four papillae (pap. 1–3, 5) consisting of two superimposed lobes, one composed of three superimposed lobes (pap. 4); narrow gap between the group of two (pap. 4, 5) and three (pap. 1–3) and remnant of fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 190): 6–8 moderately long lobes arranged along a narrow central axis (Hennig, 1949: 7–8 lobes).

CREEPING WELTS (fig. 192): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to rows of spines; first row of spines with 22–32 spines, median ones reduced in size; second row with 24–31 spines; 3–9 anteromedian spines, forming a short anterior row; spines largely fused to body wall, only weakly protruding. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 189, ventral view; fig. 191, lateral view; fig. 193, dorsal view): Bulbous, with numerous small warts between postanal protuberance and base of ventral tubercles; warts are only missing in area posterior to depression and on two diagonal lines that run from depression craniad; anal plate large, wing-shaped, pointed laterally; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate, with weakly developed, bare subanal tubercles; well posterior of each tubercle with a subanal sensory organ; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases; laterally with a distinct anterior and a posterior band of spines (see also text fig. 53 in Hennig, 1949); posterior band divided into a dorsolateral and a ventral band; area between bands pubescent; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings rather long with long dorsal tubercle; dorsal surface of last segment with three longitudinal grooves, each bordered by a row of spines on either side (see also Schumann, 1962); between grooves, except for most posterior portion, dorsal side of last segment pubescent; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 188): Flat surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 7–10 hairs, unassociated process ("d") with two unbranched hairs; one opening ("C") extending just beyond spiracular plate, a second ("A") arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 193). The arrangement of the spiracle openings is also depicted in Hennig (1949). However, Hennig did not recognize that one slit ("B") extends well beyond the spiracular plate onto the spiracle mounting (fig. 189).

BIOLOGY: *Sepsis cynipsea* is probably the sepsid for which most biological information is available. The species is very common in middle Europe where its mating behavior has been subject to several sociobiological studies (Parker, 1972 a, 1972b; Ward, 1983). *Sepsis cynipsea* is specialized on cow dung (Hammer, 1941; Parker, 1972a, 1972b; Schulz, 1989; Schumann, 1962; Ward, 1983). There are many rearing records from this substrate (Hammer, 1941; Iwasa, 1980; Kirk, 1992; Laurence, 1954; Minder, 1963; Papp, 1976; Schulz, 1989; Schumann, 1962; Schweiger, 1988). It has also been collected on sheep dung (Randall et al., 1981), and stable manure (reference in Schulz, 1989) and has been reported as being associated with the horse dung specialist *Zuskamira* (Pont, 1979). Occasionally, flowers are visited (Bährmann, 1993: *Cornus mas* and *Prunus spinosa*; van der Goot, 1986a: *Heracleum*; Warncke et al., 1993: *Saxifraga hirculus*). *Sepsis cynipsea* is particularly common in dry and sunny habitats (Bährmann, 1993).

Development times have been reported by several workers. They are 20 days (Pont, 1979: in midsummer), 12–25 days (median: 14 days; Laurence, 1954), 14 days (in laboratory, Schulz, 1989), eight days (at 24°C, personal obs.), eight or 10–14 days (first results from a laboratory culture; Schumann, 1962), 17–22 days in Denmark (Hammer, 1941) and 18–20 days in the vicinity of Moscow (Minder, 1963). Females hatch first although they pupate later than males (Schulz, 1989). In the laboratory a batch of eggs (about 30) is laid within 15–20 minutes (Parker, 1972a; Schulz, 1989). The first batch is deposited one week after eclosion and every 2.2 days a new batch can be produced under laboratory conditions (Schulz, 1989). It is unclear whether pupae (Parker, 1972 a, 1972b) or adults hibernate (Minder, 1963). Minder observed adults in October, and van der Goot (1986b) reported a swarm of sepsids including *cynipsea* in September. Such swarms are otherwise only well known for *S. fulgens* (see Pont, 1987b) and have been interpreted as aggregation of flies preparing for hibernation.

There is general agreement that in Central Europe *S. cynipsea* is the first sepsid to arrive at freshly deposited cow pat (Hammer, 1941; Minder, 1963; Parker, 1972a; Schulz, 1989). Within a few minutes, the first males arrive. Most males are found in the vegetation around the cow dung and only few on the pat where they appear to defend territories. Usually, males are much more abundant than females around a fresh cow pat and in the surrounding vegetation. As soon as females arrive, males mount the females and engage in precopulatory guarding. Females deposit their eggs while carrying a male. Only a few unmounted ovipositing females will be found on a fresh cow pat. After oviposition by the female, the precopula-pair leaves the cow pat and in 60% of all cases, the male will copulate with the female in the surrounding vegetation. At this time females no longer carry mature ova in their ovaries (Parker, 1972a, 1972b). Takeovers of a female by another male are rare. However, Ward (1983) reported that large males have a three-fold advantage over small males: (1) they are more likely to engage in a precopula, (2) they copulate with larger females and (3) they are more successful in fights with competitors. He also found that smaller males search longer at any one cow pat before they abandon the potential mating site.

McLachlan and Allen (1987) argued that small males have an advantage over large males when mating takes place on the wing. *Sepsis cynipsea* is cited as such a case, although this species never mates on the wing.

DISTRIBUTION: *Sepsis cynipsea* can be found in all of Europe, north Africa, central Asia and Japan (Hennig, 1949; Iwasa, 1980; Zuska and Pont, 1984).

Sepsis defensa Ozerov, 1985

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 3
Length: 4.11 mm (n = 1)
Largest width of body segments: 0.43–0.50 mm (n = 2)
Width of last segment: 0.52–0.55 mm (n = 3)

CEPHALIC REGION (fig. 194, ventral view; fig. 195, lateral view): Longer than wide, weakly bilobed, large lower lip; posterior pore on each lower lobe and anterior pore on one large comb to either side of mouthhooks; brace with apical tips distinctly enlarged into hooklike projections; 5–8 combs restricted to anterior section of each cephalic lobe, much wider than long with multiple small teeth; combs absent from facial mask, on the inner side of cephalic lobes, and around maxillae; facial mask composed entirely of smooth-edged ridges; the two ridges next to either side of mouth opening fused to each other at tip, ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary ridges; block next to mouth opening composed of four, second of three, the remaining of two ridges; posterior section with 5–7 short ridges dorsal to lower lobe; with a few combs behind posterior margin of facial mask.

MAXILLA: Maxillae of all specimens could not be studied because they were soiled.

ANTERIOR SPIRACLE (fig. 198): 5–7 moderately long papillae arranged along a narrow central axis.

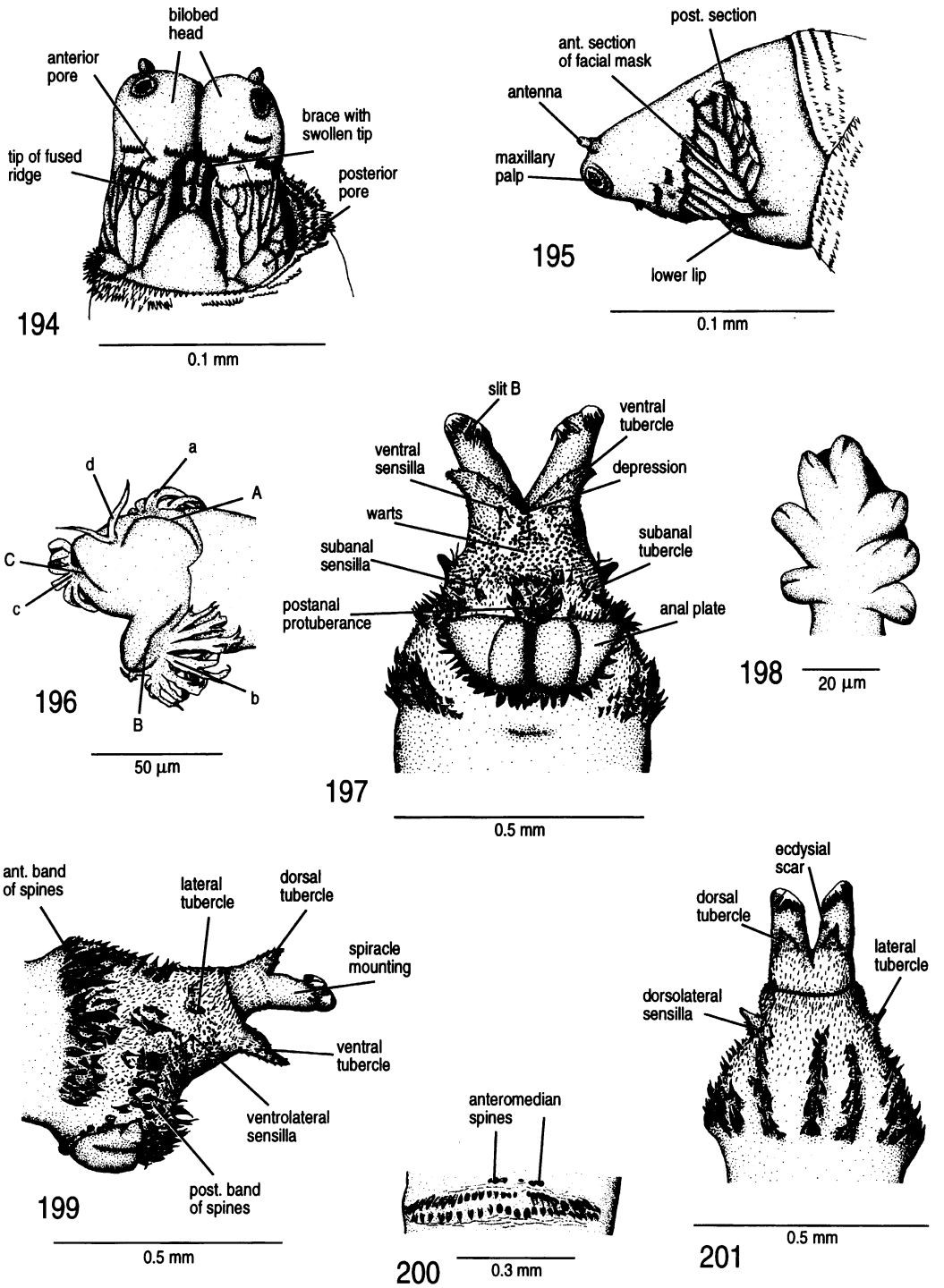


Fig. 194–201. *Sepsis defensa.* **Cephalic region:** 194: ventral, 195: lateral; **posterior spiracle:** 196; **last segment:** 197: ventral, 199: lateral, 201: dorsal; **anterior spiracle:** 198; **creeping welt:** 200.

CREEPING WELTS (fig. 200): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 24–27 spines, median ones missing or reduced in size; second row with 20–24 spines; 4–5 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 197, ventral view; fig. 199, lateral view; fig. 201, dorsal view): Slightly bulbous, with numerous small warts between postanal protuberance and base of ventral tubercles; warts are missing on two diagonal lines that run from depression at base of spiracle mountings craniad; anal plate large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate, with weakly developed, bare subanal tubercles, subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; with a distinct anterior and a posterior bands of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands pubescent; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with large dorsal tubercle; dorsum with three longitudinal grooves, each bordered by a row of spines on either side; only posterior half of integument between grooves pubescent; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 196): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") with two unbranched hairs; one opening "C" extending just beyond spiracular plate, the second, "A", arched toward base of process "d"; third opening "B" on separate extension of spiracular plate extending onto ventral side of spiracle mounting (fig. 197); ecdysial scar in dorsomedian position halfway between dorsal tubercles and spiracular plate (fig. 201).

BIOLOGY: Ozerov (1986c) reported larvae and adults of *S. defensa* from cow dung. He also found a few specimens close to a rodent carcass.

DISTRIBUTION: The species is currently only known from the Far East of Russia.

Sepsis dissimilis Brunetti, 1910

Locality: Badrshein or Shakshuk (Egypt), coll. K. Schulz, University of Arizona
Specimens examined: 16
Length: 3.99–4.64 mm ($\bar{x}$ = 4.31 1.77; n = 10)
Largest width of body segments: 0.49–0.58 mm ($\bar{x}$ = 0.52 0.05; n = 10)
Width of last segment: 0.55–0.65 mm ($\bar{x}$ = 0.60 0.03; n = 10)

CEPHALIC REGION (fig. 202, ventral view; fig. 204, lateral view): Longer than wide, monolobed, large lower lip; anterior pore on a large comb to either side of brace; posterior pore on both bulbous lower lobes; brace with tips distinctly enlarged into hooklike projections; 9–11 combs restricted to anterior section of cephalic lobes, usually considerably wider than long, arranged in transverse rows; combs absent from facial mask and around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to mouth opening fused to each other at tips; facial mask consisting of 7–9 ridges that span from cephalic lobe to anteromedian corner of lower lobe; multiple combs around entire facial mask including posterior margin.

MAXILLA (fig. 203): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 207): Consisting of 4–5 lobes; some fused to body wall; others along a short central axis.

CREEPING WELTS (fig. 209): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 21–28 spines, median ones missing or reduced in size; second row with 19–24 spines; 4–6 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 206, ven-

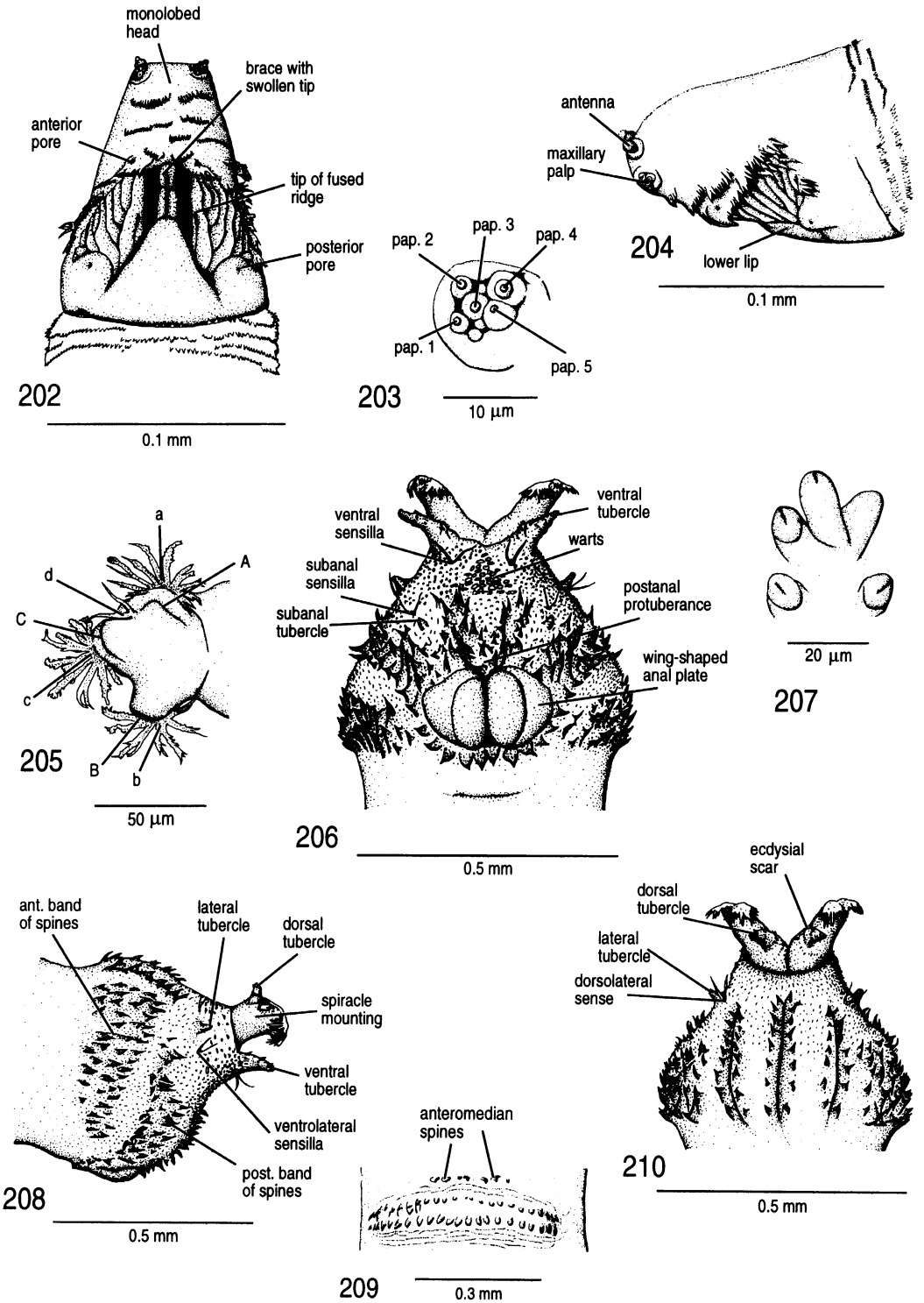


Fig. 202–210. *Sepsis dissimilis*. **Cephalic region:** 202: ventral, 204: lateral; **maxillary palp:** 203; **posterior spiracle:** 205; **last segment:** 206: ventral, 208: lateral, 210: dorsal; **anterior spiracle:** 207; **creeping welt:** 209.

tral view; fig. 208, lateral view; fig. 210, dorsal view): Distinctly bulbous, with many hairs and warts; anal plate wing-shaped, inner and outer lobes bulbous, outer lobe somewhat rounded; postanal protuberance large, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles in rather posterior position; posterior to tubercle with a subanal sensory organ; pair of ventral tubercles with distinct protuberance at half length; ventral sensory organ at base of each tubercle; shallow depression between bases of tubercles; hairs posterior to postanal protuberance transformed into numerous warts, warts in area anterior to depression and in a field circumscribed by two diagonal lines larger than those further anterior; spines arranged into an anterior and a posterior band; area between bands pubescent; lateral tubercles with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with rather long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; dorsally, pubescence restricted to posterior half of segment; sensory hairs long.

POSTERIOR SPIRACULAR DISC (fig. 205): Flat surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") always with only two hairs; opening "C" arched, extending just beyond spiracular plate, slit "A" arched at one end toward process "d"; slit "B" extending onto ventral side of spiracle mounting; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 210).

BIOLOGY: Little is known about the biology of *S. dissimilis*. I caught and reared the species on cow dung in Australia. It was not particularly common and I never observed any pre- or postcopulatory behavior. The flies caught in Egypt also bred readily in cow dung. This species belongs to the group of sepsids that have rather long development times (about three weeks).

DISTRIBUTION: Schulz collected *Sepsis dissimilis* in Egypt, providing the first record for the Palearctic region. It is otherwise known from the Afrotropical, Oriental and Australian regions (Iwasa, 1980: Japan; Zuska and Colless, 1984: Australia, New Guinea). Distributional data for Australia, including the seasonal occurrence, were published by Colless (1980).

Sepsis duplicata Haliday, 1838

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 10
Length: 3.56–3.98 mm ($\bar{x}$ = 3.76 0.13; n = 10); 7 mm (Schumann, 1962)
Largest width of body segments: 0.39–0.53 mm ($\bar{x}$ = 0.47 0.04; n = 10)
Width of last segment: 0.42–0.53 mm ($\bar{x}$ = 0.48 0.03; n = 10)

Schumann (1962) previously described all three instars of this species.

CEPHALIC REGION (fig. 211, ventral view; fig. 213, lateral view): Much longer than wide, monolobed; small lower lip; anterior pore on one large comb to either side of brace; posterior pore on both elongated lower lobes; brace with tips enlarged into hooklike projections; 10–13 combs restricted to anterior section of cephalic lobes, usually wider than long with multiple small teeth and arranged in horizontal rows; combs absent from facial mask and around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges to either side of mouth opening large and fused to each other at anterior end; no more than two long ridges spanning from cephalic lobe to elongated lower lobe; several intercalary shorter ridges as well as 2–3 short ridges dorsal to lower lobe; several combs around entire margin of facial mask. The cephalopharyngeal skeleton is depicted in Schumann (1962).

MAXILLA (fig. 212): Composed of five compound papillae, four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 216): Consisting of 5–7 lobes along a narrow central axis (fig. 49 in Schumann, 1962: 6–7 lobes).

CREEPING WELTS (fig. 218): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 18–24 spines, median ones missing or reduced in size; second row with about 18–25 spines;

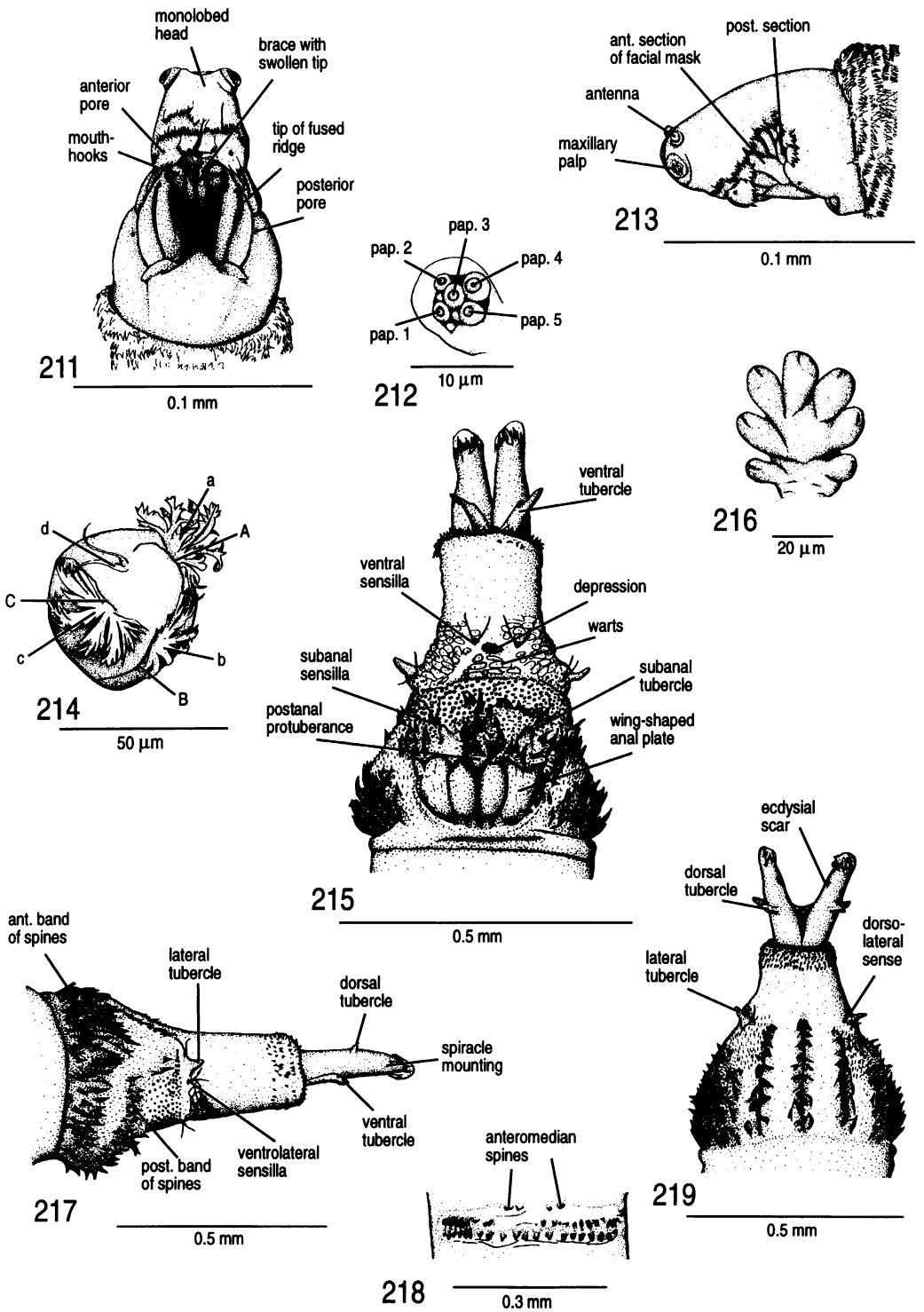


Fig. 211–219. *Sepsis duplicata.* **Cephalic region:** 211: ventral, 213: lateral; **maxillary palp:** 212; **posterior spiracle:** 214; **last segment:** 215: ventral, 217: lateral, 219: dorsal; **anterior spiracle:** 216; **creeping welt:** 218.

4–6 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 215, ventral view; fig. 217, lateral view; fig. 219, dorsal view): Distinctly bulbous at anterior end, with numerous hairs and warts; anal plate wing-shaped, with inner and outer lobe rather flattened; postanal protuberance very well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small, inconspicuous, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of small ventral tubercles with short projection at anterior third; area between bases and depression greatly expanded, thus ventral sensory organs which in other sepsids are positioned at each base of ventral tubercles, now in a more anterior position; hairs posterior to postanal protuberance transformed into warts, warts particularly large in area around depression and between two bare diagonal lines; spines arranged into an anterior and a posterior band; area between bands pubescent; lateral tubercle with a dorso- and a ventrolateral sensory organ; spiracle mountings very long, with small dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; area between grooves largely bare, hairs restricted to area between lateral two grooves and lateral field of spines; sensory organs with long hairs. Schumann (1962) depicts a lateral view of the last segment which nicely illustrates the elongated spiracle mountings.

POSTERIOR SPIRACULAR DISC (fig. 214): Bulging spiracular disc with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–6 hairs, unassociated process ("d") always with only two hairs; opening "C" extending just beyond spiracular plate, slit "A" arched at one end toward root of "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 215); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 219).

BIOLOGY: *Sepsis duplicata* is a specialist of cow dung (Schulz, 1989). There are numerous rearing records from this substrate (Hammer, 1941; Laurence, 1954; Minder, 1963; Schulz, 1989; Schweiger, 1988). Duda (1925), Frey (1908), Iwasa (1980) and van der Goot (1986a) confirmed the occurrence of *S. duplicata* close to cow pats, and van der Goot (1986a) saw *S. duplicata* visiting flowers of *Heracleum*. There is general agreement that this species is specialized on older cow pats (e.g., Papp, 1971, Schweiger, 1988). Minder (1963) reported that it favors cow pats that are 1–2 hours old. However, most authors observed that the first adults of this species were present after four hours (Schulz, 1989) and most imagines visit cow pats that are 1–2 days old (Hammer, 1941). Like all other sepsid species specialized on old dung, the development time is very long. According to Pont (1979) development takes 25 days in midsummer, Hammer (1941) reports 20–31 days, and Laurence (1954) about 30 days (26–39 days). At 24°C the first imagines emerged 15 days after the eggs had been laid (personal obs.). Larvae pupate in or below the cow pat (Hammer, 1941). Minder (1963) reported that copulation takes place in early morning hours and eggs are deposited in beetle tunnels 0.5–1.5 cm from the surface of the cow pat (Hammer, 1941; Minder, 1963). Females carry about 50–60 maturing eggs in their ovaries (Hammer, 1941). *Sepsis duplicata* hibernates as a pupa (Hammer, 1941). It is one of the few species within the Sepsidae with a courtship behavior (Hammer, 1941).

DISTRIBUTION: *Sepsis duplicata* is Palearctic in distribution. It ranges from France to Japan (e.g., Hennig, 1949; Iwasa, 1980; Zuska and Pont, 1984).

Sepsis flavimana Meigen, 1826

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 7
Length: 3.64–4.48 mm ($\bar{x}$ = 4.15 0.26; n = 7)
Largest width of body segments: 0.32–0.67 mm ($\bar{x}$ = 0.53 0.11; n = 7)
Width of last segment: 0.35–0.54 mm ($\bar{x}$ = 0.46 0.06; n = 7)

CEPHALIC REGION (fig. 220, ventral view; fig. 222, lateral view): Much longer than wide, monolobed, with moderately large lip; anterior pore on one large comb to either side of mouthhooks; posterior pore on both elongated lower lobes; brace with tips enlarged into hooklike projections; 10–13 combs restricted to anterior section of cephalic lobes,

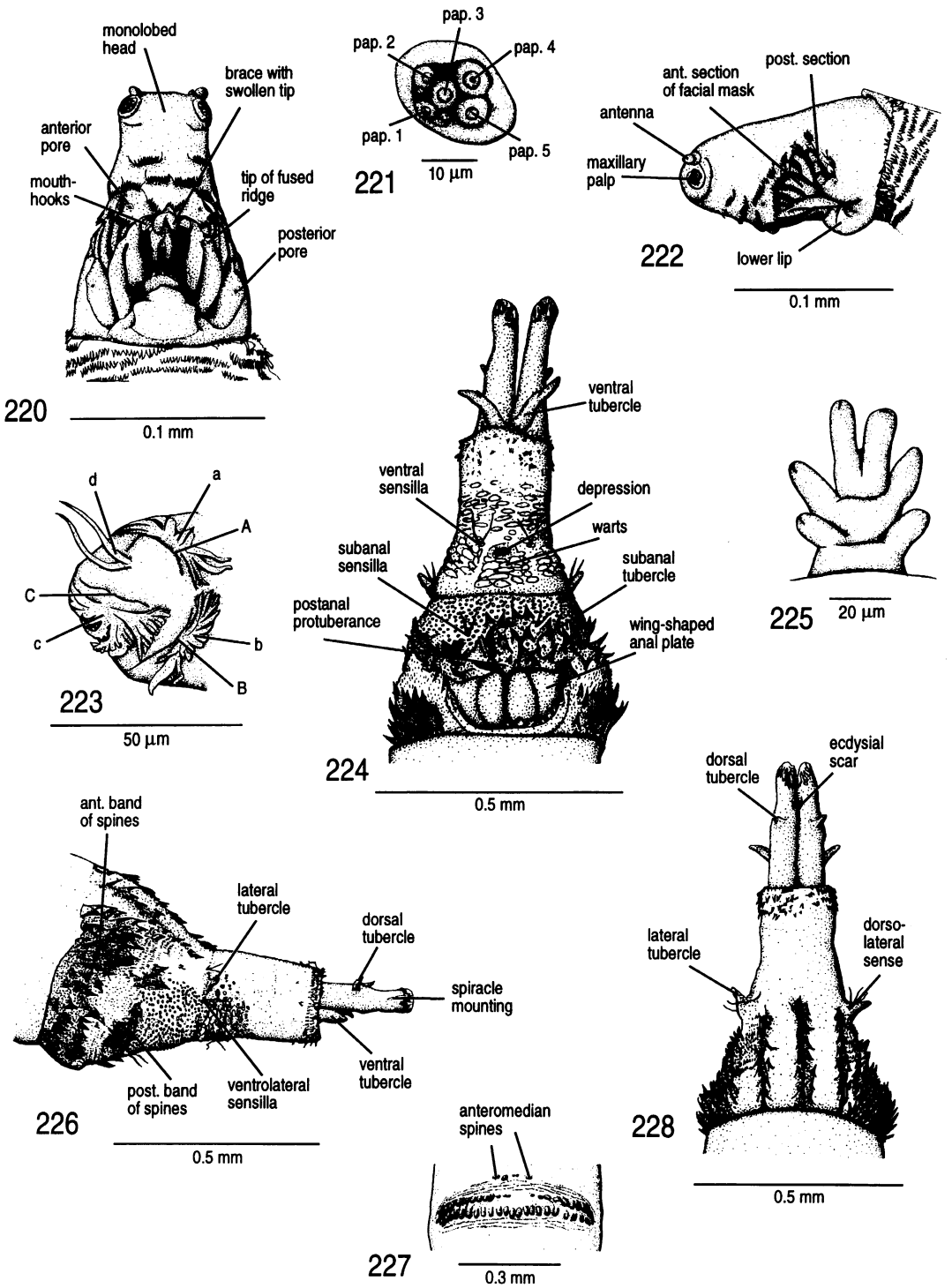


Fig. 220–228. *Sepsis flavimana.* **Cephalic region:** 220: ventral, 222: lateral; **maxillary palp:** 221; **posterior spiracle:** 223; **last segment:** 224: ventral, 226: lateral, 228: dorsal; **anterior spiracle:** 225; **creeping welt:** 227.

usually wider than long with multiple small teeth, arranged in transverse rows; no combs on facial mask or around maxillae; facial mask composed entirely of smooth-edged ridges; the two ridges next to either side of mouth opening large and fused to each other at anterior end; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into 2–3 blocks of ridges, whereby each block is formed by a primary ridge converging onto the most dorsal ridge of preceding block, and shorter intercalary ridges; block next to mouth opening with 2–4 secondary ridges, second and third with two ridges; posterior section with 2–3 short ridges dorsal to lower lobe; several combs around entire facial mask including posterior margin.

MAXILLA (fig. 221): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 225): Consisting of 6–8 long lobes along a narrow central axis.

CREEPING WELTS (fig. 227): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 18–26 spines, median ones missing or reduced in size; second row with 19–25 spines; 3–4 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 224, ventral view; fig. 226, lateral view; fig. 228, dorsal view): Distinctly bulbous at anterior end, with numerous hairs and warts; anal plate wing-shaped; postanal protuberance very well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of small ventral tubercles with short projection at anterior third; area between bases and two bare diagonal lines greatly expanded, thus ventral sensory organs which are positioned in most sepsids at bases of ventral tubercles in a more anterior position; hairs posterior to postanal protuberance transformed into warts, warts particularly large in area around a depression; spines arranged into an anterior and a posterior band; area between bands pubescent; lateral tubercle with a dorso- and a ventrolateral sensory organ; spiracle mountings very long, with small dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; area between grooves bare, hairs restricted to posterior half of integument between lateral grooves and lateral field of spines; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 223): Bulging spiracular disc with three openings and four processes of spiracular hairs; the processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") always with only two hairs; opening "C" straight, extending just beyond spiracular plate, slit "A" arched at one end toward the root of process "d"; slit "B" extending onto ventral side of spiracle mounting; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 228).

BIOLOGY: *Sepsis flavimana* is specialized for cow dung (Iwasa, 1980; van der Goot, 1986a) and has never been reared from any other substrate (Schulz, 1989), although Hennig (1949) reported imagines from stable manure of cows and Papp (1976) from yak and horse dung. Rearing records can be found in Hammer (1941), Laurence (1954), Ozerov (1989), Schulz (1989), and Schweiger (1988). There is general agreement that this species is specialized for older cow pats (Minder, 1963; Schulz, 1989; van der Goot, 1986a). The most detailed study comes from Schulz (1989) who collected the first males six hours after deposition of the pat. The species becomes the dominant sepsid after two days. Females can lay about 40 eggs every 1.5 days (in laboratory). Development time in the laboratory is rather long with all stages developing slower than *S. punctum* and *S. cynipsea*. Laurence (1954) reported a development time of 22–33 days (average of about 28 days). According to Minder (1963), it is much shorter (15–17 days) and in the laboratory at 24°C, the first imagines hatch after 14 days. These discrepancies may be explained by Schweiger's (1988) observation that *flavimana* is particularly sensitive to low temperatures. Eggs

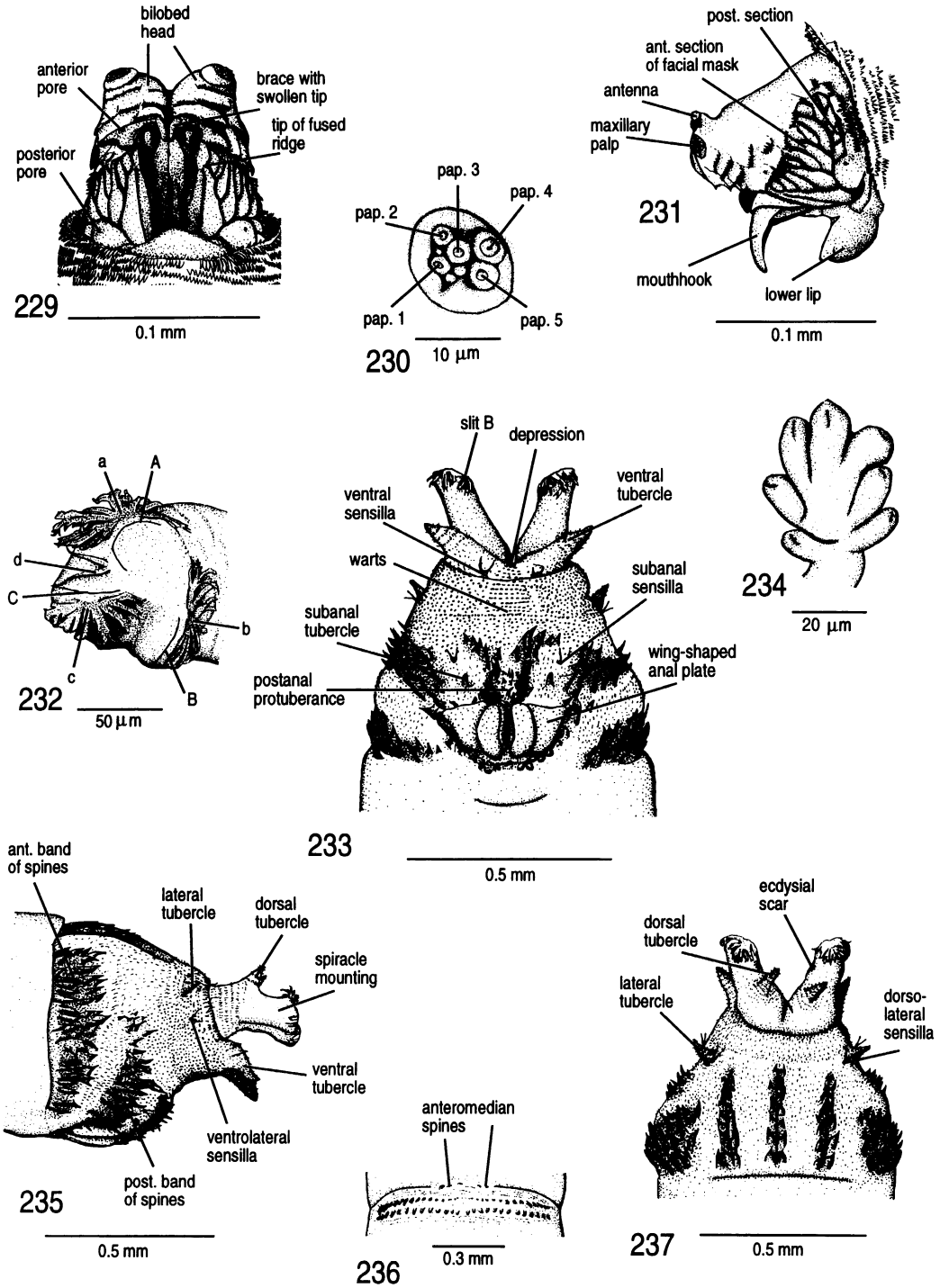


Fig. 229–237. *Sepsis fulgens*. **Cephalic region:** 229: ventral, 231: lateral; **maxillary palp:** 230; **posterior spiracle:** 232; **last segment:** 233: ventral, 235: lateral, 237: dorsal; **anterior spiracle:** 234; **creeping welt:** 236.

are deposited in beetle tunnels. Copulations take place in the vegetation surrounding the dung. Pre- or postcopulatory guarding has not been observed. Van der Goot reported this species from flowers of *Heracleum* (1986a) and *Polygonum* (1986b), Randall et al. (1981) from *Rheum* flowers and van der Goot (1986b) observed participation of *S. flavimana* in a sepsid swarm (see comments under *S. fulgens*).

DISTRIBUTION: Iwasa (1980) and Zuska and Pont (1984) reported *S. flavimana* from Europe, North America, Iran, Central Asia (China), Japan, and the Nearctic region (entire United States). The Far East of Russia can be added to the list.

Sepsis fulgens Meigen, 1826

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 15
Length: 4.39–5.46 mm ($\bar{x}$ = 4.94 0.29; n = 10)
Largest width of body segments: 0.64–0.92 mm ($\bar{x}$ = 0.76 0.11; n = 10)
Width of last segment: 0.57–0.76 mm ($\bar{x}$ = 0.67 0.06; n = 10)

CEPHALIC REGION (fig. 229, ventral view; fig. 231, lateral view): Longer than wide, distinctly bilobed, small lower lip; posterior pore on both lower lobes and anterior pore on one large comb on either side of mouthhooks; brace with tips distinctly enlarged into hook-like projections; 7–8 combs restricted to anterior section of each cephalic lobe, much wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused at tip, ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter intercalary ridges; block next to mouth opening with 3–4 secondary ridges, second and third with 2–3 and fourth with two ridges; posterior section with 2–5 short ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 230): Composed of five compound papillae (pap. 1–5); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 234): 6–7 long lobes arranged along a narrow central axis.

CREEPING WELTS (fig. 236): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 24–28 spines, median ones reduced in size, often of the size of denticles; second row with 22–30 spines; 4–5 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 233, ventral view; fig. 235, lateral view; fig. 237, dorsal view): Not bulbous, with numerous small warts between postanal protuberance and base of ventral tubercles; warts are only sparse on two diagonal lines that run from depression craniad; anal plate moderately large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; with weakly developed, bare subanal tubercles; subanal sensory organ well posterior to each tubercle; pair of large ventral tubercles with ventral sensory organ at each base; with depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band somewhat divided into dorsolateral group of spines and a ventral band; area between rows pubescent; lateral tubercle, associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; except for most posterior portion of last segment, entire dorsal side pubescent; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 232): Flat surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 7–8 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 233); ecdysial scar in dorsomedian position

halfway between dorsal tubercle and spiracular plate (fig. 237).

BIOLOGY: Compared to other species of *Sepsis*, *S. fulgens* is a generalist. It has been reared from pig dung (Papp, 1974b) and cow pats (Hammer, 1941; Papp, 1976; Schulz, 1989; van der Goot, 1986a) where it usually does not reach the abundance exhibited by *S. cynipsea* (but see Schweiger, 1988). Imagines have also been taken from horse dung (Papp, 1974a; Pont, 1979; 1987a, associated with the horse-dung specialist *Zuskamira*), compost (van der Goot, 1986a), pig swill (Pont, 1979), "steaming semiliquid manure" (Minder, 1963), silage (Hennig, 1949), and a sheep carcass (Gregor, 1966). It starts to arrive at cow dung five hours after deposition (Schulz, 1989). Development time in cow dung is about 25 days (23–30 days; Laurence, 1954). At 24°C 13 days are required in the laboratory (personal obs.). Around Moscow, *fulgens* produces about 2–3 generations per year and the imagines hibernate (Minder, 1963). There is an unusually large number of flower visits reported in the literature (Bährmann, 1993: *Cornus mas* and *Prunus spinosa*; Randall et al., 1981 on *Rheum*; van der Goot, 1986a on *Heracleum*, *Veronica*; van der Goot, 1986b on *Polygonum*).

Sepsis fulgens displays a spectacular swarming behavior which has spawned many notes in European entomology journals (summarized in Pont, 1987b). Swarms comprise up to at least 50,000–60,000 individuals and can be stationary for 40–90 days. The sex ratio is usually male biased. No copulations have been observed and the flies are sometimes seen feeding on flowers. Because the ovaries of the females are undeveloped, the spermathecae are empty, and swarming is usually observed in late summer/fall, Pont (1987b) interpreted the swarming as an hibernation phenomenon. In the literature there is some confusion over the composition of the swarms. Pont (1987b) believed that only *S. fulgens* regularly aggregates but van der Goot (1986b) observed an aberrant swarm consisting mainly of *S. cynipsea* and *S. orthocnemis*. Schweiger (1988) found that in some years *S. fulgens* can be the dominant sepsid of cow pats in Germany while it is very rare in other years. It would be interesting to know whether swarming only occurs in dominant years.

DISTRIBUTION: This species is known from most of Europe and Asia Minor (Hennig, 1949; Zuska and Pont, 1984).

Sepsis helvetica Munari, 1985

Locality: Caucasus, North Ossetia, near Alagir (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 7
Length: 4.30–5.71 mm (n = 4)
Largest width of body segments: 0.48–0.60 mm (n = 4)
Width of last segment: 0.61–0.69 mm (n = 4)

CEPHALIC REGION (fig. 238, ventral view; fig. 240, lateral view): Much longer than wide, weakly bilobed, large lower lip; posterior pore on both lower lobes and anterior pore on one large comb on either side of mouthhooks; brace with tips distinctly enlarged into hook-like projections; 6–8 combs restricted to anterior section of each cephalic lobe, combs wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges; the two ridges next to either side of mouth opening fused to each other at tip; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter, intercalary ridges; block next to mouth opening with four secondary ridges, second block with three, third with 2–3 and fourth with two ridges; posterior section with 4–5 short ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 239): Composed of five compound papillae somewhat in two groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); narrow gap between groups, with only a trace of a separating fleshy lobe.

ANTERIOR SPIRACLE (fig. 243): 6–7 moderately long lobes arranged along a central axis.

CREEPING WELTS (fig. 245): First seven segments with rows of spinules laterally and dorsally, eighth only with lateral spinules; ven-

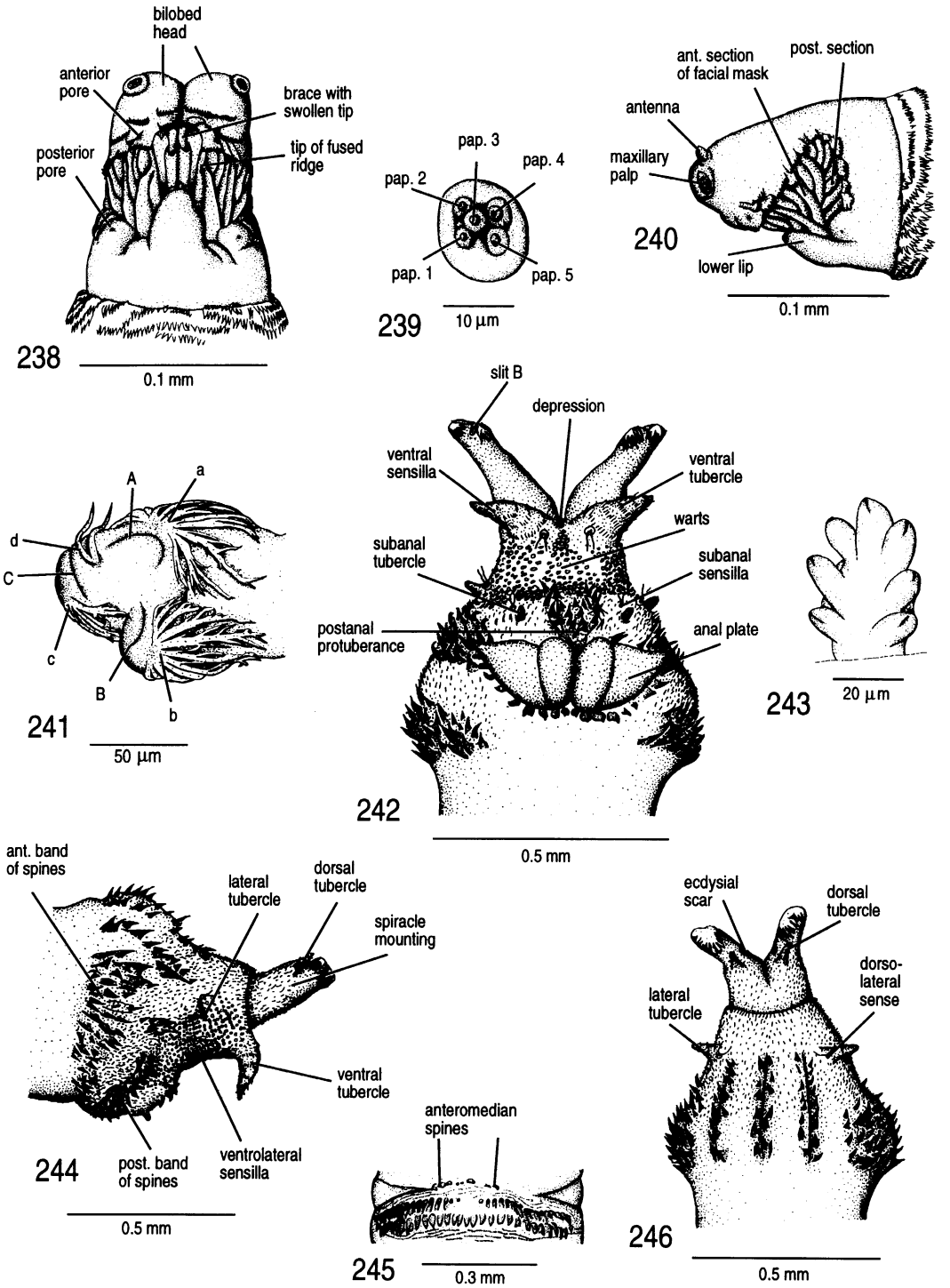


Fig. 238–246. *Sepsis helvetica.* **Cephalic region:** 238: ventral, 240: lateral; **maxillary palp:** 239; **posterior spiracle:** 241; **last segment:** 242: ventral, 244: lateral, 246: dorsal; **anterior spiracle:** 243; **creeping welt:** 245.

trally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 21–29 spines, median ones missing or extremely small; second row with 19–28 spines; 4–8 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 242, ventral view; fig. 244, lateral view; fig. 246, dorsal view): Distinctly bulbous, with numerous warts between postanal protuberance and base of ventral tubercles; warts are only sparse on two diagonal lines that run from depression craniad; anal plate large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate, with weakly developed, bare subanal tubercle; subanal sensory organ well posterior of tubercles; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between rows densely pubescent; lateral tubercle associated with a dorso- and a ventrolateral organ; spiracle mountings rather long, with rather small dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; only posterior half of dorsal aspect of last segment pubescent; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 241): Flat surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 7–9 hairs, unassociated process ("d") with two unbranched hairs; spiracular hairs unusually long and branched; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 242); ecdysial scar in dorsomedian position fairly close to dorsal tubercle (fig. 246).

BIOLOGY: Unknown.

DISTRIBUTION: Currently only known from the locus typicus in Switzerland (Munari, 1985) and the Caucasus Mountains (Georgia).

Sepsis indica (Allosepsis) Wiedemann, 1824

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 4
Length: 6.06–6.12 mm (n = 2)
Largest width of body segments: 0.46–0.56 mm (n = 4)
Width of last segment: 0.38–0.56 mm (n = 3)

CEPHALIC REGION (fig. 247, ventral view; fig. 249, lateral view): Much longer than wide (especially elongated is section anterior to facial mask), cephalic lobes largely adjacent, thus cephalic region only weakly bilobed, small lower lip; posterior pore on both lower lobes and anterior pore on one comb to either side of brace; tips of brace enlarged into a hooklike projection; 7–10 combs restricted to anterior section of cephalic lobes, almost as wide as long with multiple long teeth; combs absent from facial mask, inner side of cephalic lobes, and around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges on either side of mouth opening fused to each other at anterior end; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into five blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary ridges; block next to mouth opening composed of 4–5, second of 3–4, the remaining of 2–3 ridges; posterior section with 7—8 rather long ridges dorsal to lower lobe; no combs posterior to facial mask.

MAXILLA (fig. 248): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 252): 5–6 short and stout lobes arranged along a central axis.

CREEPING WELTS (fig. 254): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 17–24 spines, median ones reduced in size; second row with 23–29 spines; 4–6 anterome-

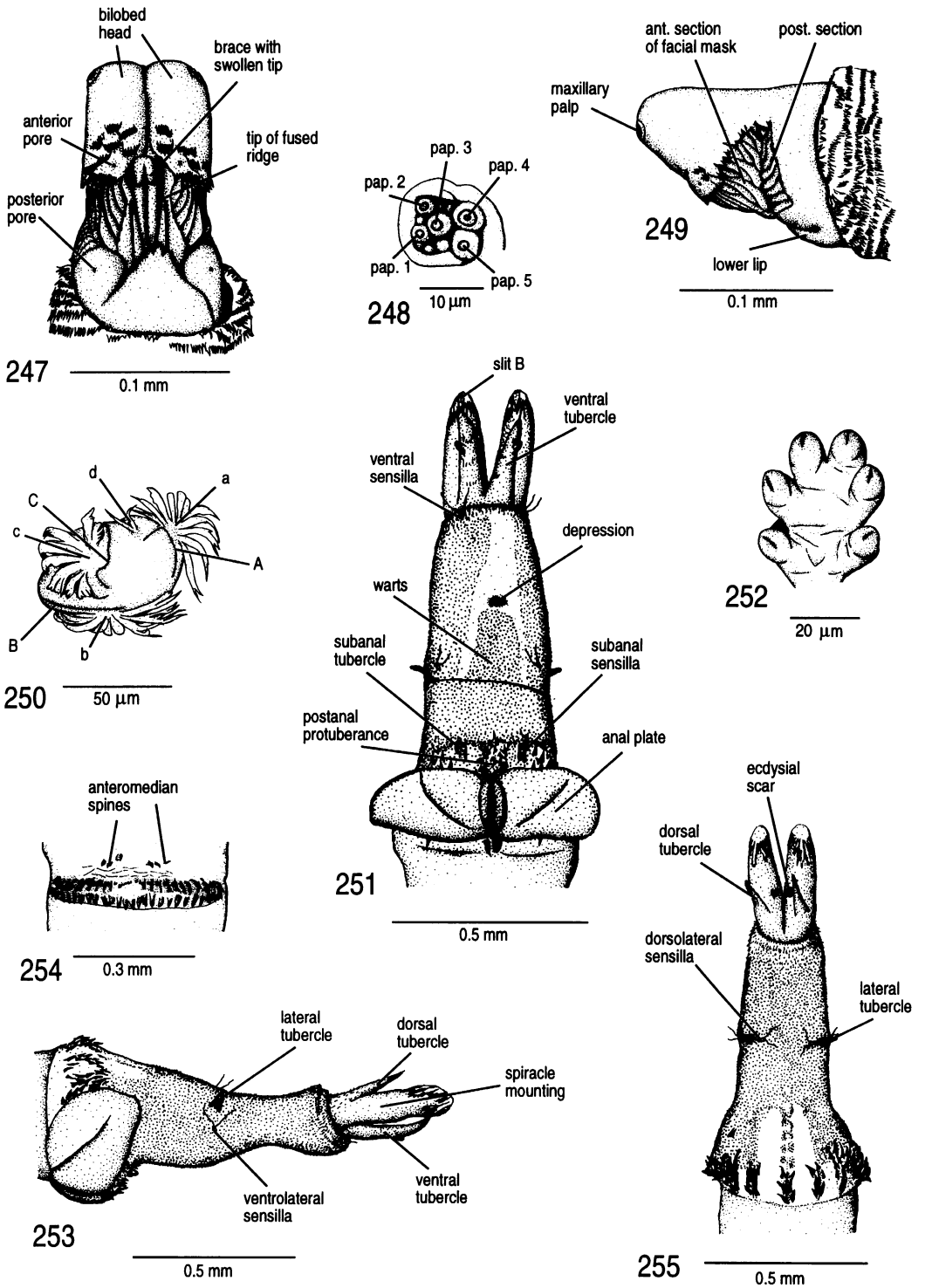


Fig. 247–255. *Sepsis indica.* **Cephalic region:** 247: ventral, 249: lateral; **maxillary palp:** 248; **posterior spiracle:** 250; **last segment:** 251: ventral, 253: lateral, 255: dorsal; **anterior spiracle:** 252; **creeping welt:** 254.

dian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 251, ventral view; fig. 253, lateral view; fig. 255, dorsal view): Anterior section slightly bulbous, posterior section greatly elongated; numerous small warts between postanal protuberance and base of ventral tubercles as well as most of dorsal and lateral aspects of last segment; warts are only missing in an area posterior to a depression and on two diagonal lines from depression craniad; anal plate very large, rounded laterally with diagonal fold; postanal protuberance very small; few preanal spines anterior to anal plate; pair of bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of very long ventral tubercles with small projection at 3/4 of their length; ventral tubercles associated with a ventral sensory organ at each base; due to large anal plate, lateral bands of spines undeveloped, only represented by field of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings long, with long, slender, dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a short row of spines on either side; pattern of spines is regular, however, spines replaced by groups of small warts in posterior section of rows; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 250): Bulging surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–7 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" distinctly arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 251); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 255).

BIOLOGY: Iwasa (1980) reported this species on cow dung in Japanese pastures.

DISTRIBUTION: Iwasa (1980; 1987) found *S. indica* from Taiwan and Japan but it is also known from the Far East of Russia (see above). Duda (1925, 1926) mentioned specimens from Sri Lanka.

Sepsis kaszabi Soós, 1972

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 2
Length: 4.55–4.80 mm (n = 2)
Largest width of body segments: 0.61–0.64 mm (n = 2)
Width of last segment: 0.57–0.60 mm (n = 2)

CEPHALIC REGION (fig. 256, ventral view; fig. 258, lateral view): Much longer than wide, monolobed; large lower lip; anterior pore on one large combs to either side of brace and posterior pore on both elongated lower lobes; brace with tips enlarged into hooklike projections; combs restricted to anterior section of cephalic lobes, none on facial mask; combs arranged in horizontal rows, usually wider than long with multiple long teeth; no combs around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening large, and fused to each other at anterior end; ridges somewhat organized into anterior and posterior sections separated by indistinct midfurrow; anterior section organized into three blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsolateral ridges of preceding block, and intercalary shorter ridges; first block next to mouth opening composed of four, remaining ones of two ridges; posterior section with three short ridges dorsal of elongated lower lobe; several combs around entire facial mask including posterior margin.

MAXILLA (fig. 257): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

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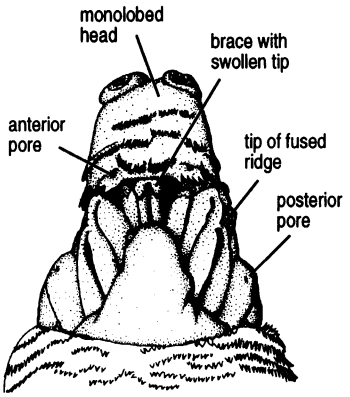
Fig. 256–264. *Sepsis kaszabi*. **Cephalic region:** 256: ventral, 258: lateral; **maxillary palp:** 257; **posterior spiracle:** 259; **last segment:** 260: ventral, 262: lateral, 264: dorsal; **anterior spiracle:** 261; **creeping welt:** 263.



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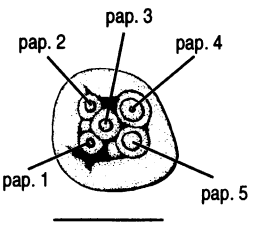

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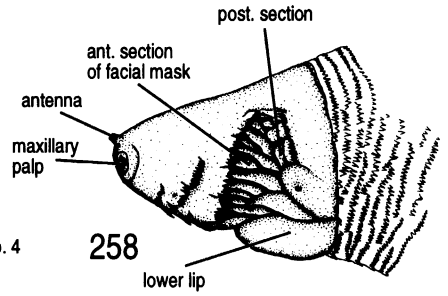

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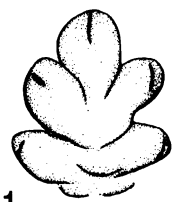

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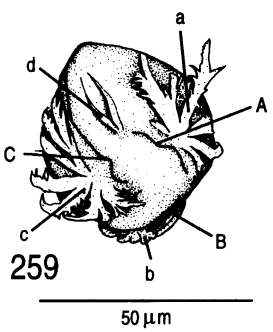

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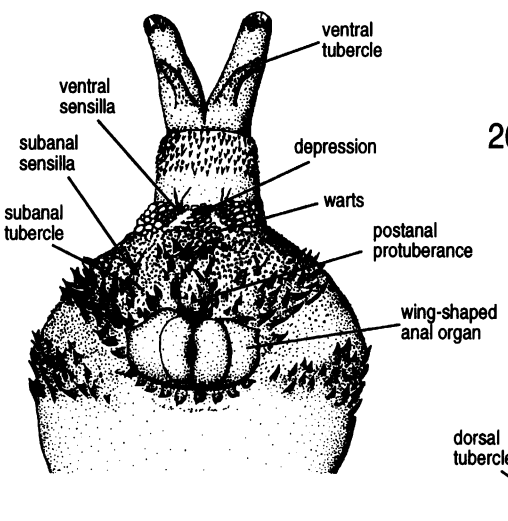

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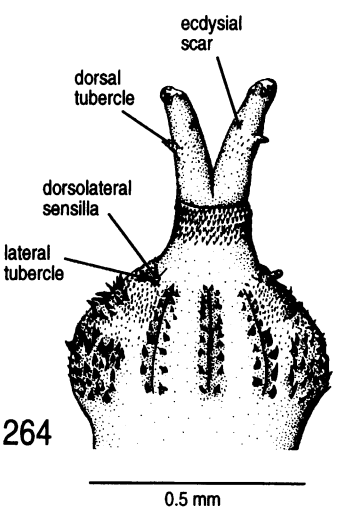

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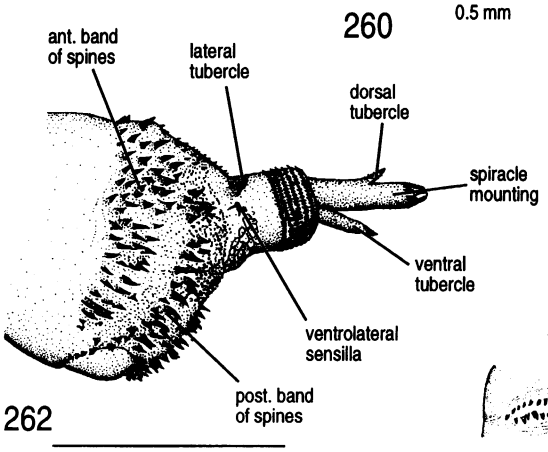

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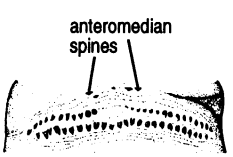


263

ANTERIOR SPIRACLE (fig. 261): Consisting of 5 lobes along a narrow central axis.

CREEPING WELTS (fig. 263): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 20–24 spines, median ones small or missing; second row with about 19–25 spines; 4–5 anterior spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 260, ventral view; fig. 262, lateral view; fig. 264, dorsal view): Distinctly bulbous at anterior end, with numerous hairs and warts; anal plate wing-shaped, inner and outer lobes flattened; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of small ventral tubercles at base of spiracle mountings; compared to most sepsids, area between bases of ventral tubercles and depression greatly expanded, thus ventral sensory organs which are usually positioned at base of each ventral tubercle now in a more anterior position to either side of depression; hairs posterior to postanal protuberance transformed into warts; warts particularly large in area around depression which also strongly constricted; spines arranged into an anterior and a posterior band; area between bands pubescent; lateral tubercle with a dorso- and a ventrolateral sensory organ; spiracle mountings very long, with small, slender dorsal tubercle; dorsal surface of last segment with three longitudinal grooves, each bordered by a row of spines on either side; areas between grooves not pubescent, hairs restricted to posterior half of area between lateral two grooves and lateral field of spines.

POSTERIOR SPIRACULAR DISC (fig. 259): Bulging spiracular disc with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–6 hairs, unassociated process ("d") always with only two hairs; opening "C" more or less straight, extending beyond spiracular plate, slit "A" weakly arched toward the root of process "d"; slit "B" extending onto ventral side of spiracle mounting; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 264).

BIOLOGY: Ozerov (1989) collected larvae of this species in cow dung, and Papp (1976) found adults on yak dung in Mongolia.

DISTRIBUTION: According to Zuska and Pont (1984) this species is only known from Asia (Mongolia, Far East of Russia).

Sepsis lateralis Wiedemann, 1830

Locality: Honde-Valley (Eastern Highlands, Zimbabwe), coll. R. Meier
Specimens examined: 16
Length: 5.62–6.48 mm ($\bar{x}$ = 6.14 0.82; n = 10); 3.5–4.5 mm (Hafez, 1939)
Largest width of body segments: 0.71–0.97 mm ($\bar{x}$ = 0.82 0.07; n = 10)
Width of last segment: 0.71–1.06 mm ($\bar{x}$ = 0.92 0.07; n = 10)

All three larval instars and the eggs of *S. lateralis* were previously described by Hafez (1939).

CEPHALIC REGION (fig. 265, ventral view; fig. 267, lateral view): Longer than wide, distinctly bilobed, moderately large lower lip; posterior pore on both lower lobes and anterior pore on one large comb on either side of mouthhooks; brace with tips distinctly enlarged into hooklike projections; 11–12 combs restricted to anterior section of each cephalic lobe, combs much wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a long ridge converging onto most dorsal ridge of preceding block, and shorter, intercalary ridges; block next to mouth opening with 4–5 ridges, second block with four, third with three and fourth with 2–3 ridges; posterior section with 4–6 ridges dorsal to lower lobe; numerous combs posterior to facial mask. According to Hafez (1939) "this segment is produced dorsally in middle into six hooklike structures which are short and thick." I could not find these structures and cannot imagine what they could have been.

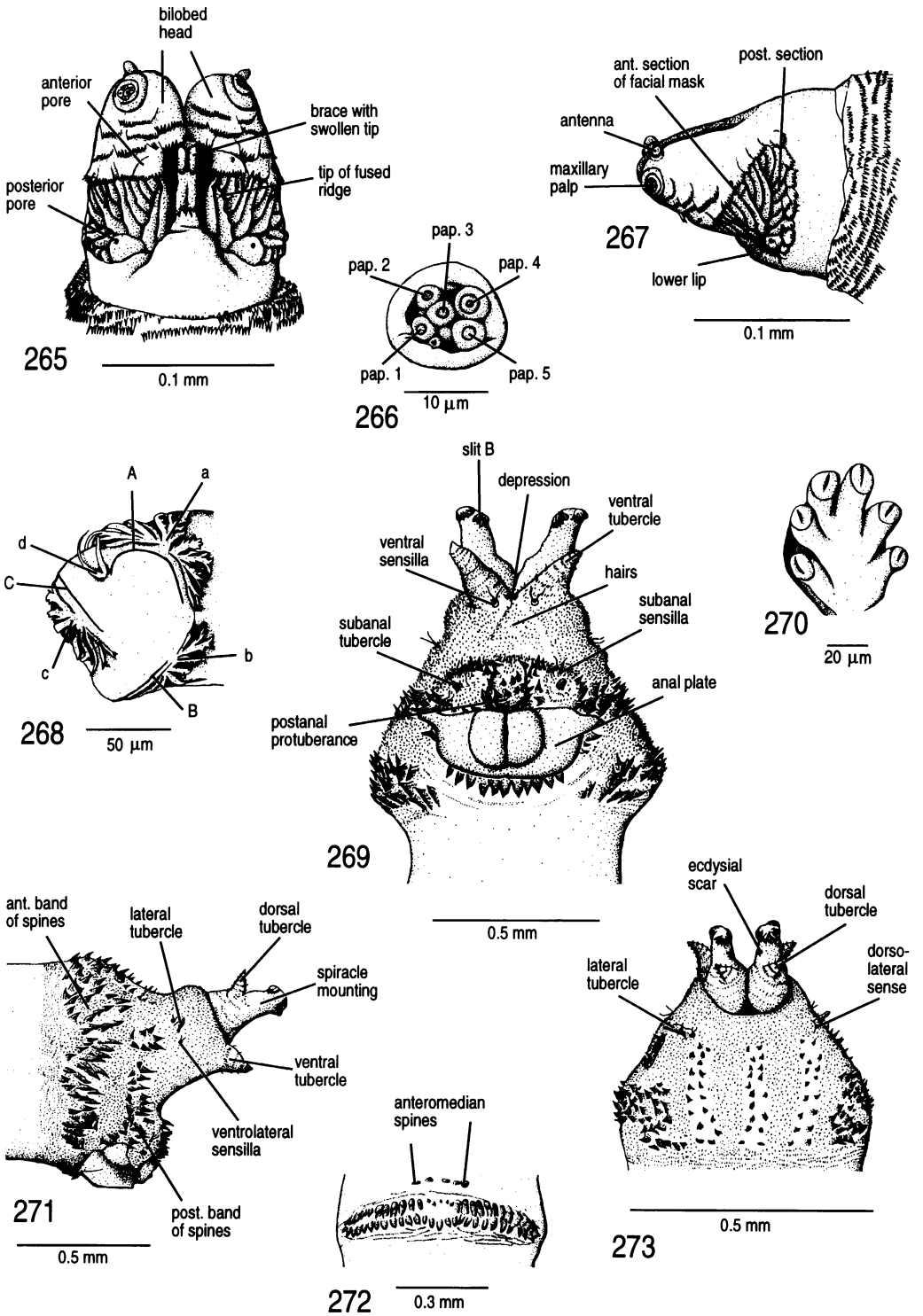


Fig. 265–273. *Sepsis lateralis*. **Cephalic region:** 265: ventral, 267: lateral; **maxillary palp:** 266; **posterior spiracle:** 268; **last segment:** 269: ventral, 271: lateral, 273: dorsal; **anterior spiracle:** 270; **creeping welt:** 272.

Hafez (1939) illustrated cephalopharyngeal skeleton.

MAXILLA (fig. 266): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 270): 6–8 moderately long lobes arranged along a central axis (Hafez, 1939: four lobes).

CREEPING WELTS (fig. 272): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 25–29 spines, median ones missing or reduced in size; second row with 21–27 spines; 3–5 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 269, ventral view; fig. 271, lateral view; fig. 273, dorsal view): Distinctly bulbous; unlike most other *Sepsis*, with hairs instead of warts between postanal protuberance and base of ventral tubercles (see also Hafez, 1939); pubescence sparse only along two diagonal lines that run from depression craniad; anal plate large, wing-shaped, laterally pointed and drawn out; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate, with weakly developed, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands densely pubescent; pubescence extending craniad from anterior band of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with moderately large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of very small spines on either side; entire dorsal aspect of last segment densely pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 268): Flat surface with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 6–9 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 269); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 273). Hafez (1939) described only three processes of spiracular hairs. He must have overlooked the fourth ("d") which consists of only two hairs.

BIOLOGY: *Sepsis lateralis* is a generalist breeding on several different substrates. It has been reared from cow dung (Hafez, 1939; 1947; Iwasa, 1980; personal obs.), chicken dung (Disney, 1973), ostrich dung (personal obs.), and even a dead locust (Deeming, 1969). The females deposit their eggs readily in cow dung. Fresh substrate is preferred. At 26–28°C development takes only six to seven days. Hafez (1939) stated that in the presence of cow dung the species avoids camel and horse feces and is less abundant in pig dung. It can be extremely common on fresh cow dung. There is no precopulatory guarding.

DISTRIBUTION: This species is extremely widespread in the Palearctic, Afrotropical, Australian (New Guinea) and Oriental regions (Iwasa, 1987; 1989; Zuska and Pont, 1984). It has also colonized numerous islands (e.g., Baez, 1982: Canary Islands).

Sepsis latiforceps Duda, 1926

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 2
Length: 5.58–5.70 mm (n = 2)
Largest width of body segments: 0.73–0.76 mm (n = 2)
Width of last segment: 0.75–0.77 mm (n = 2)

CEPHALIC REGION (fig. 274, ventral view; fig. 276, lateral view): Longer than wide, distinctly bilobed, moderately large lower lip; posterior pore on both lower lobes and anterior pore on one comb to either side of mouthhooks; brace with tips distinctly enlarged into narrow hooklike projections; 10 to 12 combs restricted to anterior section of each cephalic lobe, combs wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around

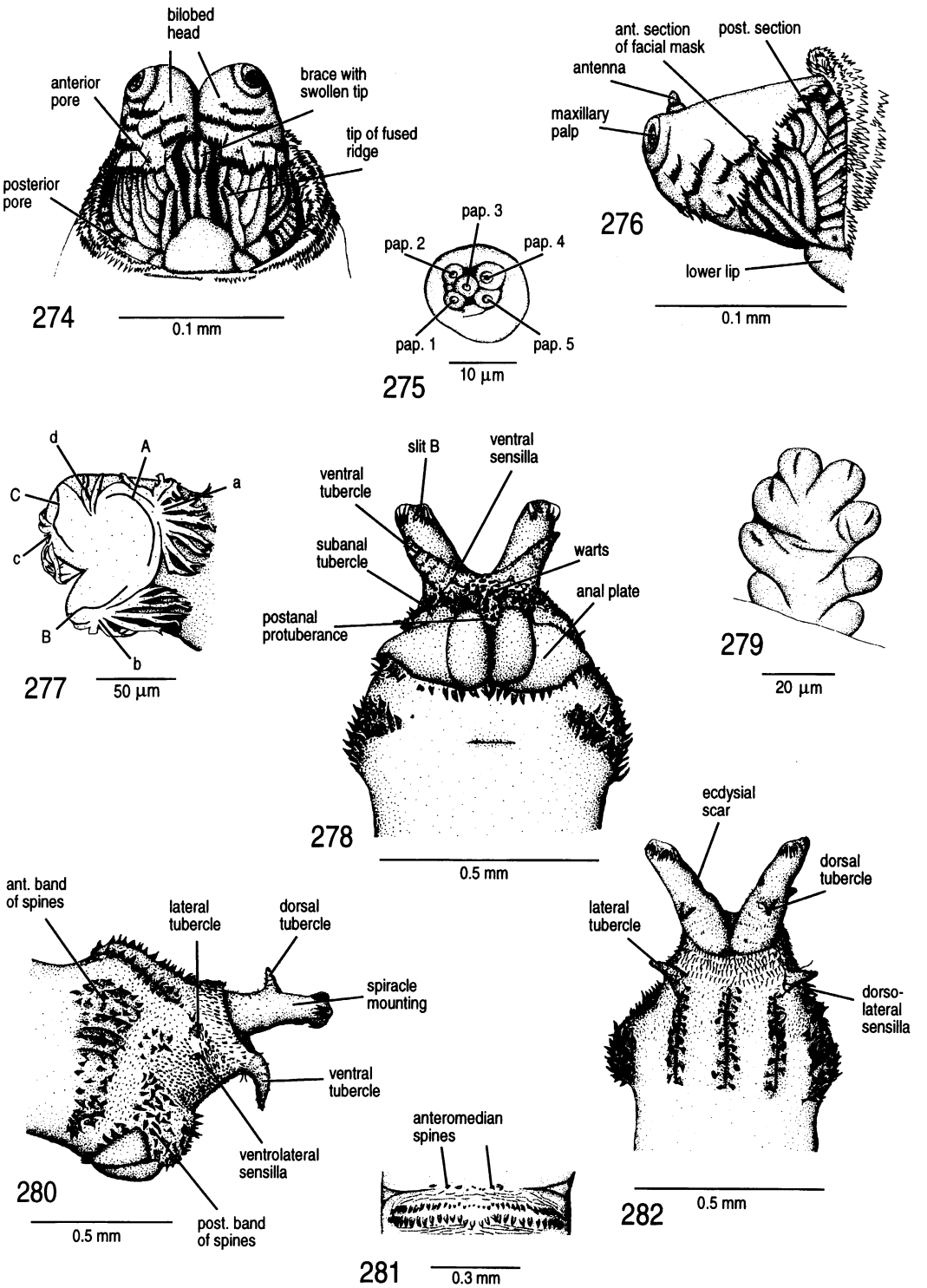


Fig. 274–282. *Sepsis latiforceps*. **Cephalic region:** 274: ventral, 276: lateral; **maxillary palp:** 275; **posterior spiracle:** 277; **last segment:** 278: ventral, 280: lateral, 282: dorsal; **anterior spiracle:** 279; **creeping welt:** 281.

maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges on either side of mouth opening fused to each other at tips; ridges somewhat organized into anterior and posterior sections somewhat separated by mid-furrow; anterior section organized into three blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary intercalary ridges; first two blocks next to mouth opening with four ridges, third block with 3–4 ridges; posterior section with ten rather long ridges dorsal to lower lobe.

MAXILLA (fig. 275): Composed of five compound papillae; four papillae (pap. 1–3, 5) consisting of two superimposed lobes, one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 279): 7–8 moderately long lobes arranged along a central axis.

CREEPING WELTS (fig. 281): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of rows of spinules; remaining six welts ventrally with two long rows of reclinate spines and short additional rows of spinules anterior and posterior to spines; first row of spines with 26–30 spines, median ones very small; second row with 22–28 spines; 4–6 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 278, ventral view; fig. 280, lateral view; fig. 282, dorsal view): Distinctly bulbous, with numerous warts between postanal protuberance and base of ventral tubercles; warts are only missing on two diagonal lines that run from depression craniad; anal plate large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, pair of bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands pubescent; lateral tubercle associated with a dorso- and ventrolateral sensory organ; spiracle mountings long, with long dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; only posterior half of dorsal aspect of last segment pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 277): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–9 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 278); hairs unusually long and branched; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 282).

BIOLOGY: The only rearing record is provided by Ozerov (1989) who found larvae in cow dung.

DISTRIBUTION: This species is known from the Palearctic and Oriental regions of Asia (China, Taiwan and Japan; Zuska and Pont, 1984; Far East of Russia, see above).

Sepsis monostigma Thomson, 1869

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 8
Length: 4.56–5.62 mm ($\bar{x}$ = 4.94 0.35; n = 6)
Largest width of body segments: 0.50–0.73 mm ($\bar{x}$ = 0.61 0.07; n = 6)
Width of last segment: 0.54–0.73 mm ($\bar{x}$ = 0.63 0.08; n = 6)

CEPHALIC REGION (fig. 283, ventral view; fig. 285, lateral view): Longer than wide, distinctly bilobed, moderately large lower lip; posterior pore on both lower lobes and anterior pore on one large comb to either side of mouthhooks; brace with tips distinctly enlarged into hooklike projections; 6–8 combs restricted to anterior section of each cephalic lobe, combs wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip; ridges somewhat organized into anterior and posterior sections separated by mid-furrow; anterior section organized into three blocks

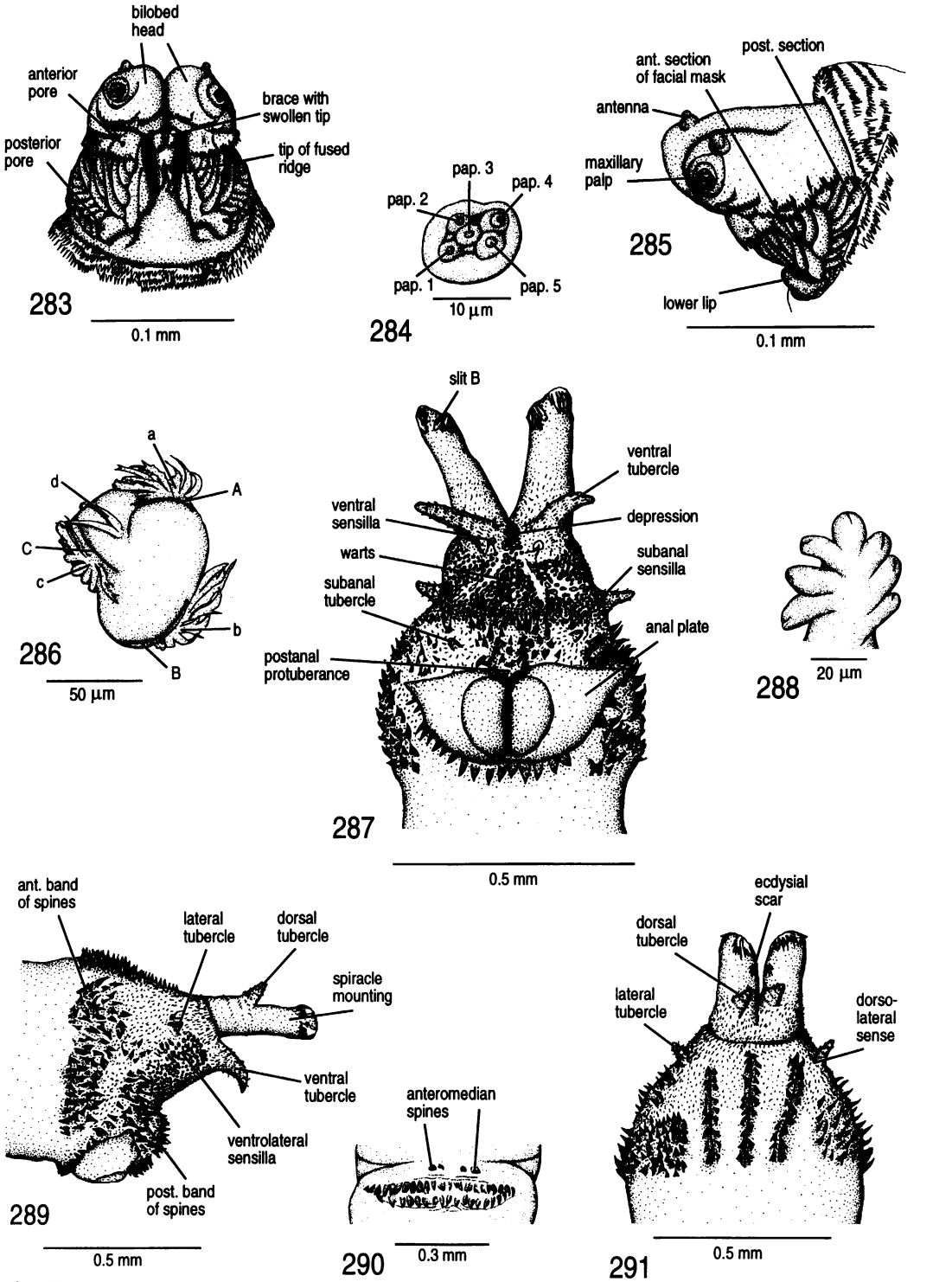


Fig. 283–291. *Sepsis monostigma.* **Cephalic region:** 283: ventral, 285: lateral; **maxillary palp:** 284; **posterior spiracle:** 286; **last segment:** 287: ventral, 289: lateral, 291: dorsal; **anterior spiracle:** 288; **creeping welt:** 290.

of ridges, whereby each block is formed by a large primary ridge converging onto most dorsal ridge of preceding block, and shorter, intercalary ridges; block next to mouth opening with 4–6 secondary ridges, second and third block with 3–4 ridges; posterior section with 8–10 long ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 284): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 288): 6–7 moderately long lobes arranged along a central axis.

CREEPING WELTS (fig. 290): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 23–30 spines, median ones missing or reduced in size; second row with 18–23 spines; 2–4 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 287, ventral view; fig. 289, lateral view; fig. 291, dorsal view): Moderately bulbous, with warts between postanal protuberance and base of ventral tubercles; warts are only missing on two diagonal lines that run from depression craniad; anal plate large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of bare subanal tubercle; each tubercle with subanal sensory organ well posterior to tip; pair of large ventral tubercles with ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral groups of spines and a ventral band; area between bands pubescent; lateral tubercles associated with a dorso- and a ventrolateral sensory organ; spiracle mountings rather long, with moderately large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; only posterior half of dorsal aspect of last segment pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 286): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 6–9 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 287); ecdysial scar in dorsomedian position halfway between spiracular plate and dorsal tubercle (fig. 291).

BIOLOGY: *Sepsis monostigma* deposits eggs in fresh cow dung in shaded and moist locations (Ozerov, 1989). Ozerov collected larvae from this substrate and Nishijma and Iwasa (1979) reared *S. monostigma* from brown bear dung.

DISTRIBUTION: This species is distributed throughout the Oriental and East Palearctic regions. It also occurs in Japan (Iwasa, 1980; 1987).

Sepsis neglecta Ozerov, 1986

Locality: Turkmenistan, 40 km W Ashkhabad, coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 2
Length: 4.66–4.98 mm (n = 2)
Largest width of body segments: 0.71–0.72 mm (n = 2)
Width of last segment: 0.70–0.71 mm (n = 2)

CEPHALIC REGION (fig. 292, ventral view; fig. 294, lateral view): Much longer than wide, weakly bilobed because cephalic lobes are largely adjacent, moderately large lower lip; posterior pore on both bulbous lower lobes and anterior pore on one large comb to either side of mouthhooks; brace with tips distinctly enlarged into hooklike projections; 6–8 combs restricted to anterior section of each cephalic lobe; combs wider than long with multiple small teeth; no combs on facial mask, on the inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter, in-

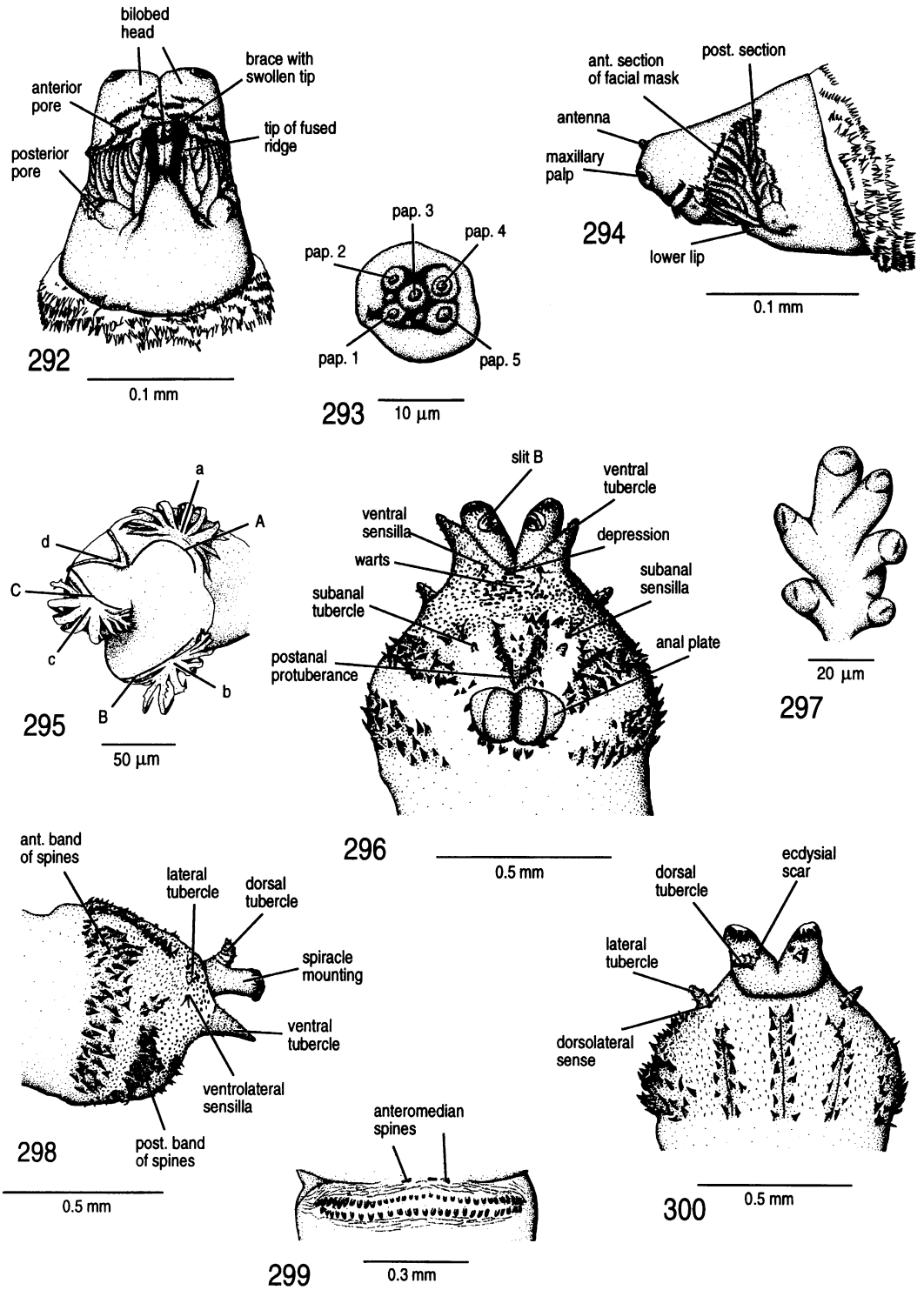


Fig. 292–300. *Sepsis neglecta.* **Cephalic region:** 292: ventral, 294: lateral; **maxillary palp:** 293; **posterior spiracle:** 295; **last segment:** 296: ventral, 298: lateral, 300: dorsal; **anterior spiracle:** 297; **creeping welt:** 299.

tercalary ridges; block next to mouth opening with 4–5 ridges, second and third block with 3–5, fourth with three ridges; posterior section with 5–7 short ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 293): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 297): 5–6 moderately long lobes arranged along a central axis.

CREEPING WELTS (fig. 299): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 19–34 spines, median ones somewhat reduced in size; second row with 19–27 spines; 3–4 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 296, ventral view; fig. 298, lateral view; fig. 300, dorsal view): Moderately bulbous, with moderate number of warts between postanal protuberance and base of ventral tubercles; warts are only missing on two diagonal lines that run from depression craniad; anal plate very small, wing-shaped, lateral lobe small and rounded; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercle; subanal sensory organ well posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral groups of spines and a ventral band; area between bands densely pubescent; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; entire dorsal aspect of last segment pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 295): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 6–9 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" bent toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 296); ecdysial scar in dorsomedian position halfway between spiracular plate and dorsal tubercle (fig. 300).

BIOLOGY: Unknown.

DISTRIBUTION: Ozerov (1986b) described this species from Atbasar in Kazakhstan but it is also known from Turkmenistan (see above).

Sepsis neocynipsea Melander and Spuler, 1917

Locality: Ithaca (New York, USA), coll. R. Meier
Specimens examined: 10
Length: 5.60–6.89 mm ($\bar{x}$ = 6.19 0.38; n = 10)
Largest width of body segments: 0.80–1.06 mm ($\bar{x}$ = 0.910.09; n = 9)
Width of last segment: 0.85–1.30 mm ($\bar{x}$ = 0.930.10; n = 10)

Mangan (1977) provided a sketch of a ventral view of the last segment which was apparently intended to be a part of his master's thesis on the morphology of sepsid immatures. However, the thesis mentioned in the acknowledgments was never written (Foote, in litt.).

CEPHALIC REGION (fig. 301, ventral view; fig. 303, lateral view): Much longer than wide, distinctly bilobed, small lower lip; posterior pore on both lower lobes and anterior pore on one large comb to either side of mouthhooks; brace with tips enlarged into hooklike projections (distorted on figure due to protruding mouthhooks); about 11 combs restricted to anterior section of each cephalic lobe, combs wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at anterior end; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into six blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter, inter-

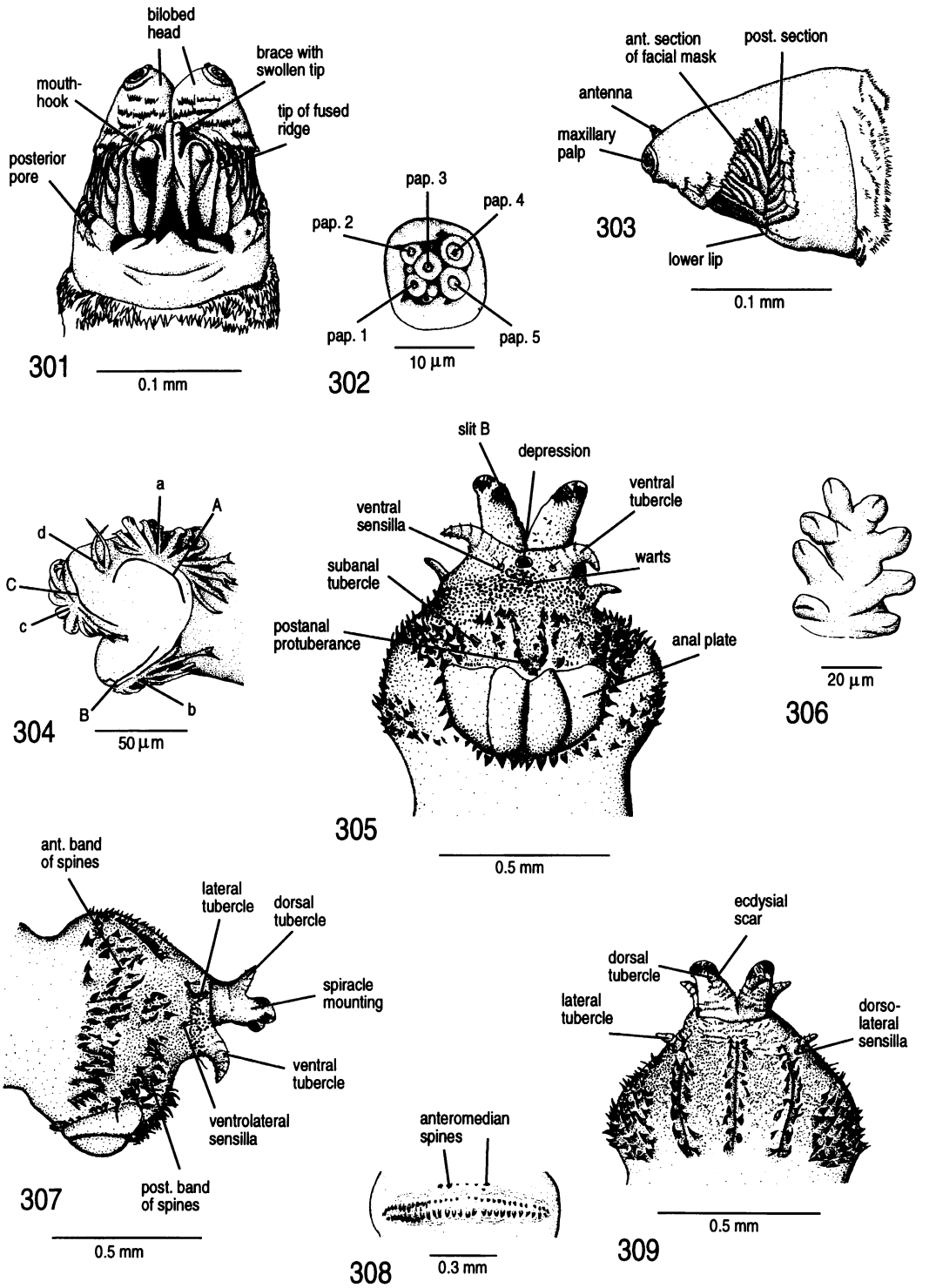


Fig. 301–309. *Sepsis neocynipsea*. **Cephalic region:** 301: ventral, 303: lateral; **maxillary palp:** 302; **posterior spiracle:** 304; **last segment:** 305: ventral, 307: lateral, 309: dorsal; **anterior spiracle:** 306; **creeping welt:** 308.

calary ridges; block next to mouth opening composed of 4–5 ridges, next three of 3–4 and the remaining of two ridges; posterior section with ten ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 302): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 306): 7–8 moderately long lobes arranged along a central axis.

CREEPING WELTS (fig. 308): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 30–34 spines, median ones reduced in size; second row with 21–29 spines; 4–6 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 305, ventral view; fig. 307, lateral view; fig. 309, dorsal view): Distinctly bulbous, with numerous warts between postanal protuberance and base of ventral tubercles; anal plate large, wing-shaped, laterally somewhat pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercle, subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands densely pubescent; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings rather short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; entire dorsal integument of last segment densely pubescent; hairs of sensory organ long.

POSTERIOR SPIRACULAR DISC (fig. 304): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 7–11 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 305); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 309). Mangan (1977) correctly observed that one spiracular slit extends far beyond the spiracular plate.

BIOLOGY: *Sepsis neocynipsea* is the most common sepsid in North America but the species is restricted to mountainous regions in middle Europe (Hennig, 1949; Randall et al., 1981; Püchel, personal commun.). Immatures have frequently been found in cow dung (Blume, 1970; Coffey, 1966; Duda 1925; Iwasa, 1980; Mangan, 1977; Valiela, 1969; 1974, Wharton and Moon, 1979; personal obs.). Larvae have also been reported from dung of horses (Coffey, 1966), sheep (Coffey, 1966), mink (Coffey, 1966), pig (Coffey, 1966; Iwasa, 1980), fox (Iwasa, 1980), and brown bear (Iwasa, 1980). Imagines can also occur on small mammal feces (Mangan 1977), sheep dung (Randall, et al., 1981), horse dung (Papp, 1976), and carrion (Mangan, 1977; Reed, 1958). In North America it is one of the first sepsids to appear on freshly deposited cow pats. It can be very common. The males display neither post- nor precopulatory guarding. Based on the form of the surstylus and a bristle character of the legs, Hennig placed *S. neocynipsea* and *S. cynipsea* in a monophyletic species group. Both species are particularly common visitors of fresh cow pats. However, in Europe where they are sympatric, *S. neocynipsea* is usually rare at low elevations. This may be the result of competitive exclusion. A similar phenomenon is observed for *S. biflexuosa* and *S. flavimana*. Both belong to Hennig's *S. flavimana* species group and breed in older cow pats. They are sympatric in Europe where *S. biflexuosa* is very rare while it is very common in the USA where *S. flavimana* is missing.

DISTRIBUTION: *Sepsis cynipsea* has a Holarctic distribution (Iwasa, 1980: Japan; 1989; Zuska and Pont, 1984). Mangan (1977) listed American localities. The southern most point from which *S. neocynipsea* is known is Mexico City.

Sepsis orthocnemis Frey, 1908

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 22
Length: 4.35–5.04 mm ($\bar{x}$ = 4.68 0.25; n = 10)
Largest width of body segments: 0.65–1.01 mm ($\bar{x}$ = 0.77 0.11; n = 10)
Width of last segment: 0.67–0.82 mm ($\bar{x}$ = 0.74 0.05; n = 10)

CEPHALIC REGION (fig. 310, ventral view; fig. 312, lateral view): Much longer than wide, distinctly bilobed, with rather narrow lower lip; posterior pore on both lower lobes and anterior pore on one large comb on either side of mouthhooks; brace with tips enlarged into hooklike projections; 8–9 combs restricted to anterior section of each cephalic lobe; combs wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip; ridges somewhat organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary, shorter and intercalary ridges; block next to mouth opening with 3–4 secondary ridges, second row with three, third and fourth with 2–3; posterior section with 3–4 short ridges dorsal to lower lobe; combs posterior to facial mask.

MAXILLA (fig. 311): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 315): 3–6 (normally 5–6) moderately long lobes arranged along a short central axis.

CREEPING WELTS (fig. 317): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 20–27 spines, median ones considerably reduced in size, denticle-size; second row with 20–26 spines; 4–5 anteromedian spines forming a short anterior row; spines largely fused to body wall with rather blunt tips. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 314, ventral view; fig. 316, lateral view; fig. 318: dorsal view; fig. 467: detail): Moderately bulbous, with numerous warts between postanal protuberance and bases of ventral tubercles; warts are only sparse on two diagonal lines that run from depression craniad; anal plate moderately large, wing-shaped, laterally pointed, outer lobe somewhat flattened and weakly developed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercles; subanal sensory organ well posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands densely pubescent; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings long, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; only posterior half of dorsal aspect of last segment pubescent; sensory organs with long hairs.

POSTERIOR SPIRACULAR DISC (fig. 313): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 314); ecdysial scar in dorsomedian position halfway between spiracular plate and dorsal tubercle (fig. 318).

BIOLOGY: *Sepsis orthocnemis* breeds in cow dung (Hammer, 1941; Laurence, 1954; Papp, 1976; Schweiger, 1988; Schulz, 1989). Schulz (1989) collected this species on pats that were at least one day old. Development times are reported by several authors (Hammer, 1941: less than 24 days; Laurence, 1954: 22–24 days; Pont, 1979: midsummer: 25 days) and in the laboratory at 24°C 12–14 days (personal obs.).

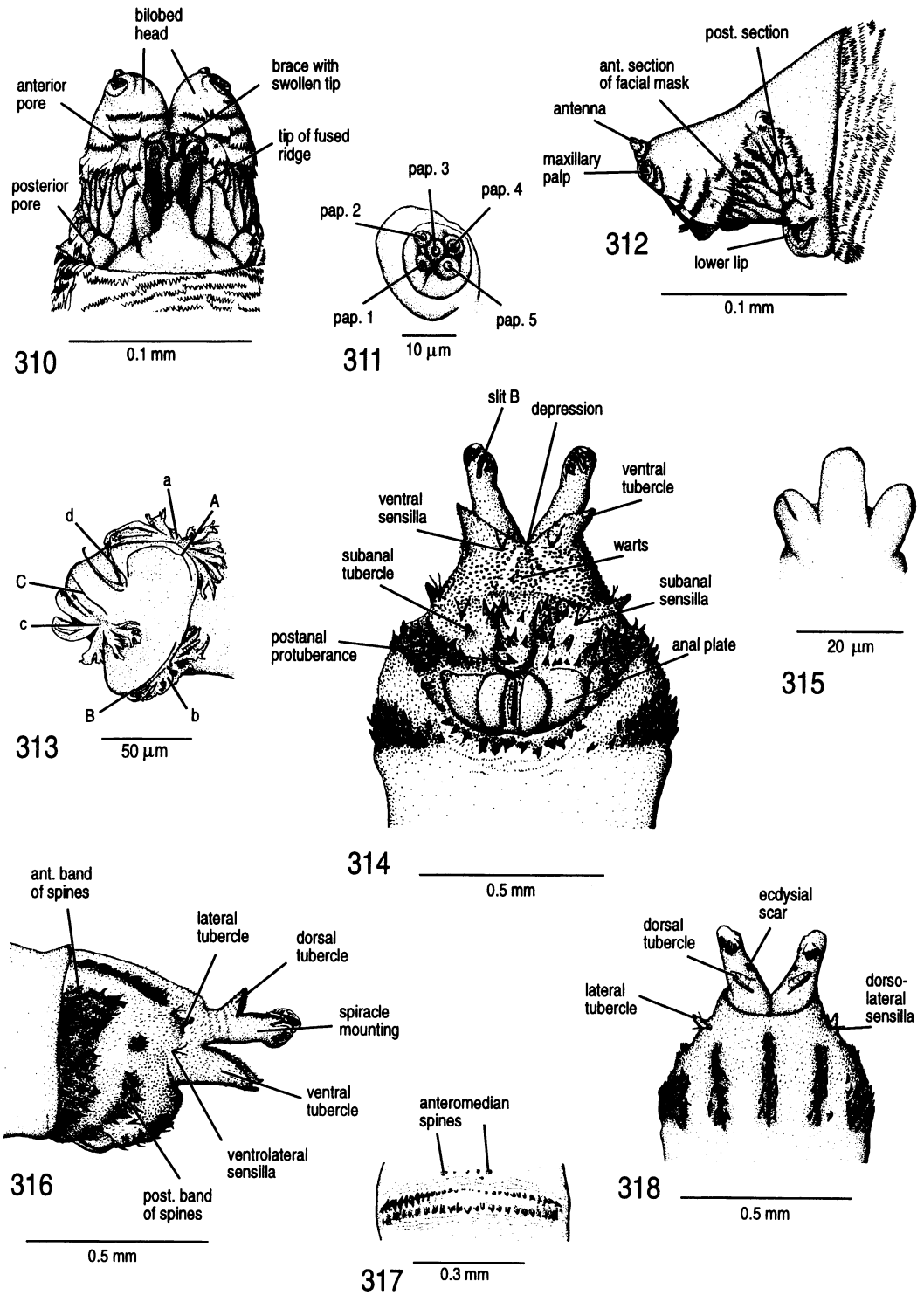


Fig. 310–318. *Sepsis orthocnemis*. **Cephalic region:** 310: ventral, 312: lateral; **maxillary palp:** 311; **posterior spiracle:** 313; **last segment:** 314: ventral, 316: lateral, 318: dorsal; **anterior spiracle:** 315; **creeping welt:** 317.

Sepsis orthocnemis has also been collected from human excrement (Gregor, 1966; personal obs.), sheep dung (Randall et al., 1981), and probably horse dung (Pont, 1987: association with the horse-dung specialist *Zuskamira*). Van der Goot (1986a, 1986b) reported visits at *Heracleum* and *Polygonum*-flowers and Randall et al. (1981) reported visits at *Rheum* flowers. On one occasion this species participated in the formation of a sepsid swarm (see *S. fulgens*; van der Goot, 1986b). As Pont (1979) found adults in December (England), *S. orthocnemis* hibernates as imagines.

DISTRIBUTION: This species can be found in all of the Palearctic region including North Africa and Afghanistan.

Sepsis punctum (Fabricius, 1794)

Locality: Berlin (Germany), coll. R. Meier; Tucson (Arizona, USA), coll. K. Schulz, University of Arizona
Specimens examined: 23
Length: 3.27–5.66 mm ($\bar{x}$ = 4.540.68; n = 10); 5 mm (Schumann, 1962)
Largest width of body segments: 0.49–0.84 mm ($\bar{x}$ = 0.70 0.10; n = 10)
Width of last segment: 0.54–0.82 mm ($\bar{x}$ = 0.68 0.08; n = 10)

All three larval instars and the eggs of *S. punctum* are described and depicted in Schumann (1962). Some figures of the third instar are also provided by Mangan (1977).

CEPHALIC REGION (fig. 319, ventral view; fig. 321, lateral view): Longer than wide, distinctly bilobed, moderately large lower lip; posterior pore on both lower lobes and anterior pore on one large comb on either side of mouthhooks; brace with tips enlarged into hooklike projections; 9–15 combs restricted to anterior section of each cephalic lobe; combs much wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tip; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into four blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary, intercalary ridges; block next to mouth opening with 5–6 secondary ridges, second row with 3–5, third and fourth with 3–4; posterior section with 9–13 ridges dorsal to lower lobe; few combs posterior to facial mask. The cephalopharyngeal skeleton is depicted in Schumann (1962).

MAXILLA (fig. 320): Composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); narrow gap between groups.

ANTERIOR SPIRACLE (fig. 324): 5–7 moderately long lobes arranged along a short central axis (fig. 42 in Schumann, 1962: 6 lobes; fig. in Mangan, 1977: 7 lobes).

CREEPING WELTS (fig. 326): First seven segments with rows of spinules laterally and dorsally; eighth with only lateral spinules; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 27–35 spines, median ones missing or reduced in size; second row with 22–30 spines; four anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 323, ventral view; fig. 325, lateral view; fig. 327, dorsal view): Bulbous, with numerous warts between postanal protuberance and base of ventral tubercles; warts are only sparse on two diagonal lines that run from depression craniad; anal plate moderately large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercles; subanal sensory organ well posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral groups of spines and a ventral band; area between bands densely pubescent; rather large lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings long and wide, with rather large

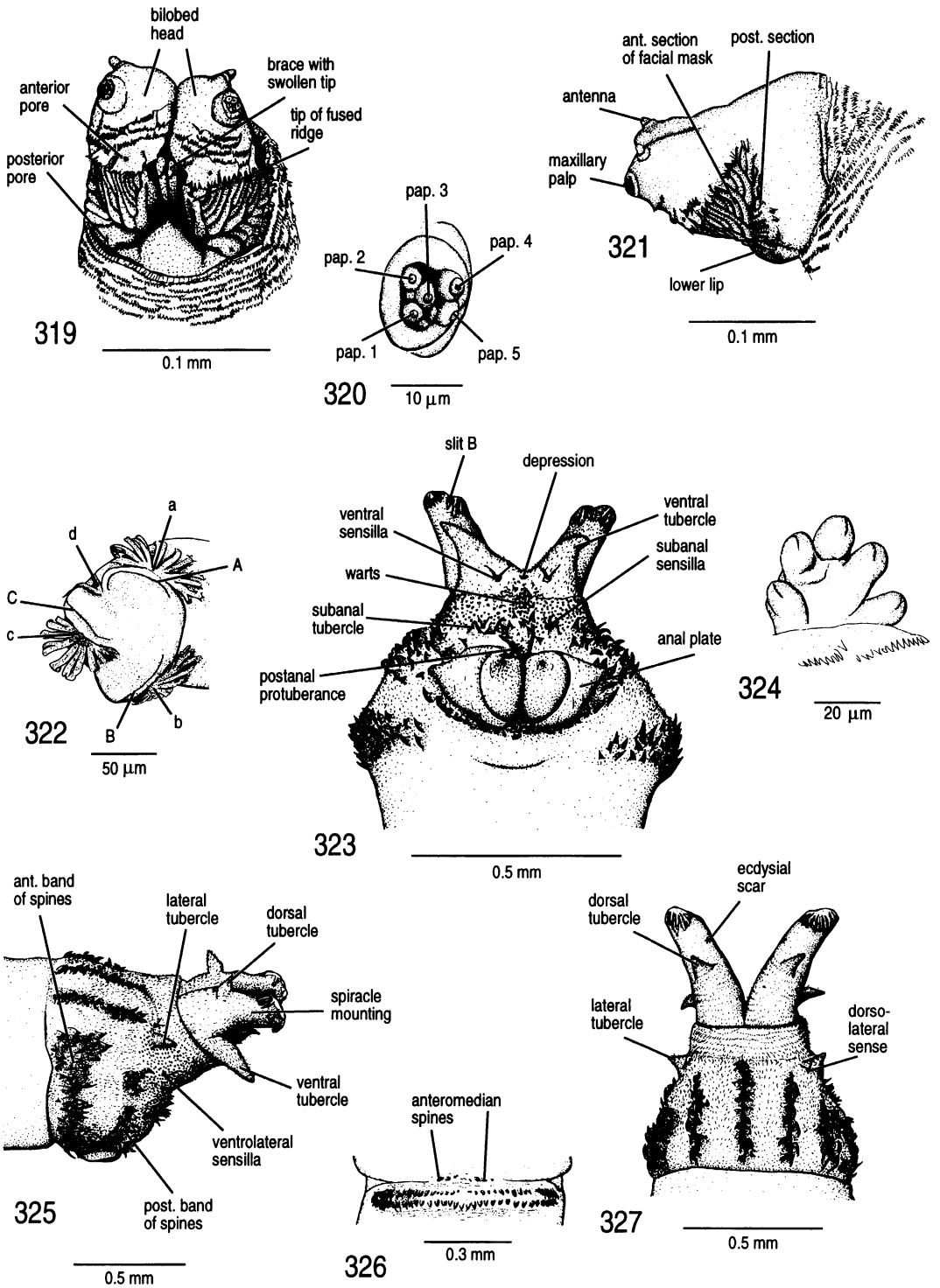


Fig. 319–327. *Sepsis punctum.* **Cephalic region:** 319: ventral, 321: lateral; **maxillary palp:** 320; **posterior spiracle:** 322; **last segment:** 323: ventral, 325: lateral, 327: dorsal; **anterior spiracle:** 324; **creeping welt:** 326.

dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; except for most anterior section, entire dorsal side of last segment pubescent; sensory organ with long sensory hairs. There are additional published figures of lateral (Schumann, 1962) and ventral views (Schumann, 1962; Mangan, 1977) of the last segment which agree with description provided here.

POSTERIOR SPIRACULAR DISC (fig. 322): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 7–10 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "B" extending onto ventral side of spiracle mounting (fig. 323); slit "A" arched toward base of process "d"; ecdysial scar in a dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 327). Mangan (1977) noted that no spiracular slit extends beyond spiracular plate. This observation does not concur with any of my results.

BIOLOGY: Compared to other *Sepsis* species, *S. punctum* is a generalist. It breeds in pig manure (Hammer, 1941), dog feces, and cow dung (Minder, 1963; Schulz, 1989; Schumann, 1962; Schweiger, 1988; Wharton and Moon, 1979; Zerbe, 1993). It belongs to the group of *Sepsis* species that appear soon after the deposition of the dung (Schulz, 1989; Zerbe, 1993). Adults have been reported from feeding pens, small mammal feces, carrion, rotting vegetation (Mangan, 1977), horse dung (Pont, 1987a: associated with the horse-dung specialist *Zuskamira*), fox feces (Iwasa, 1980), human excrement (Gregor, 1966) and bear dung (see Schulz, 1989). The species is mesophilic (Bährmann, 1993; Minder, 1963) and is rarely found on dry pastures. Occasionally flowers are visited (Bährmann, 1993: *Cornus mas*). Minder reported a development time of 15–18 days which is in agreement with the 16 days that Schulz (1989) observed for laboratory cultures. At 24°C the development is considerably faster with the first imagines hatching after 11 days. Females can be highly fecund. Under laboratory conditions an average of 82 eggs are produced every 0.8 days and the females become receptive 3–5 days after eclosion. *Sepsis punctum* hibernates as adults. Parker (1972a, 1972b) found imagines in December and Minder caught adults with developed fat body from the Moscow region in late fall.

Parker (1971a, 1972b) first reported precopulatory guarding for this species. He noticed that male take-overs of females attacking a precopula pair are much more common in this species than in *S. cynipsea*. Body size varies dramatically (when measured by body weight by a factor of 10; Zerbe, 1993) and is linked to the abundance of food during the larval development. Males arrive earlier at the substrate than females and are much more common on a fresh cow pat (Zerbe, 1993). Males try to establish territories on the cow pat. Small males are forced into the surrounding vegetation. On a fresh cow pat, only small females succeed in depositing eggs without being mounted by a male. Large females are immediately mounted by large males. Precopula pairs are subject to attacks by males looking for a mate. Of 14 pairs that Zerbe (1993) observed, seven pairs were attacked once and four pairs were attacked several times. The outcome is almost invariably that large males displace small males that may have initially succeeded in mounting a female. Take-over fights can be very violent. After egg deposition, copulation almost always takes place in the surrounding vegetation. Interestingly, in the American populations of *S. punctum* precopulatory guarding is never observed (Schulz, personal commun.).

Small males follow a different strategy in searching for mates than large males: they wait in the surrounding vegetation or at old cow pats which females will occasionally visit (Zerbe, 1993). Since Schulz (1989) found under laboratory conditions that small males live longer than large males, their disadvantage at fresh cow pats may be partly overcome by a greater longevity.

DISTRIBUTION: *Sepsis punctum* has a Holarctic distribution including numerous European and Asian records (Iwasa, 1980; Zuska and Pont, 1984). It also occurs on the Canary Islands (Baez, 1982). Mangan (1977) reported this species from all of eastern United States, California and Texas.

Sepsis secunda Melander and Spuler, 1917

Locality: Santa Rita Experimental Range, Pima County (Arizona, USA), coll. K. Schulz University of Arizona
Specimens examined: 9
Length: 4.44–5.53 mm ($\bar{x}$ = 4.80 0.39; n = 9)
Largest width of body segments: 0.48–0.70 mm ($\bar{x}$ = 0.59 0.08; n = 9)
Width of last segment: 0.56–0.69 mm ($\bar{x}$ = 0.62 0.05; n = 9)

CEPHALIC REGION (fig. 328, ventral view; fig. 330, lateral view): Much longer than wide, monolobed, large lower lip; anterior pore on one large comb to either side of brace and posterior pore on both elongated lower lobes; brace with tips enlarged into hooklike projections; combs restricted to anterior section of cephalic lobes, none on facial mask or around maxillae; combs arranged in horizontal rows, usually wider than long with multiple long teeth; facial mask composed entirely of smooth-edged ridges; the two ridges next to either side of mouth opening large and fused to each other at anterior end; ridges somewhat organized into anterior and posterior sections separated by mid-furrow; anterior section organized into three blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and shorter, intercalary ridges; block next to mouth opening composed of three ridges, second and third block of two ridges; posterior section with 2–4 short ridges dorsal to lower lobe; several combs around entire facial mask including posterior margin.

MAXILLA (fig. 329): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 333): Consisting of 4–6 lobes along a narrow central axis.

CREEPING WELTS (fig. 335): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 18–21 spines, median ones missing or the size of denticles; second row with about 19–23 spines; 3–4 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 332, ventral view; fig. 334, lateral view; fig. 336, dorsal view): Distinctly bulbous at anterior end, with numerous hairs and warts; anal plate wing-shaped; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; pair of small inconspicuous, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of narrow but long ventral tubercles at bases of spiracle mountings; depression between bases of tubercles; compared to most sepsids, area between depression and ventral tubercles greatly expanded, thus ventral sensory organ which is usually positioned at base of tubercles now in a more anterior position; hairs posterior to postanal protuberance transformed into warts, warts particularly large in area around depression; here last segment also strongly constricted; spines arranged into an anterior and a posterior band; posterior band divided into dorsolateral group of spines and a ventral band; area between bands pubescent; lateral tubercle with a dorso- and a ventrolateral sensory organ; spiracle mountings very long, with small dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; areas between grooves not pubescent, hairs restricted to posterior half of area between lateral two grooves and lateral field of spines; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 331): Bulging spiracular disc with three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–7 hairs, unassociated process ("d") always with only two hairs; opening "C" straight, extending just beyond spiracular plate, slit "A" at one end weakly arched toward the root of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 332); ecdysial scar in dorsomedian position above dorsal tubercle (fig. 336).

BIOLOGY: Blume (1970) and Schulz (personal commun.) collected and reared this species from cow droppings.

DISTRIBUTION: Melander and Spuler (1917) report *S. secunda* from the west coast of the

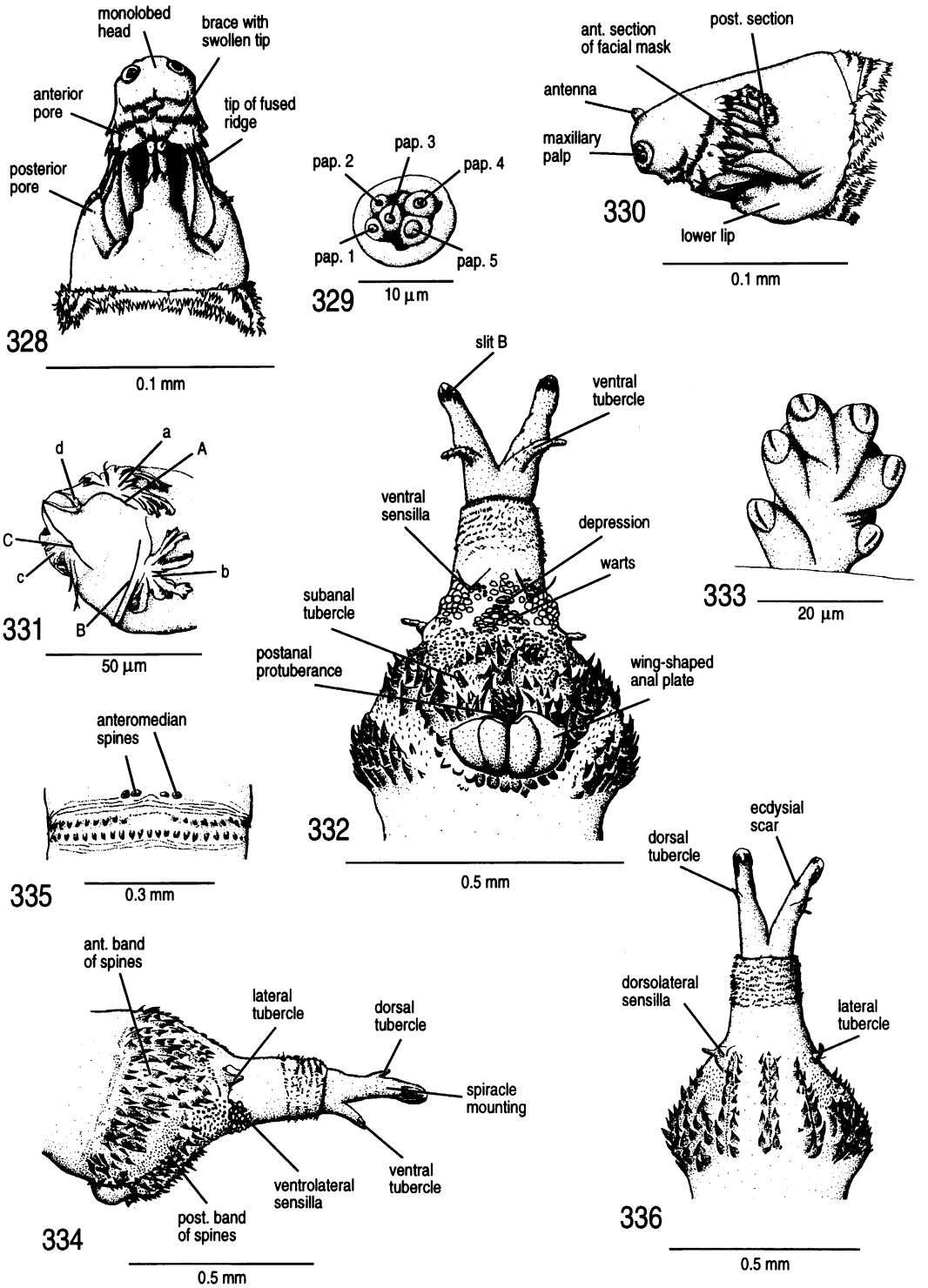


Fig. 328–336. *Sepsis secunda.* **Cephalic region:** 328: ventral, 330: lateral; **maxillary palp:** 329; **posterior spiracle:** 331; **last segment:** 332: ventral, 334: lateral, 336: dorsal; **anterior spiracle:** 333; **creeping welt:** 335.

United States and Pennsylvania. Schulz also collected this species in Arizona (personal commun.).

Sepsis thoracica (Robineau-Desvoidy, 1830)

Locality: Setla (Alicante, Spain), leg K. Schulz, University of Arizona
Specimens examined: 8
Length: 4.59–5.82 mm ($\bar{x}$ = 5.28 0.38; n = 8)
Largest width of body segments: 0.61–0.97 mm ($\bar{x}$ = 0.84 0.13; n = 8)
Width of last segment: 0.64–0.88 mm ($\bar{x}$ = 0.72 0.07; n = 8)

Hennig (1949) provided a description of the larva in which he stated that it very much resembles *S. cynipsea*. According to Hennig, it differs only with respect to the number of lobes on the anterior spiracles (5 instead of 7—8). He overlooked the three double rows of spines on the dorsum of the last segment and his figures are very sketchy. In Peterson (1960) there is also a description of the larvae of a species that was identified as *S. pectoralis*. *Sepsis pectoralis* is, according to Hennig (1949), a synonym of *S. thoracica*. It is nevertheless unlikely that the larvae Peterson studied belonged to *S. thoracica* since this species is unknown from the Nearctic region, and Peterson's book was dedicated to the Nearctic fauna.

CEPHALIC REGION (fig. 337, ventral view; fig. 339, lateral view): Longer than wide, moderately bilobed, moderately large lower lip; posterior pore on both lower lobes and anterior pore on one large comb to either side of mouthhooks; brace with tips enlarged into hooklike projections (not visible on figure); 6–8 combs restricted to anterior section of each cephalic lobe; combs much wider than long with multiple small teeth; no combs on facial mask, inner side of cephalic lobes or around maxillae; facial mask composed entirely of smooth-edged ridges, the two ridges next to either side of mouth opening fused to each other at tips (not visible in figure); ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into five blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary, intercalary ridges; block next to mouth opening with 4–5 ridges, the remaining blocks with two, rarely one or three ridges; posterior section with 5–6 short ridges dorsal to lower lobe; combs along posterior margin of facial mask. For an illustration of cephalopharyngeal skeleton, see Hennig (1949).

MAXILLA (fig. 338): Composed of five compound papillae in two groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); narrow gap between groups.

ANTERIOR SPIRACLE (fig. 342): 5–7 moderately long lobes arranged along a short central axis (text fig. 35 in Hennig, 1949: 5 lobes).

CREEPING WELTS (fig. 344): First eight segments with rows of spinules laterally and first seven dorsally; ventrally, first four welts consisting of rows of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 28–30 spines, median ones reduced in size; second row with 23–29 spines; 4–7 anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 341, ventral view; fig. 343, lateral view; fig. 345, dorsal view): Moderately bulbous, with numerous warts between postanal protuberance and base of ventral tubercles; warts scarce only on two diagonal lines that run from depression craniad; anal plate small, wing-shaped, laterally somewhat pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercles, subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; posterior band divided into dorsolateral group of spines and a ventral band; area between bands densely pubescent; rather large lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long and wide, with rather large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; except for anterior third, dorsal aspect of last segment pubescent; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 340): Has

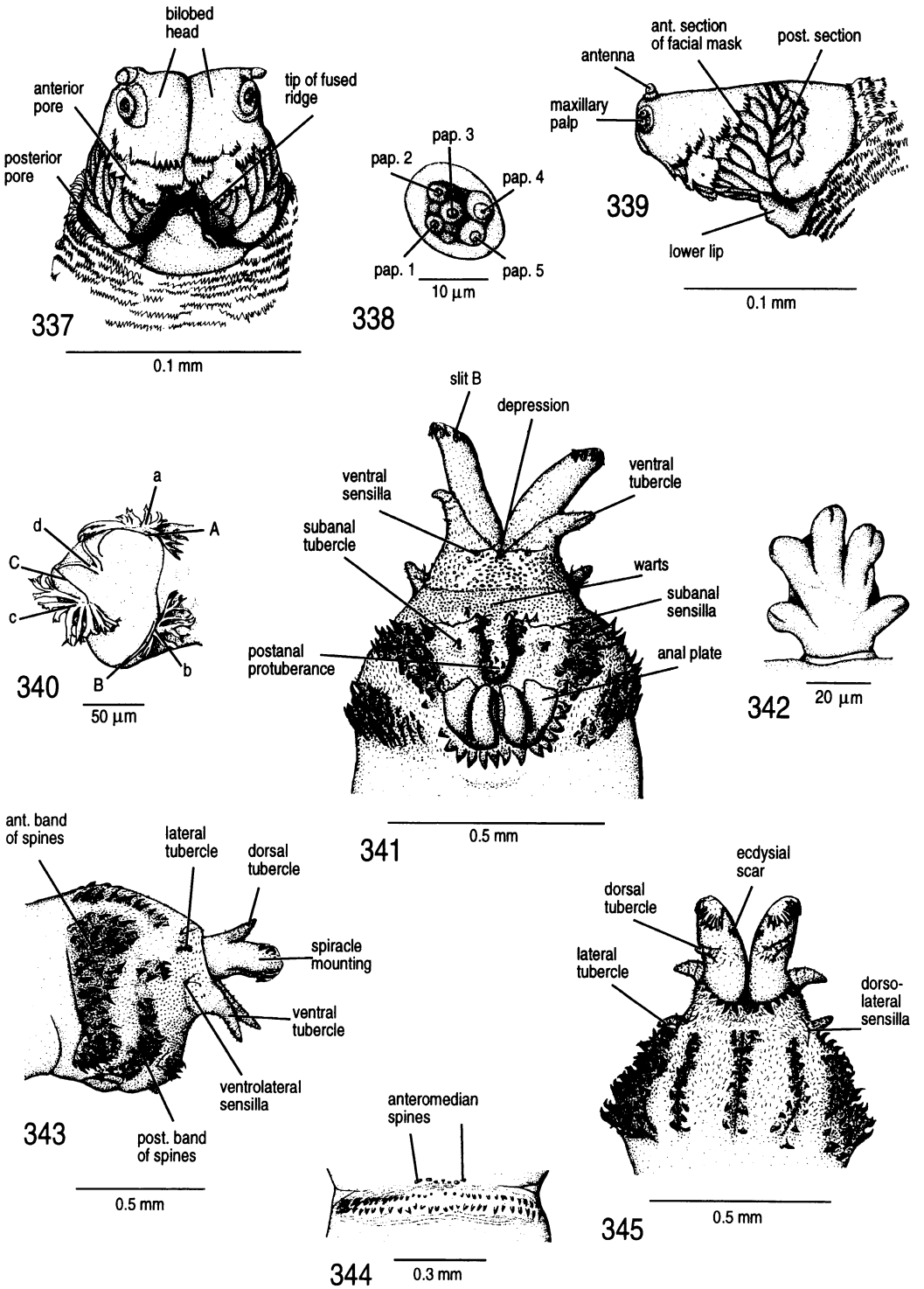


Fig. 337–345. *Sepsis thoracica.* **Cephalic region:** 337: ventral, 339: lateral; **maxillary palp:** 338; **posterior spiracle:** 340; **last segment:** 341: ventral, 343: lateral, 345: dorsal; **anterior spiracle:** 342; **creeping welt:** 344.

three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–8 hairs, unassociated process ("d") with two unbranched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 341); ecdysial scar in a dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 345). The arrangement of the spiracle opening is also depicted in Hennig (1949). However, Hennig did not recognize that opening "B" extends beyond the spiracular plate.

BIOLOGY: *Sepsis thoracica* breeds in cow (Hafez, 1947; Hennig, 1949; Kirk, 1992; Papp, 1971; 1976; Pont 1979; Schweiger, 1988) and buffalo dung (Hafez, 1948) where the development time of larvae is known to be four days and 5 h at 26–28°C. In the laboratory at 24°C, development requires 7–8 days. In cow dung the total development time is 15–22 days (Laurence 1954). Adults have also been taken on horse (Iwasa, 1980; Papp, 1976), pig (Papp, 1974b), and yak dung (Papp, 1976). In Europe this species does not have any pre- or postcopulatory guarding. In Zimbabwe I commonly collected a species that is considered conspecific with *S. thoracica*. At mid-elevation it was very common on cow dung and was the earliest visitor of freshly deposited cow pats. Here the males displayed precopulatory guarding. Single females on the cow pat were exceedingly rare. Copulations took place in the surrounding vegetation. Take-over attempts were rarely observed, and the precopulatory guarding very closely resembled that of *S. cynipsea*. Since the larvae of these African *S. thoracica* are morphologically different from the larvae of the European specimens, I believe that the African *S. thoracica* is a different species.

DISTRIBUTION: The distribution of *S. thoracica* is fairly wide. It is found throughout the Palearctic (including Japan and the Canary Islands), Oriental (including Taiwan) and Australian regions (Iwasa, 1987; 1989; Zuska and Pont, 1984).

Sepsis violacea Meigen, 1826

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 27
Length: 3.04–4.54 mm ($\bar{x}$ = 3.98 0.42; n = 10)
Largest width of body segments: 0.67–0.97 mm ($\bar{x}$ = 0.79 0.12; n = 10)
Width of last segment: 0.56–0.88 mm ($\bar{x}$ = 0.73 0.09; n = 10)

CEPHALIC REGION (fig. 346, ventral view; fig. 348, lateral view): Longer than wide, distinctly bilobed; posterior pore on both small lower lobes and anterior pore on one large comb to either side of mouthhooks; brace with tips enlarged into hooklike projections; 10–11 combs restricted to anterior section of each cephalic lobe, much wider than long with multiple small teeth; combs absent on facial mask and around maxillae; facial mask composed entirely of smooth-edged ridges, ridges much narrower and more numerous than in other species of *Sepsis*, apparently the result of longitudinal fission of "normal," wide ridges; anterior tips of ridges on either side of mouth opening fused to each other at anterior end; ridges organized into anterior and posterior sections separated by mid-furrow; anterior section organized into 3–4 blocks of ridges, whereby each block is formed by a primary ridge converging onto most dorsal ridge of preceding block, and secondary, shorter and intercalary ridges; block next to mouth opening with 5–7 secondary ridges, second, third and fourth blocks with 4–6; posterior section with 15–17 or in case of specimens with four blocks 12–13 very long ridges dorsal to lower lobe; combs along posterior margin of facial mask.

MAXILLA (fig. 347): Composed of five compound papillae; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4).

ANTERIOR SPIRACLE (fig. 351): 5–8 moderately long lobes arranged along a short central axis.

CREEPING WELTS (fig. 353): Laterally first eight segments, dorsally first seven with rows of spinules; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and few short additional rows of spinules anterior and posterior to spines; first row of spines with 20–27 spines, median ones reduced in size; second row with 22–25 spines; 3–4 anteromedian spines forming a short anterior row; spines rather small. Except for last abdominal segment, integument without hairs.

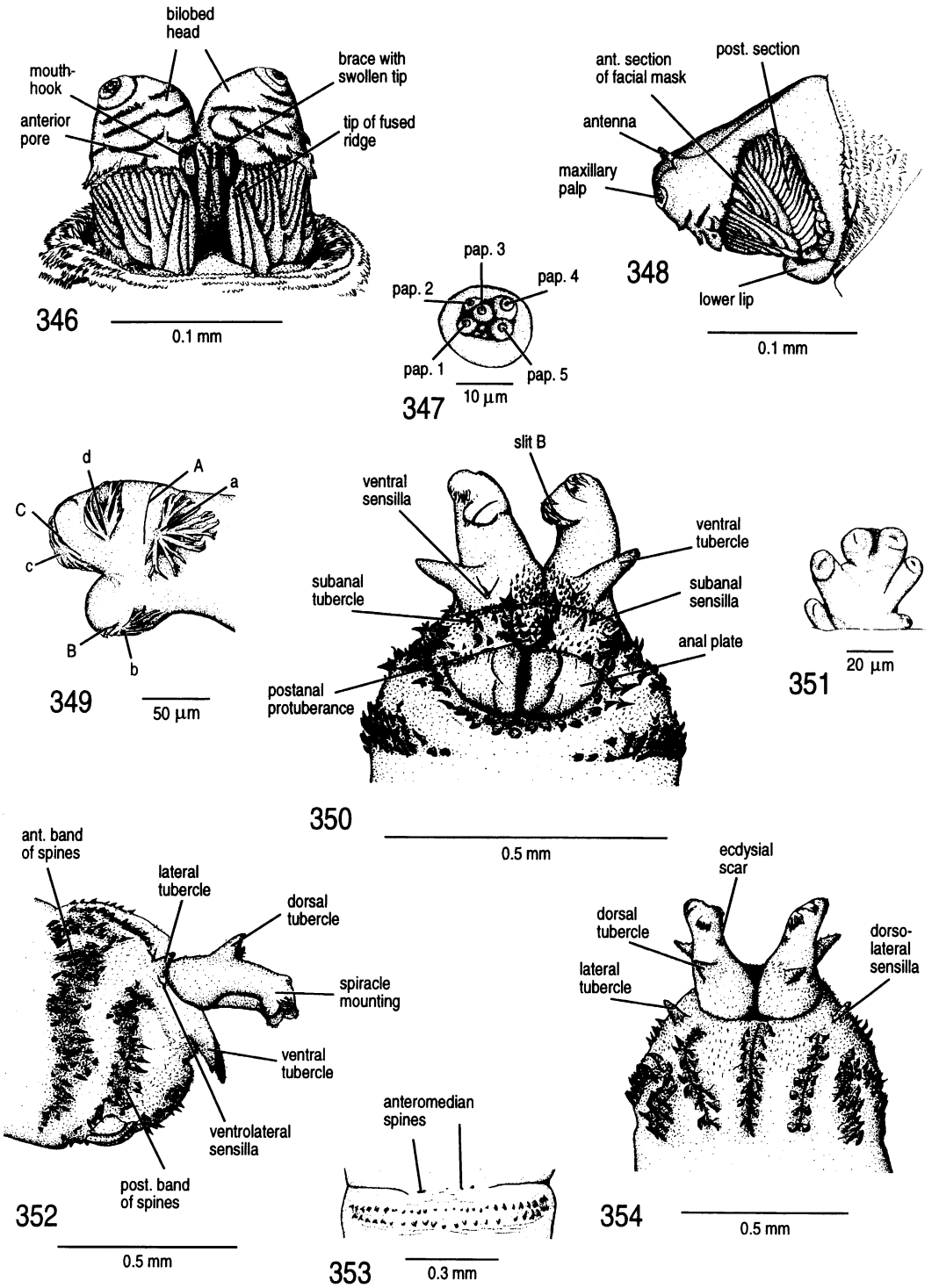


Fig. 346–354. *Sepsis violacea.* **Cephalic region:** 346: ventral, 348: lateral; **maxillary palp:** 347; **posterior spiracle:** 349; **last segment:** 350: ventral, 352: lateral, 354: dorsal; **anterior spiracle:** 351; **creeping welt:** 353.

LAST ABDOMINAL SEGMENT (fig. 350, ventral view; fig. 352, lateral view; fig. 354, dorsal view): Moderately bulbous, with numerous hairs but unlike most other *Sepsis* with hairs instead of warts between postanal protuberance and base of ventral tubercles; hairs are missing only on two diagonal lines that run from depression craniad; anal plate large, wing-shaped, laterally pointed; postanal protuberance well developed, tongue-shaped and spiny; preanal row of spines along anal plate; weakly developed, bare subanal tubercles; subanal sensory organ posterior to each tubercle; pair of large ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; with a distinct anterior and a posterior band of spines laterally; area between rows pubescent; rather large lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long and wide, with rather large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of spines on either side; hairs restricted to posterior half of segment; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 349): Has three spiracular openings positioned on drawn-out processes, three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 5–7 hairs, unassociated process ("d"), unique for genus *Sepsis*, with 3–4 branched hairs; opening "C" extending just beyond spiracular plate, slit "A" arched toward base of process "d"; slit "B" extending onto ventral side of spiracle mounting (fig. 350); ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 354).

BIOLOGY: Adults of *S. punctum* and *S. violacea* are morphologically very similar, but they differ remarkably in larval morphology, behavior and ecology (Schweiger, 1988). Some of the older reports on the ecology of *S. violacea* should be judged with care since they may actually pertain to *S. punctum*. This is particularly the case for Hinton's (1960) indication that this species has a precopula. I never observed any kind of pre-or postcopulatory guarding. The species breeds in cattle (Hinton, 1960; Mohr, 1943; van der Goot, 1987a; in lab, personal obs.) and pig dung (Papp, 1974b). Development time at 24°C is 7–10 days. Adults have also been collected from rotting vegetation, horse, pig, sheep, human, chicken, bear and small mammal dung (Pont, 1979; for additional references, see Schulz, 1989). *Sepsis violacea* is one of the very few sepsids commonly encountered in buildings (Minder, 1963; van der Goot, 1985; 1987a). Van der Goot (1987a) noticed that this species is becoming increasingly common in the Netherlands and attributes this phenomenon to the increasing number of cattle raised indoors. Pont (1987b) lists a large number of cases where *S. violacea* formed aggregations at places where ammonia is used for either printing or cleansing. I can confirm Zuska's (1960) report on an association of this species with manure (personal obs.). *Sepsis violacea* appears to hibernate as a puparium in North America (see references in Schulz, 1989), but Pont reported that imagines from England can be collected in December. Occasionally, flowers are visited (Bährmann, 1993: *Cornus mas*).

DISTRIBUTION: The species is found throughout the Palearctic region including Europe, Asia and north Africa (Zuska and Pont, 1984). Records from North America need to be checked for accuracy of species identification.

14. GENUS *SUSANOMIRA* PONT, 1987
Susanomira caucasica Pont, 1987

Locality: Caucasus, North Ossetia, 10 km SE Alagir, near 1600 m (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 9
Length: 7.1–8.81 mm ($\bar{x}$ = 8.30 0.59; n = 9)
Largest width of body segments: 1.09–1.41 mm ($\bar{x}$ = 1.21 0.10; n = 9)
Width of last segment: 1.18–1.41 mm ($\bar{x}$ = 1.29 0.08; n = 9)

CEPHALIC REGION (fig. 355, ventral view; fig. 357, lateral view): Longer than wide, distinctly bilobed, large lower lip; posterior pore on both lower lobes and anterior pore on one comb to either side of brace; brace simple; 7–8 combs restricted to anterior section of cephalic lobes, wider than long with multiple small teeth; combs absent from facial mask, inner side of cephalic lobes and around maxillae; facial mask composed entirely of smooth-edged ridges, some primary ridges

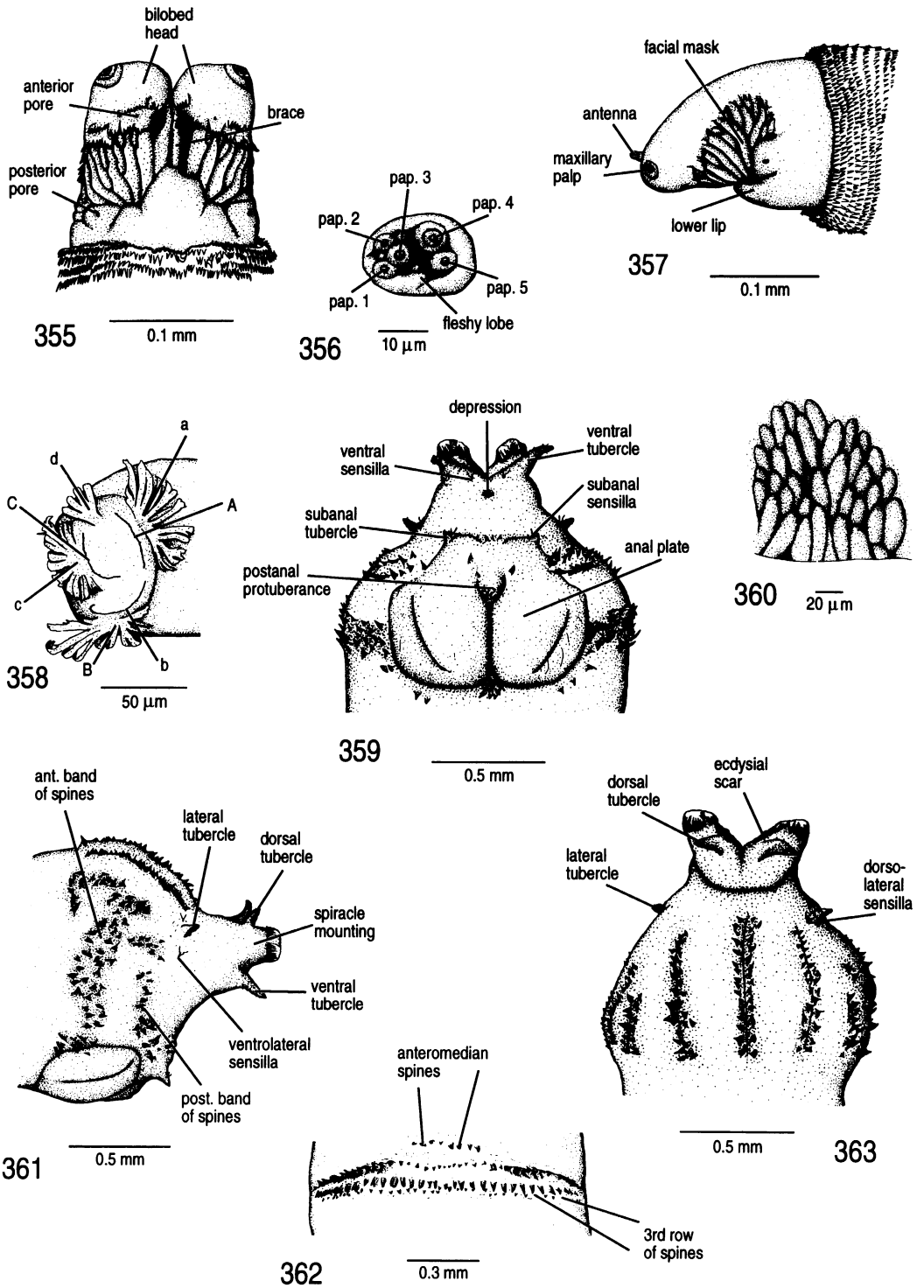


Fig. 355–363. *Susanomira caucasica.* **Cephalic region:** 355: ventral, 357: lateral; **maxillary palp:** 356; **posterior spiracle:** 358; **last segment:** 359: ventral, 361: lateral, 363: dorsal; **anterior spiracle:** 360; **creeping welt:** 362.

spanning across anterior section of facial mask and 1–2 intercalary secondary ridges, secondary ridges increasing in length toward dorsal; ridges above lower lobe shorter, pointing toward anterodorsal corner of lower lobe; no combs around posterior margin of facial mask.

MAXILLA (fig. 356): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); distinct gap between groups and a remnant of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 360): Has unusual morphology: lobes not arranged along a central axis, but in a "spiracle field" with 34–39 lobes.

CREEPING WELTS (fig. 362): First eight segments with rows of spinules laterally and dorsally; ventrally, first three welts consisting of spinules, fourth with a single row of spines; remaining six welts ventrally with three long rows of reclinate spines and additional rows of spinules anterior and posterior to spines; first row of spines with 23–41 spines, median ones missing or reduced in size; second row with 23–34 spines; third row more irregular with 29–31 smaller spines, often in spaces between spines of second row; in addition to long rows, with about eight anteromedian spines forming a short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 359, ventral view; fig. 361, lateral view; fig. 363, dorsal view): Not distinctly bulbous, but about equal to diameter of widest body segment, segment largely bare; anal plate large, rounded laterally with diagonal fold; postanal protuberance consisting of 7–8 spines on swelling; preanal protuberance consisting of a number of small spines; weakly developed, bare subanal tubercle; posterior to tubercle with a subanal sensory organ; pair of ventral tubercles with a ventral sensory organ at each base, depression between bases of tubercles; anterior band of spines present, not meeting ventrally; posterior band of spines divided into a dorsolateral group of spines and a ventrolateral band; lateral tubercle, associated with a dorso- and a ventrolateral sensory organ; spiracle mountings comparatively short and stout, with dorsal tubercle; dorsal surface of abdominal segment with three longitudinal grooves, each bordered by a row of spines on either side; area between rows bare; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 358): Has three openings and four processes of spiracular hairs, the processes ("a–c") associated with openings with 9–11 hairs, unassociated process ("d") with four hairs; curved openings arranged in rectangular fashion with "B" shifted toward "C" in some specimens; ecdysial scar at base of dorsal tubercle (fig. 363).

BIOLOGY: *Susanomira caucasica* was described by Pont (1987a) who collected the type specimens on dry horse dung.

DISTRIBUTION: *Susanomira caucasica* is known from the Caucasus Mountains (Georgia), but appears to be more widespread.

15. GENUS *THEMIRA* ROBINEAU-DESVOIDY, 1830

Key to the species.

Subgenus *Enicita*

1. Last segment with numerous hairs on dorsal side and laterally between bands of spines (figs. 370, 372) ..... *T. annulipes*
– Last segment with very few or no hairs on dorsal and lateral aspect (figs. 441, 443) ..... *T. simplicipes*

Subgenus *Themira*

1. Anal plate with drawn-out lateral corners (fig. 386); seven creeping welts consisting of a double row of spines ..... *T. leachi*
– Last segment with simple (e.g., fig. 377) or swollen anal plate with diagonal fold (e.g., fig. 395); with six creeping welts consisting of a double row of spines 2
2. Last segment with simple anal plate consisting of one lobe to either side of anal opening (e.g., fig. 377); entire anterior and lateral margin of anal plate surrounded by a row of strong spines (e.g., fig. 377) 3
– Last segment with swollen anal plate; anal plate never entirely surrounded by strong spines, but at best with a few rather weak spines along anterior margin of anal plate 4
3. Last abdominal segment lacking ventrally hairs between anal plate and ventral tubercles (e.g., figs. 377, 422) .. *T. flavicoxa, T. nigricornis*
– Last abdominal segment with hairs between anal plate and ventral tubercles (fig. 404) ... *T. lutulenta*

4. Dorsal aspect of last segment with at best three weakly expressed grooves, but without row of spines on either side of the grooves (fig. 453) ..... *T. superba*
- Dorsal aspect of last segment with three grooves that are lined with one row of spines on either side (e.g., figs. 399, 417) 5
5. Facial mask with numerous ridges converging onto a median furrow (fig. 409) .. *T. minor*
- Facial mask almost entirely covered with combs; very few or a few ridges close to lower lip (e.g., figs. 391, 427) 6
6. Facial mask with several ridges close to lower lip (fig. 427)..... *T. putris*
- Facial mask more or less completely covered with combs; never more than 4–5 ridges (e.g., figs. 391, 445) 7
7. Last segment with three grooves dorsally and an irregularly spaced row of spines on either side (fig. 399) .....*T. lucida*
- Last segment dorsally with regularly spaced spines not arranged in rows (fig. 453) .... *T. superba*

Themira (Enicita) annulipes (Meigen, 1826)

Locality: Caucasus, North Ossetia, near Alagir (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 4
Length: 3.12–4.85 mm (n = 4)
Largest width of body segments: 0.46–0.68 mm (n = 4)
Width of last segment: 0.48–0.73 mm (n = 4)

A figure of the cephalopharyngeal skeleton and ventral view of the last segment of this species is provided by Mangan (1977).

CEPHALIC REGION (fig. 364, ventral view; fig. 366, lateral view): Wider than long, cephalic lobes distinctly bilobed, with moderately sized lower lip; anterior pore on one comb on either side of mouthhooks; one posterior pore on both lower lobes; brace consisting of two ridges which are largely adjacent and fuse only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing comb, wider than long with numerous rather coarse teeth; numerous combs on the inner side of cephalic lobes or around maxillae; facial mask small, few ridges close to lower lobe.

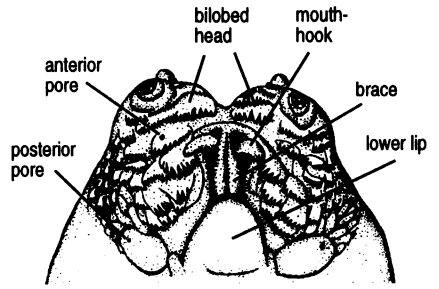
MAXILLA (fig. 365): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); gap between groups rather wide with remnant of a fleshy lobe partly separating them.

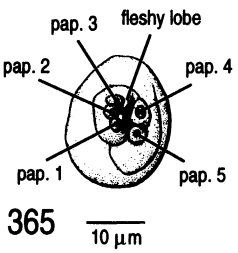
ANTERIOR SPIRACLE (fig. 369): 12–14 lobes arranged along a wide central axis which narrows toward tip (see also, Mangan, 1977).

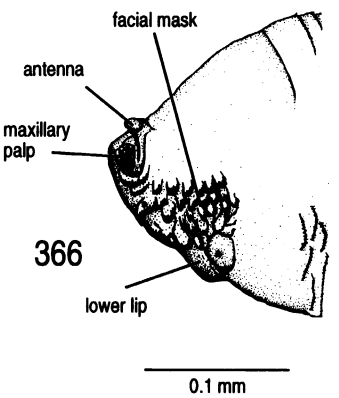
CREEPING WELTS (fig. 371): First eight segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple short additional rows of spinules anterior and posterior to spines; first row of spines with 19–21 spines, discounting median ones which are the size of denticles; second row with 24–27 spines. Except for last abdominal segment, body otherwise lacking hairs.

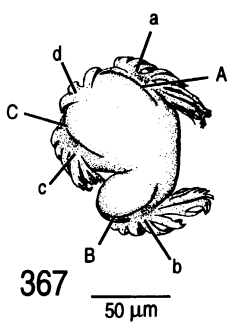
LAST ABDOMINAL SEGMENT (fig. 368, ventral view; fig. 370, lateral view; fig. 372, dorsal view): Slightly bulbous, with few hairs between anal plate and ventral tubercles; anal plate very large almost as wide as last segment, with diagonal fold; spiny postanal protuberance; preanal protuberance very conspicuous bulbous, buttonlike, consisting of fused spines; small, hairy subanal tubercle; posterior to tubercle with a subanal sensory organ; pair of well developed, long ventral tubercles with a sensory organ at each base; depression between bases of tubercles; spines on last segment very small; anterior band of spines not well defined, not meeting ventrally; posterior band with few spines; between bands numerous spinules; small lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with moderately large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of irregularly spaced spines on either side; no hairs or spinules between grooves; hairs of sensory organs short.

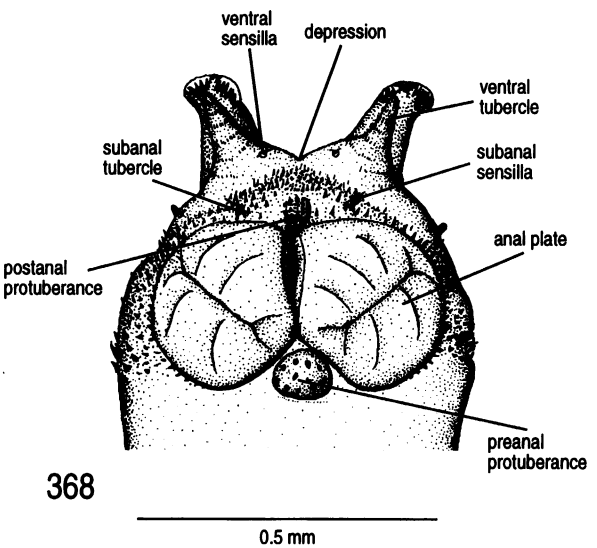
POSTERIOR SPIRACULAR DISC (fig. 367): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 6–10 hairs, unassociated process ("d") with three hairs; weakly curved openings in rectangular arrangement with opening "B" displaced toward slit "C" by half the width of spiracular plate; ecdysial scar in dorsomedian position just below spiracular plate (fig. 372).

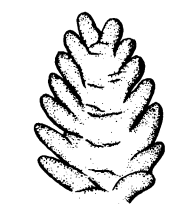


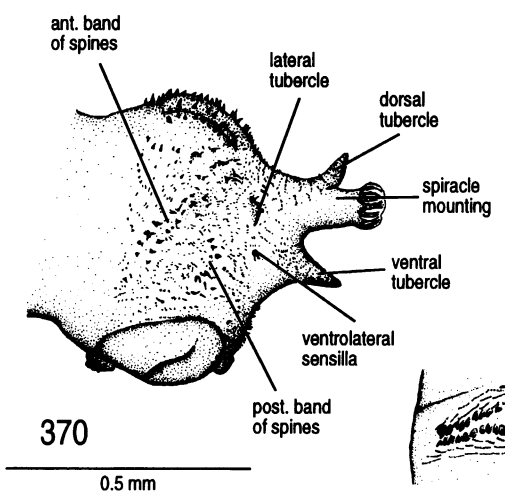












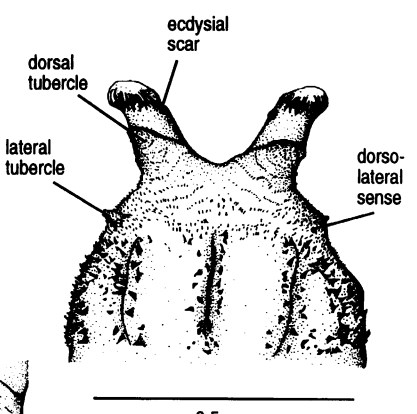


Fig. 364–372. *Themira annulipes.* **Cephalic region:** 364: ventral, 366: lateral; **maxillary palp:** 365; **posterior spiracle:** 367; **last segment:** 368: ventral, 370: lateral, 372: dorsal; **anterior spiracle:** 369; **creeping welt:** 371.

BIOLOGY: *Themira annulipes* appears to be associated with manure (personal obs.). Mangan (1977) reported it from cattle feeding pens, sewage leaks and overflows, and Pont (1987a) found it associated with the horse-dung specialist *Zuskamira*. In the lab, I bred the species on cow dung, but only a few eggs were laid and few larvae survived. I am convinced that the substrate was not optimal. The development time was quite long (at 24°C: 14 days). *Themira annulipes* appears to be most common in moist habitats (Bährmann, 1993).

DISTRIBUTION: The distribution of this species is Holarctic with numerous records throughout the Holarctic (Mangan, 1977; Zuska and Pont, 1984).

Themira flavicoxa Melander and Spuler, 1917

Locality: Ithaca (New York, USA), coll. R. Meier
Specimens examined: 15
Length: 6.79–8.59 mm ($\bar{x}$ = 7.53 0.59; n = 10)
Largest width of body segments: 0.65–1.16 mm ($\bar{x}$ = 0.91 0.12; n = 10)
Width of last segment: 0.73–0.96 mm ($\bar{x}$ = 0.86 0.07; n = 10)

CEPHALIC REGION (fig. 373, ventral view; fig. 375, lateral view): Wider than long, distinctly bilobed, small lower lip; anterior pore on one comb to either side of mouthhooks; posterior pore on both lower lobes; both lower lobes surrounded by a crescent-shaped ridge; brace consisting of two ridges, tips not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing comb, on the inner side of cephalic lobes or around maxillae; combs mostly wider than long with numerous fine teeth; large facial mask, only anteromedian section covered by combs, remainder consisting of serrate ridges converging onto anteromedian corner of lower lobe.

MAXILLA (fig. 374): Composed of five compound papillae in two groups of two and three; four papillae consisting of two superimposed lobes (pap. 1—3, 5), one composed of three superimposed lobes (pap. 4); gap between groups distinct with remnant of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 378): 13–16 lobes arranged along a broad central axis which narrows toward tip and stands perpendicular to body axis; lobes with secondary annulations.

CREEPING WELTS (fig. 380): First five segments with rows of spinules laterally and dorsally; sixth only with lateral spinules; ventrally, first four welts consisting of spinules, remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 13–17 spines, median ones reduced to the size of denticles, second row with 21–24 spines; four anteromedian spines in no apparent order; body segments otherwise without hairs.

LAST ABDOMINAL SEGMENT (fig. 377, ventral view; fig. 379, lateral view; fig. 381, dorsal view): Bulbous, bare; anal plate simple consisting of single lobe; postanal protuberance moderately large and spiny; preanal protuberance absent but with a more or less complete row of spines along anterior margin of anal plate; large, hairy subanal tubercle, immediately lateral to tip with a subanal sensory organ; pair of well developed ventral tubercles and a ventral sensory organ at each base; shallow depression between the bases of the tubercles; spines on last segment moderately large; with a distinct anterior and a posterior band of spines, anterior band not meeting ventrally; area between rows of spines without denticles or hairs; pair of lateral tubercle associated with a dorso- and ventrolateral sensory organ; moderately long, wide spiracle mountings, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves which are accompanied by a row of irregularly spaced spines on either side; no hairs between grooves; hairs of sensory organs short, sometimes with three instead of two sensory hairs.

POSTERIOR SPIRACULAR DISC (fig. 376): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 5–7 hairs, unassociated process ("d") with four hairs; weakly curved openings in rectangular arrangement with opening "B" somewhat shifted toward slit "C"; ecdysial scar immediately below spiracular plate in median position (fig. 381).

BIOLOGY: *Themira flavicoxa* is the most common *Themira* species in upstate New York. It is particularly abundant in early spring when it is one of the first sepsid species

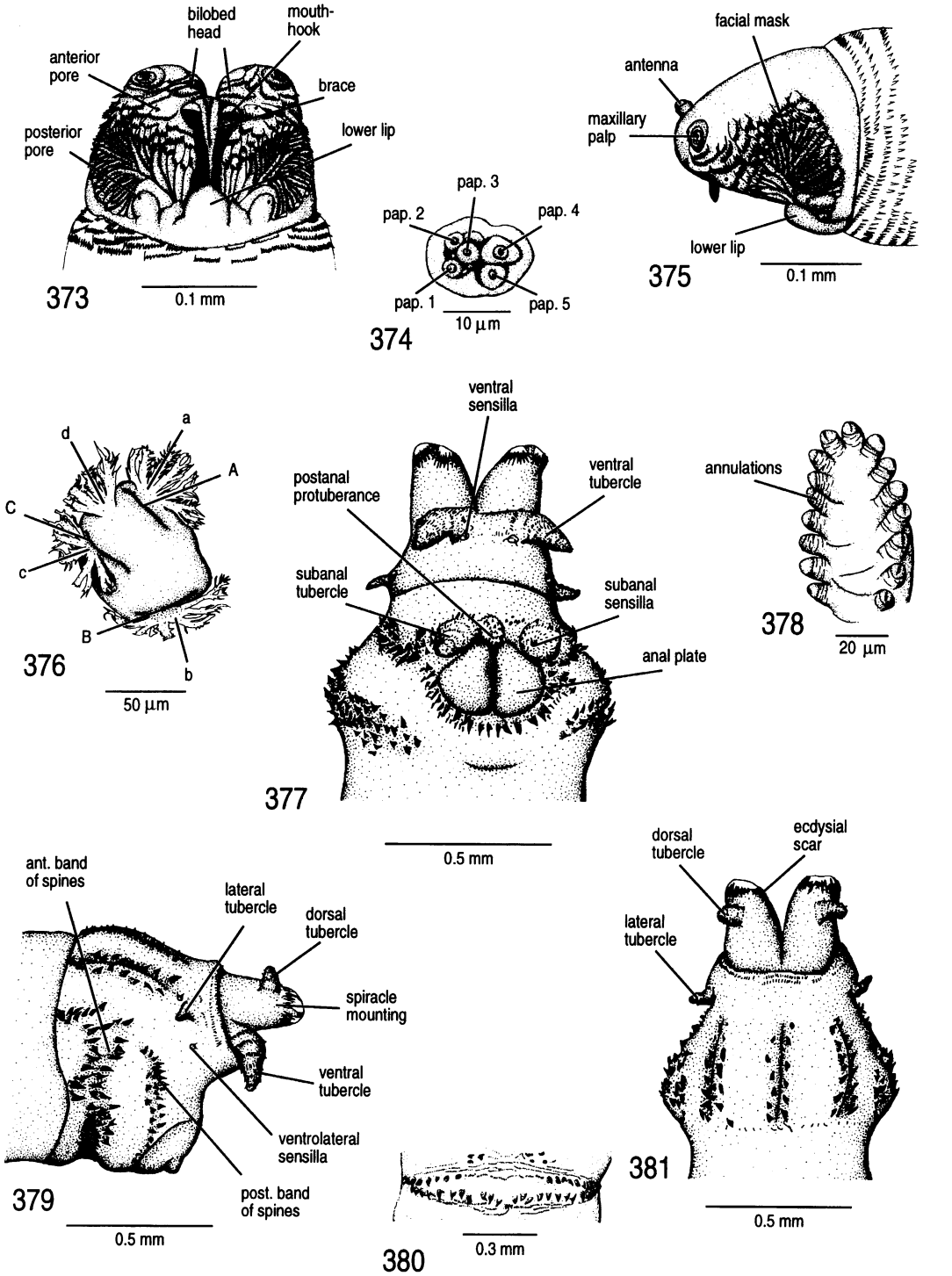


Fig. 373–381. *Themira flavicoxa.* **Cephalic region:** 373: ventral, 375: lateral; **maxillary palp:** 374; **posterior spiracle:** 376; **last segment:** 377: ventral, 379: lateral, 381: dorsal, **anterior spiracle:** 378; **creeping welt:** 380.

to appear. It can be very common on compost but I also collected it close to rodent carcasses. It readily breeds on cow dung. There is no evidence of pre- or postcopulatory guarding as in species such as *Sepsis cynipsea*. However, the females are mounted several minutes prior to copulation and many males are rejected by the females during that time.

DISTRIBUTION: This species only occurs in the Nearctic region. Melander and Spuler (1917) described it from the northern east coast of the United States.

Themira leachi (Meigen, 1826)

Locality: Primorskiy kray, Glazkovka, 20 km SW Valentin (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 3
Length: 5.42–5.90 mm (n = 3)
Largest width of body segments: 0.78–0.89 mm (n = 3)
Width of last segment: 0.65–0.92 mm (n = 3)

CEPHALIC REGION (fig. 382, ventral view; fig. 384, lateral view): Wider than long, distinctly bilobed, with large lip; anterior pore on one comb on either side of mouthhooks; posterior pore on both lower lobes; brace consisting of two ridges which are adjacent and fuse only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing combs, on the inner side of cephalic lobes or around maxillae; large facial mask entirely covered with combs arranged in a pattern converging onto anteromedian corner of lower lobe; combs wider than long with numerous fine teeth.

MAXILLA (fig. 383): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); gap between groups distinct with incomplete fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 387): 8–11 lobes arranged along a wide central axis which narrows toward tip; perpendicular to body axis.

CREEPING WELTS (fig. 389): All segments have spinules dorsally and laterally; ventrally, first four welts only consisting of spinules; remaining seven welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 30–36 spines, median ones reduced in size; second row with 23–29 spines. Except for last abdominal segment, body without hairs.

LAST ABDOMINAL SEGMENT (fig. 386, ventral view; fig. 388, lateral view; fig. 390, dorsal view): Not bulbous, with numerous denticle-like hairs; anal plate rather small with diagonal fold, and posteromedian and lateral corners being distinctly protruding; spiny postanal protuberance; preanal protuberance absent but with a short row of spines along anterior margin of anal plate; large, hairy subanal tubercle and a subanal sensory organ below tip; pair of well developed ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; spines on last segment rather small; anterior band of spines well defined, meeting ventrally and here consisting of a double row (probably homolog of creeping welt of last abdominal segment); very few spines forming a posterior band; numerous denticles between bands; several rows of denticles in front of anterior band of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings very short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves with a row of equally spaced spines on either side; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 385): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 4–6 hairs, unassociated process ("d") with four hairs; weakly curved openings in rectangular arrangement with opening "B" displaced by half the width of spiracular plate toward slit "C"; ecdysial scar immediately below spiracular plate in a dorsomedian position.

BIOLOGY: According to Pont (1979) *T. leachi* can be reared from manured soil, and females are frequently found on cow dung and human feces. I never collected the species in Berlin which may be because, according to Zuska (1960), it is predominantly a mountainous species living in forests close to creeks.

DISTRIBUTION: *Themira leachi* has a Palearctic distribution. There are numerous records in Europe and a few in Asia (east to Mongolia; Zuska and Pont, 1984 and Far East of Russia).

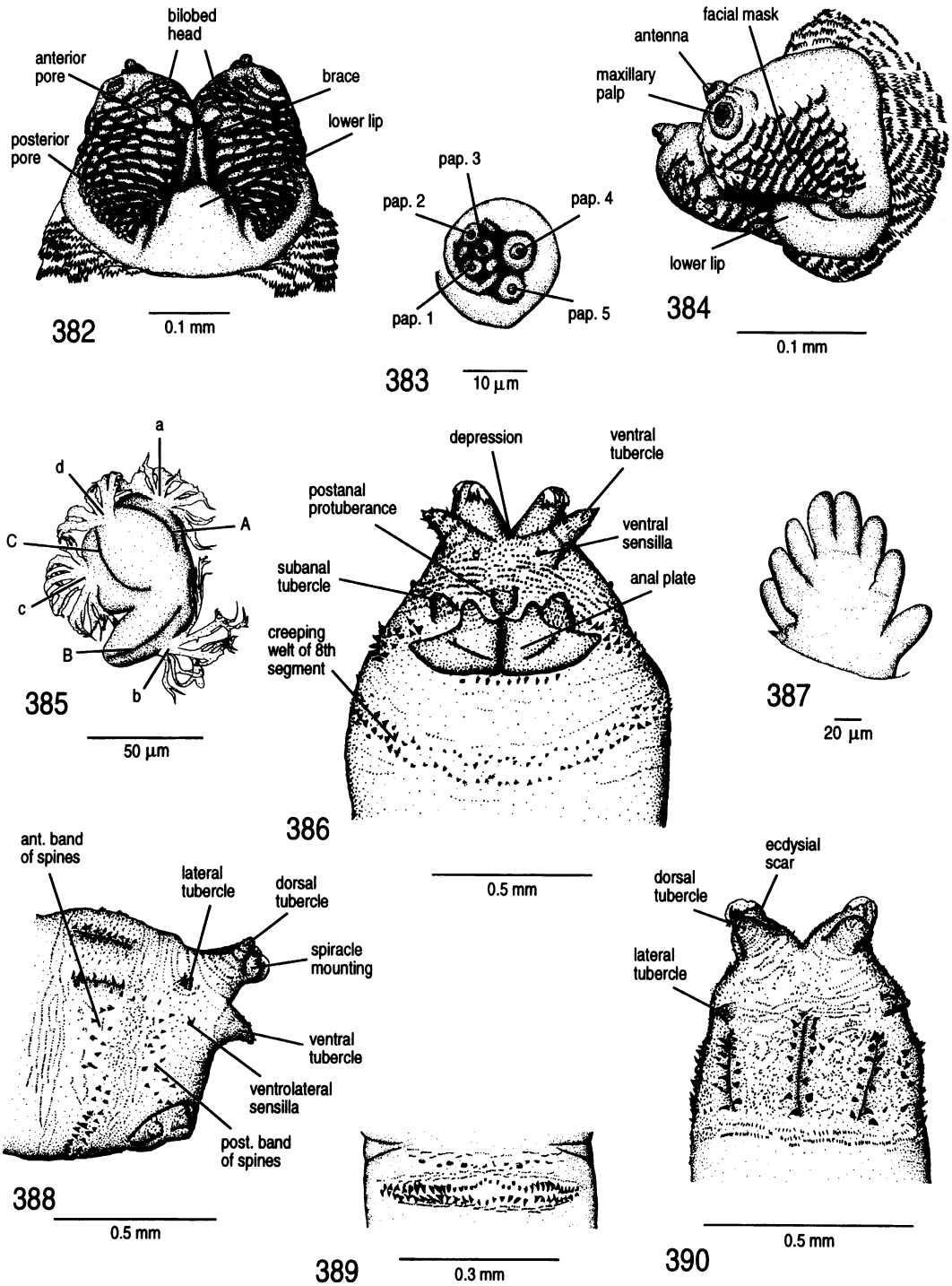


Fig. 382–390. *Themira leachi.* **Cephalic region:** 382: ventral, 384: lateral; **maxillary palp:** 383; **posterior spiracle:** 385; **last segment:** 386: ventral, 388: lateral, 390: dorsal; **anterior spiracle:** 387; **creeping welt:** 389.

Themira lucida (Staeger, 1844)

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 17
Length: 3.77–4.51 mm ($\bar{x}$ = 4.18 0.22; n = 10)
Largest width of body segments: 0.73–0.98 mm ($\bar{x}$ = 0.80 0.11; n = 10)
Width of last segment: 0.65–0.81 mm ($\bar{x}$ = 0.70 0.06; n = 10)

CEPHALIC REGION (fig. 391, ventral view; fig. 393, lateral view): Wider than long, distinctly bilobed, small lower lip; anterior pore on one comb to either side of mouthhooks; posterior pore on both lower lobe; brace consisting of two ridges which are adjacent and fuse only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing combs, on the inner side of cephalic lobes or around maxillae; combs about as wide as long with fine teeth; large facial mask almost entirely covered by combs, rows of combs converging onto anteromedian corner of lower lobe; few ridges close to lower lobe.

MAXILLA (fig. 392): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups distinct with an incomplete fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 396): 13–17 lobes arranged along a wide central axis which narrows toward tip; axis of spiracle stands perpendicular to body axis.

CREEPING WELTS (fig. 398): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 21–27 spines, median ones reduced to denticle-size; second row with 19–22 spines; no anteromedian spines, but occasionally large denticles anterior to row of spines. Except for last abdominal segment, body without hairs.

LAST ABDOMINAL SEGMENT (fig. 395, ventral view; fig. 397, lateral view; fig. 399, dorsal view): Not bulbous, with numerous denticle-like hairs; large, swollen anal plate with diagonal fold; postanal protuberance small and spiny; preanal protuberance absent but with spines anterior to anal plate; moderately sized, hairy subanal tubercles, immediately lateral to tips with subanal sensory organs; pair of large, well developed ventral tubercles with a ventral sensory organ at each base; small, shallow depression at base of ventral tubercles; spines on last segment rather small; with an anterior and a posterior band of spines but not well defined, anterior band not meeting ventrally; numerous denticles between bands; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short and wide, with very large dorsal tubercle; dorsal side of segment with three longitudinal grooves, with spines on either side; dorsal side of segment of last segment covered with denticles; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 394): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 5–7 hairs, unassociated process ("d") with 4–5 hairs; weakly curved openings in rectangular arrangement with opening "B" not displaced toward slit "C"; ecdysial scar immediately below spiracular plate in median position (fig. 399).

BIOLOGY: In Germany, Duda (1925) observed that *T. lucida* is common everywhere on pastures and around creeks. Gregor (1966) collected this species on bait whereby fruits were favored over meat and fish. There are no published rearings, but F. Püchel (personal commun.) told me that he caught and reared this species repeatedly on waterfowl dung. My attempts to establish a culture on cow dung were not successful. The flies bred only on the substrate on which they had been originally caught. The development time at 24°C was ten days. The dung could not be associated with any animal but resembled goose dung. O'Toole (1978) reported larvae as scavengers in a nest of *Vespula vulgaris*. What they fed on remains a mystery.

DISTRIBUTION: *Themira lucida* is a Palearctic species occurring mainly in Europe but there are some records from North Africa and throughout Russia including the Far East (Zuska and Pont, 1984).

Themira lutulenta Ozerov, 1986

Locality: Primorskiy kray, 40 km SE Ussuriysk (Far East of Russia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow

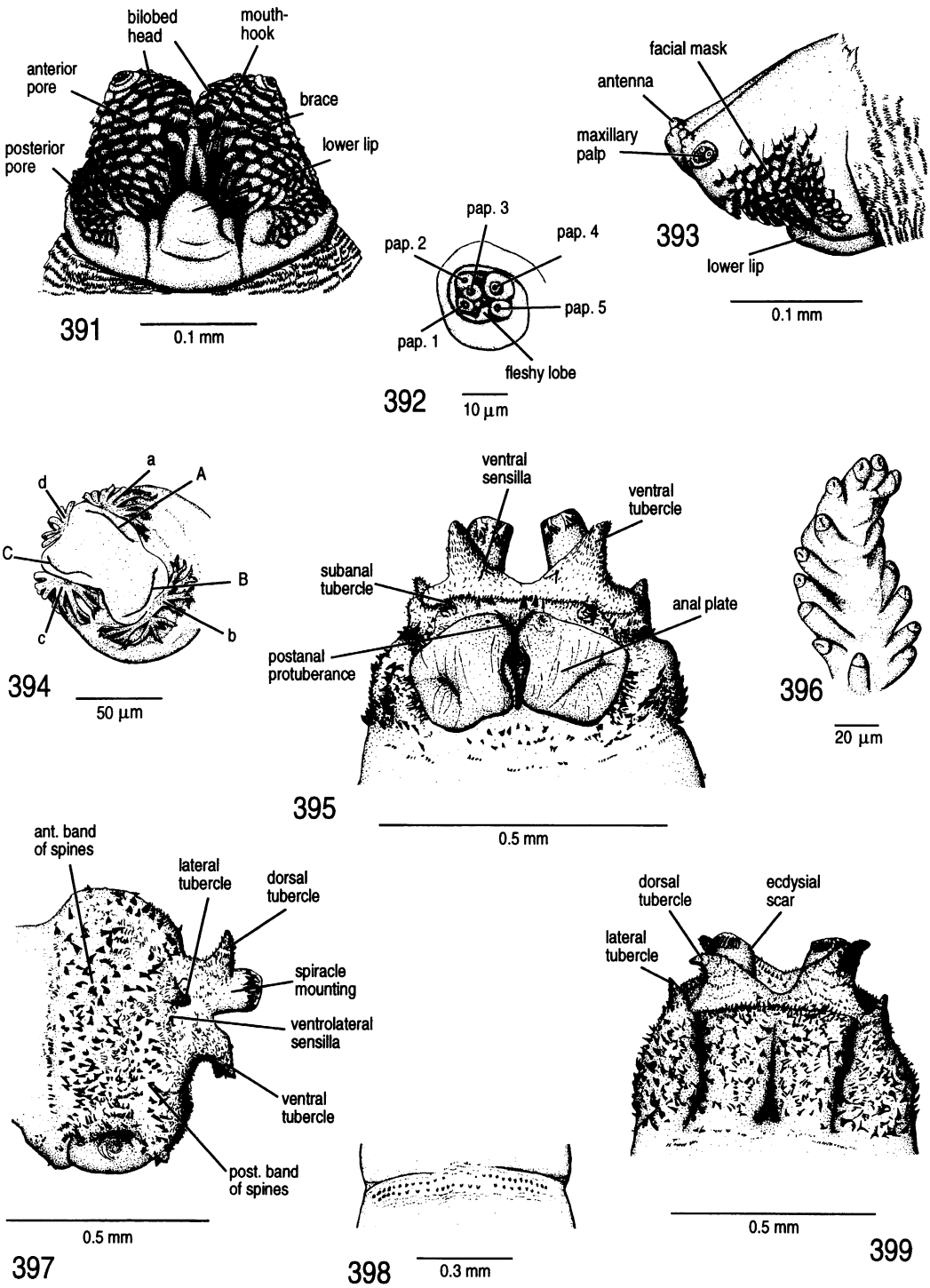


Fig. 391–399. *Themira lucida.* **Cephalic region:** 391: ventral, 393: lateral; **maxillary palp:** 392; **posterior spiracle:** 394; **last segment:** 395: ventral, 397: lateral, 399: dorsal; **anterior spiracle:** 396; **creeping welt:** 398.

Specimens examined: 6
Length: 7.78–8.33 mm ($\bar{x}$ = 7.96 0.19; n = 6)
Largest width of body segments: 0.79–0.95 mm ($\bar{x}$ = 0.87 0.06; n = 6)
Width of last segment: 0.72–0.91 mm ($\bar{x}$ = 0.82 0.06; n = 6)

CEPHALIC REGION (fig. 400, ventral view; fig. 402, lateral view): Wider than long, distinctly bilobed; anterior pore on one comb to either side of mouthhooks; lower lobe was not visible on any specimen, but is apparently surrounded by crescent-shaped ridge; brace consisting of two ridges which are adjacent along full length; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing comb, on the inner side of cephalic lobes, and around maxillae; combs mostly wider than long with numerous teeth; large facial mask, only anteromedian section covered by combs, remainder of facial mask consisting of serrate ridges converging onto anteromedian corner of lower lobe.

MAXILLA (fig. 401): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups small with only remnant of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 405): 14–16 lobes arranged along a broad central axis which narrows toward tip, lobes with annulations.

CREEPING WELTS (fig. 407): First six segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules; six remaining welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 11–28 spines, median ones missing or reduced in size; second row with 19–23 spines; about four anteromedian spines. Except for last abdominal segment, body without hairs.

LAST ABDOMINAL SEGMENT (fig. 404, ventral view; fig. 406, lateral view; fig. 408, dorsal view): Slightly bulbous; anal plate simple consisting of single lobe to either side of anal opening; postanal protuberance moderately large and spiny; preanal protuberance absent but with a more or less complete row of large spines along anterior margin of anal plate; large, hairy subanal tubercle, immediately lateral of tip with a subanal sensory organ; pair of well developed ventral tubercles with a ventral sensory organ at each base; with hairs in rows between anal plate and ventral tubercles (in contrast to the close relatives *T. flavicoxa* and *T. nigricornis*); spines on last segment rather large and arranged in a distinct anterior and a posterior band, anterior band not meeting ventrally; few hairs between rows of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; rather short and stout spiracle mountings, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves accompanied by a row of more or less irregularly spaced spines on either side; no additional hairs between grooves; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 403): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 6–8 hairs, unassociated process ("d") with 3–4 hairs; straight openings in rectangular arrangement; ecdysial scar in dorsomedian position just below spiracular plate (fig. 408).

BIOLOGY: Unknown.

DISTRIBUTION: *Themira lutulenta* is currently only known from the Far East of Russia.

Themira minor (Haliday, 1833)

Locality: Kevelaer (Nordrhein-Westfalen, Germany); Berlin (Germany), coll. R. Meier
Specimens examined: 62
Length: 3.52–4.59 mm ($\bar{x}$ = 4.23 0.31; n = 10)
Largest width of body segments: 0.73–1.1 mm ($\bar{x}$ = 0.94 0.10; n = 10)
Width of last segment: 0.56–0.92 mm ($\bar{x}$ = 0.79 0.10; n = 10)

CEPHALIC REGION (fig. 409, ventral view; fig. 411, lateral view): Wider than long, distinctly bilobed, small lower lip, with anterior pore on one comb to either side of mouthhooks; posterior pore on both lower lobes; brace consisting of two ridges, adjacent and fused only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing combs, on the inner side of cephalic lobes or around maxillae; combs wider than

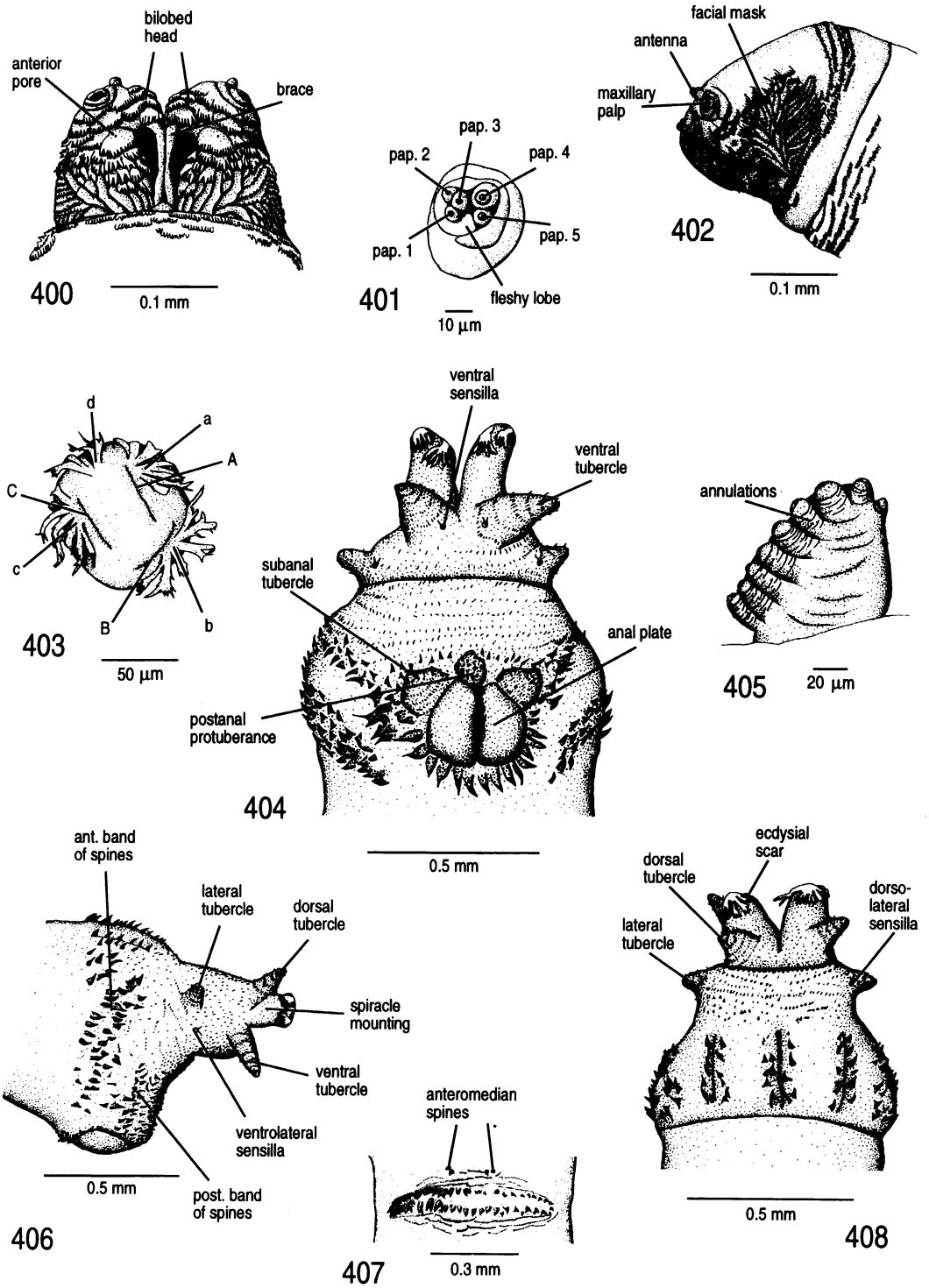


Fig. 400–408. *Themira lutulenta.* **Cephalic region:** 400: ventral, 402: lateral; **maxillary palp:** 401; **posterior spiracle:** 403; **last segment:** 404: ventral, 406: lateral, 408: dorsal; **anterior spiracle:** 405; **creeping welt:** 407.

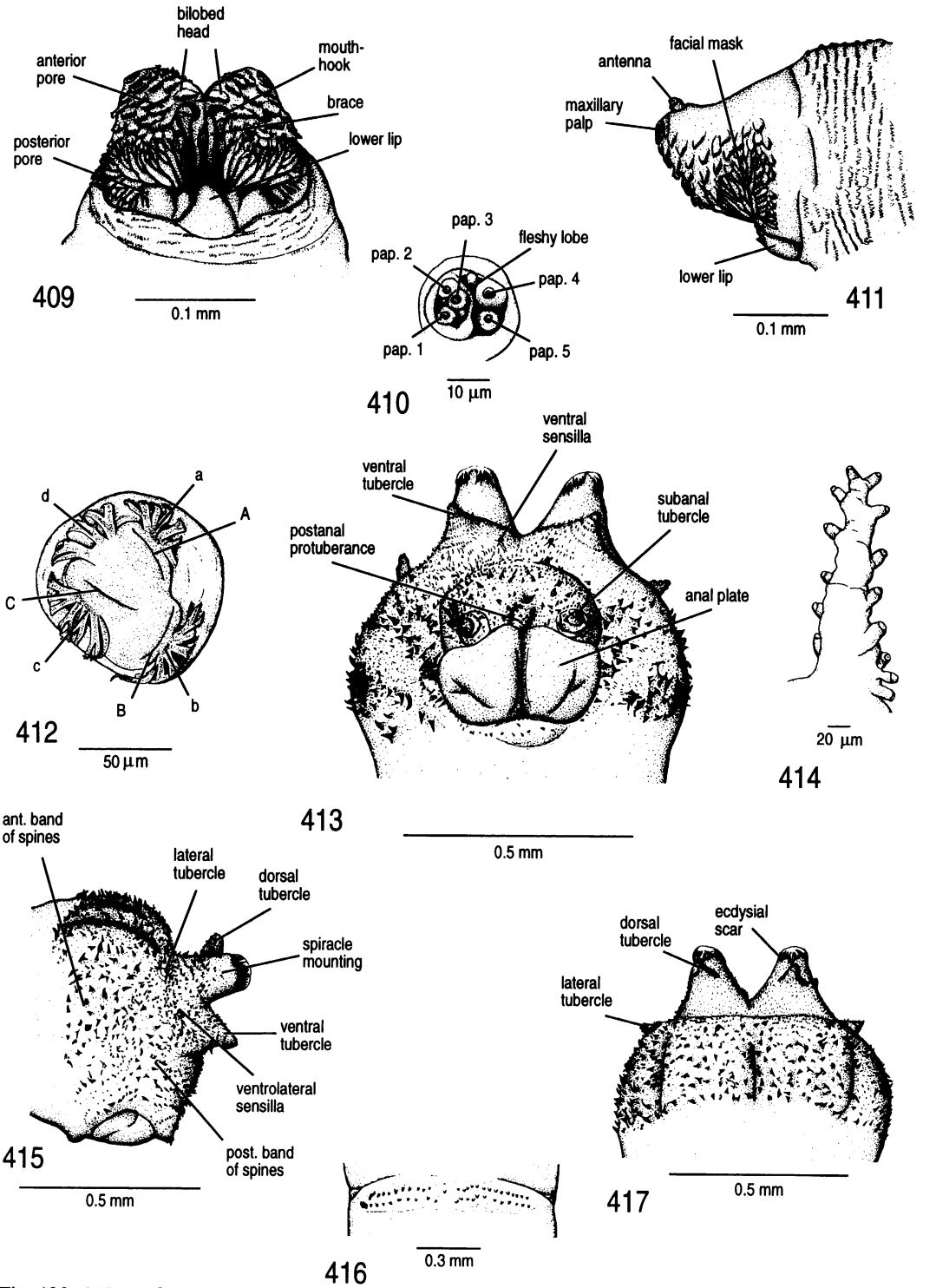


Fig. 409–417. *Themira minor*. **Cephalic region:** 409: ventral, 411: lateral; **maxillary palp:** 410; **posterior spiracle:** 412; **last segment:** 413: ventral, 415: lateral, 417: dorsal; **anterior spiracle:** 414; **creeping welt:** 416.

long with numerous fine teeth; large facial mask, only anteromedian section covered by combs, rest of facial mask consisting of ridges converged onto anteromedian corner of lower lobe.

MAXILLA (fig. 410): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups distinct with a complete but very narrow fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 414): 11–15 lobes arranged along central axis, narrowing toward tip (see also Mangan, 1977); central axis perpendicular to body axis.

CREEPING WELTS (fig. 416): First seven segments with rows of spinules laterally and dorsally; ventrally, first four welts consisting of spinules, remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 23–26 spines, median spines denticle-size, second row with 13–23 spines; no large spines anterior to two long rows; spines generally very small. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 413, ventral view; fig. 415, lateral view; fig. 417, dorsal view): Bulbous, with numerous denticles; anal plate enlarged with diagonal fold, plate about one-third as wide as posterior segment; postanal protuberance moderately large and spiny; preanal protuberance weakly developed as a row of spines along anterior margin of anal plate; large, hairy subanal tubercles, posterior to tips with a subanal sensory organ; pair of well-developed ventral tubercles with a ventral sensory organ at each base; spines on last segment rather small; anterior and posterior band of spines not very well separated and not well defined; anterior band not meeting ventrally; between bands with numerous denticles and hairs; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves with spines on either side; spines in irregular row along grooves and across entire dorsal side of last segment; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 412): Has three openings and four processes of spiracular hairs, ones associated with openings ("a–c") with 5–9 hairs, unassociated process ("d") with 3–4 hairs; weakly curved openings in rectangular arrangement with opening "B" displaced toward slit "C"; ecdysial scar in dorsomedian position just below spiracular plate (fig. 417).

BIOLOGY: *Themira minor* is a very common species that Mangan (1977) reported from cattle feeding pens, Coffey (1966) from horse droppings, and Papp (1974b) and Coffey (1966) from pig dung. It has been reared from cow dung (Pont, 1979) and larvae have been found in manure heaps and/or the compost of cattle dung (Iwasa, 1981). I collected this species also on sewage and on the muddy banks of a creek. It is frequently associated with *T. putris*. In the laboratory it breeds very well on cow dung and the development time is the shortest I have observed for any *Themira* (24°C: 8 days from egg to imagines). I never observed any pre- or postcopulatory guarding. *Themira minor* is one of the few species in this genus for which flower visits have been recorded (van der Goot, 1986a: on flowers of *Angelica sylvestris*).

DISTRIBUTION: *Themira minor* is Holarctic with numerous records in both regions including Georgia and the Far East of Russia (Iwasa, 1980: Japan; 1989; Mangan, 1977; Zuska and Pont, 1984)

Themira nigricornis (Meigen, 1826)

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 6
Length: 6.79–7.62 mm ($\bar{x}$ = 7.06 0.28; n = 6)
Largest width of body segments: 0.82–0.98 mm ($\bar{x}$ = 0.89 0.06; n = 6)
Width of last segment: 0.75–1.04 mm ($\bar{x}$ = 0.83 0.11; n = 6)

CEPHALIC REGION (fig. 418, ventral view; fig. 420, lateral view): Wider than long, distinctly bilobed, small lower lip; anterior pore on one comb to either side of mouthhooks; posterior pores on both lower lobes; lobe surrounded by crescent-shaped ridge; brace consisting of two ridges, tips not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to porebearing combs, on the inner side of cephalic lobes or around maxillae; combs most-

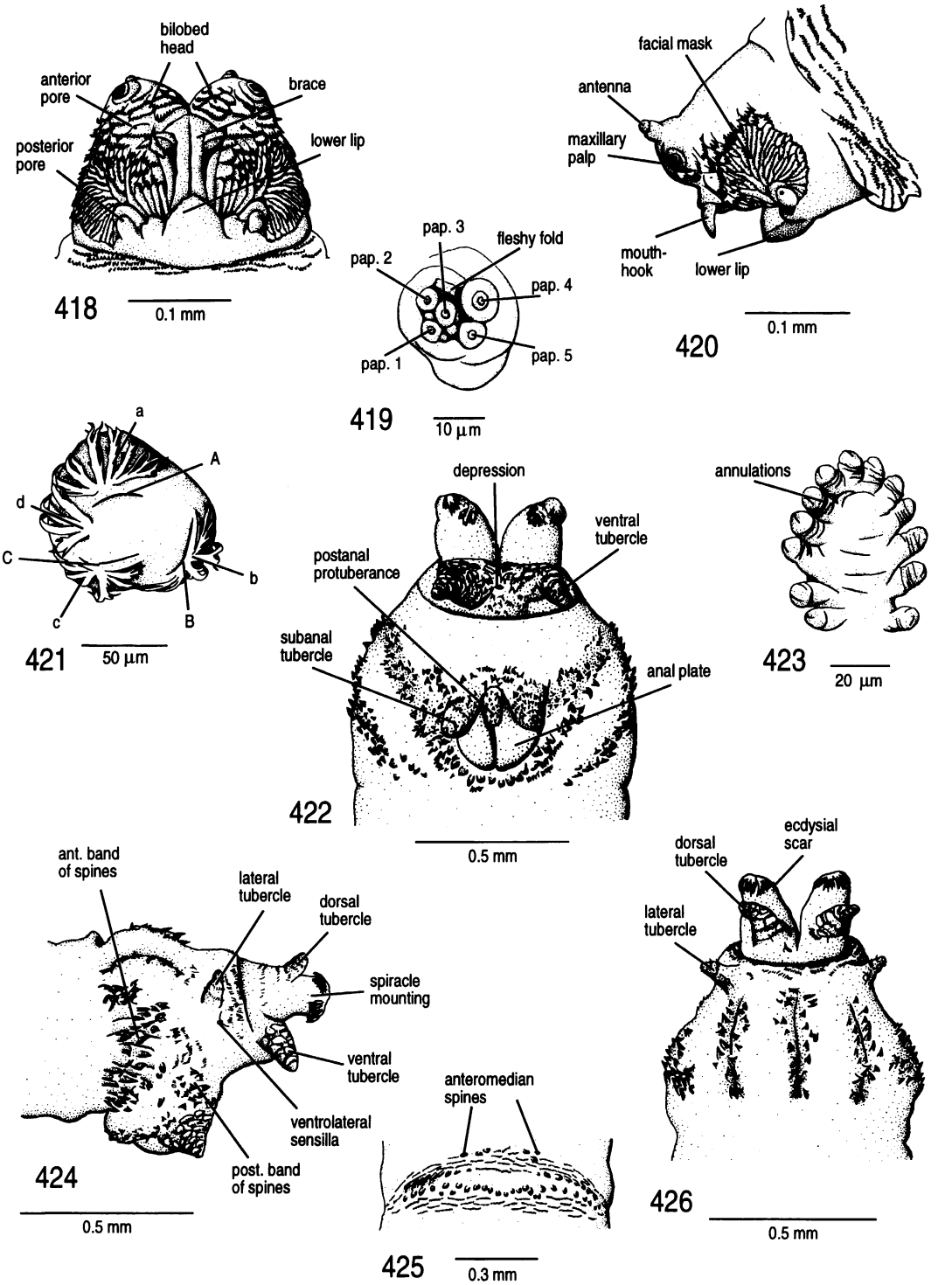


Fig. 418–426. *Themira nigricornis.* **Cephalic region:** 418: ventral, 420: lateral; **maxillary palp:** 419; **posterior spiracle:** 421; **last segment:** 422: ventral, 424: lateral, 426: dorsal; **anterior spiracle:** 423; **creeping welt:** 425.

ly wider than long with numerous fine teeth; large facial mask with serrate ridges converging onto anteromedian corner of lower lobe.

MAXILLA (fig. 419): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups distinct with remnant of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 423): 17–21 lobes arranged along a broad central axis, narrowing toward tip and standing perpendicular to body axis; in some specimens with additional lobes at base of axis; lobes with secondary annulations.

CREEPING WELTS (fig. 425): First five segments with rows of spinules laterally and dorsally; sixth only with lateral spinules; ventrally, first four welts consisting of spinules, remaining six welts ventrally with two long rows of reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 19–27, median ones reduced to the size of denticles, second row with 25–27 spines; 2–4 anteromedian spines forming a short anterior row; no hairs on body segments.

LAST ABDOMINAL SEGMENT (fig. 422, ventral view; fig. 424, lateral view; fig. 426, dorsal view): Moderately bulbous; anal plate simple, consisting of single lobe; postanal protuberance moderately large and spiny; preanal protuberance absent, but with a more or less complete row of spines along anterior margin of anal plate; large, hairy subanal tubercle, immediately lateral to tip with a subanal sensory organ; pair of well-developed ventral tubercles, ventral sensory organ at each base; small and shallow depression between bases of tubercles; spines on last segment small, arranged in an anterior and a posterior band; anterior band not meeting ventrally; without denticles or hairs between rows of spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; short, wide spiracle mountings, with large dorsal tubercle; dorsal side of segment has three longitudinal grooves accompanied by row of irregularly spaced spines on either side; no hairs between grooves; hairs of sensory organs short, sometimes with three instead of two sensory hairs.

POSTERIOR SPIRACULAR DISC (fig. 421): Has three openings and four processes of spiracular hairs, those ("a–c") associated with openings with 7–9 hairs, unassociated process ("d") with four hairs; weakly curved openings in rectangular arrangement with opening "B" barely shifted toward slit "C"; ecdysial scar immediately below spiracular plate in median position (fig. 426).

BIOLOGY: Duda (1925) found large numbers of *T. nigricornis* in a sheep pasture. Iwasa (1981) reported it from cow dung mixed with litter (straw or rice stem) and Gregor (1966) observed adults on rotting meat (see also Pont, 1979) and fungi. It has been reared from garden soil and human excrement (Pont, 1979) and in Alaska from pupae floated from marsh material (Mangan, 1976). There is general agreement that this species is almost exclusively found in early spring (Gregor, 1966; Minder, 1963; Steyskal, 1946; personal obs.).

DISTRIBUTION: This species is Holarctic with numerous records in Europe and Asia including Japan (Iwasa, 1981; 1989; Zuska and Pont, 1984). Steyskal (1946) and Mangan (1976) furnished records for this species in North America including Alaska.

Themira putris (Linnaeus, 1758)

Locality: Berlin (Germany), Kevelaer (Nordrhein-Westfalen, Germany), coll. R. Meier
Specimens examined: 61
Length: 6.55–8.2 mm ($\bar{x}$ = 7.42 0.45; n = 10)
Largest width of body segments: 0.66–1.08 mm ($\bar{x}$ = 0.93 0.12; n = 10)
Width of last segment: 0.77–1.02 mm ($\bar{x}$ = 0.90 0.10; n = 10)

Immatures were previously described by Hennig (puparia: Hennig, 1949:19). He provided length measurements for first instars and a drawing of the cephalopharyngeal skeleton of the first and second instar. Mangan (1977) depicted the anterior spiracles and cephalic region of the third instar.

CEPHALIC REGION (fig. 427, ventral view; fig. 429, lateral view): Wider than long, distinctly bilobed, small lower lip, with anterior pore on one comb to either side of mouthhooks; posterior pores on both lower lobes; brace consisting of two adjacent ridges that are fused only at tip, tips not enlarged; combs not restricted to anterior section of cephalic

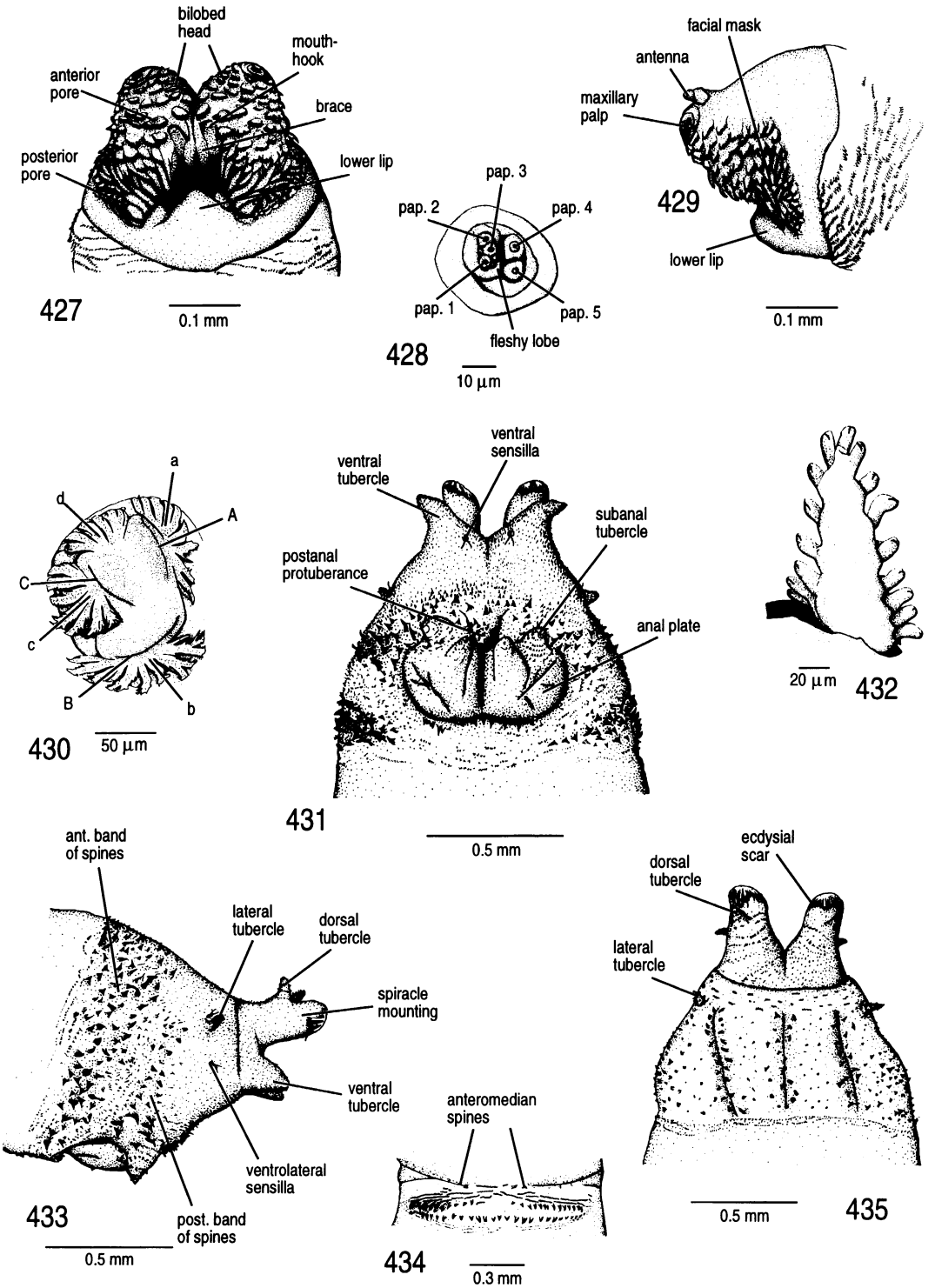


Fig. 427–435. *Themira putris*. **Cephalic region:** 427: ventral, 429: lateral; **maxillary palp:** 428; **posterior spiracle:** 430; **last segment:** 431: ventral, 433: lateral, 435: dorsal; **anterior spiracle:** 432; **creeping welt:** 434.

lobes, but also on facial mask posterior to pore-bearing combs, on the inner side of cephalic lobes, and around maxillae; combs wider than long with numerous fine teeth; large facial mask partly covered by combs, partly by ridges; ridges restricted to posterior part of facial mask, rows of combs and ridges both converging onto anteromedian corner of lower lobe (for illustrations of cephalopharyngeal skeleton, see Hennig, 1949).

MAXILLA (fig. 428): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), gap between groups distinct with incomplete fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 432): 15–23 lobes arranged along a central axis which narrows toward tip. Hennig (1949, with text fig. 34) and Mangan (1977: fig. 6) confirmed large number of lobes. Hennig found 23 lobes on one puparium, apparently, always with some basal lobes at base of central axis (cannot be seen on figure; missing in Mangan's sketch); central axis perpendicular to body axis.

CREEPING WELTS (fig. 434): First eight segments with rows of spinules laterally; first seven with spinules dorsally; ventrally, first four welts consisting of spinules; remaining six welts ventrally with two long rows of reclinate spines and multiple short additional rows of spinules anterior and posterior to spines; first row with 21–25 spines, median ones missing or reduced in size; second row with 22–28 spines. Except for last abdominal segment, no hairs on integument.

LAST ABDOMINAL SEGMENT (fig. 431, ventral view; fig. 433, lateral view; fig. 435, dorsal view): Not bulbous, with denticlelike hairs; anal plate enlarged with diagonal fold and posteromedian corner drawn out, anal plate half as wide as last segment; postanal protuberance large and spiny; preanal protuberance absent but with a row of spines along anterior margin of anal plate; rather large, hairy subanal tubercles; subanal sensory organ, posterior to their tips; pair of well developed ventral tubercles with a ventral sensory organ at each base; shallow depression between bases of tubercles; spines on last segment small, arranged in an anterior and a posterior band, anterior band not meeting ventrally; numerous denticles and hairs between bands of spines and in front of anterior band; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with medium-sized dorsal tubercle; dorsal side of segment with three longitudinal grooves with a row of irregularly spaced spines on either side; additional spinules between grooves; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 430): Has three openings and four processes of spiracular hairs, those associated with openings ("a–c") with 7—10 hairs, unassociated process ("d") with 3–4 hairs; weakly curved openings in rectangular arrangement with opening "B" displaced toward slit "C"; ecdysial scar in dorsomedian position just below spiracular plate (fig. 435); spiracular plates of all three instars are also depicted in Hennig (1949).

BIOLOGY: *Themira putris* is probably the most common *Themira* in Germany. It has been reported from human excrement (Pont, 1979; Zetterstedt in Hennig, 1949), cow dung (Duda, 1925), horse dung (Wainstein and Rodowa in Hennig 1949), liquid manure (Andersson, 1975; Coffey, 1966; Duda, 1925; Hennig, 1949; Minder, 1963; numerous personal obs.), sewage (Cole, 1969; Melander and Spuler, 1917) pig dung (Papp, 1974b), cattle feeding pens, rotting vegetation (Andersson, 1975; Mangan, 1977), green algae on the Baltic Sea (observed by Remmert, reported in Moeller, 1965) and sea wrack (van der Goot, 1986a). It is notorious for large outbreaks in sewage works (Pont, 1979; personal obs.) and can be caught on fish bait but also visits fruits and feces (Gregor, 1966). It has been reared from liquid pig manure (Coffey, 1966; Papp, 1974b) and such unusual substrates as a bird's nest (Pont, 1979) and sea wrack that had been exposed to fresh water (Moeller, 1965). According to Minder (1963), copulations mainly take place in late afternoon, but can also be observed at other times of the day (personal obs.). The development time is 20–30 days and at least some pupae hibernate. There is no pre- or postcopulatory guarding. *Themira putris* occasionally visits flowers (Bährmann, 1993: *Cornus mas*; van der Goot, 1986a: *Heracleum*).

DISTRIBUTION: *Themira putris* is Holarctic with records throughout both regions (Iwasa,

1981: Japan; Zuska and Pont, 1984; Mangan, 1977). Cole (1969) speculated that this species was introduced to the USA.

Themira (Enicita) simplicipes (Duda, 1926)

Locality: Caucasus, North Ossetia, near Alagir (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 5
Length: 3.34–3.87 mm ($\bar{x}$ = 3.65 0.21; n = 5)
Largest width of body segments: 0.47–0.58 mm ($\bar{x}$ = 0.51 0.05; n = 5)
Width of last segment: 0.38–0.53 mm ($\bar{x}$ = 0.46 0.06; n = 5)

CEPHALIC REGION (fig. 436, ventral view; fig. 438, lateral view): Wider than long, bilobed, small lower lip; anterior pore on one comb to either side of mouthhooks; posterior pore on both lower lobes; brace consisting of two ridges adjacent and fused only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, but also on facial mask posterior to pore-bearing comb, on the inner side of cephalic lobes, and around maxillae; combs wider than long with numerous rather coarse teeth; facial mask small, covered with combs arranged in rows, with only few ridges around lower lobe.

MAXILLA (fig. 437): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4), distinct gap between groups with remnants of a fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 441): Ten lobes arranged along a central axis; spiracle not perpendicular to body axis.

CREEPING WELTS (fig. 443): First seven segments with rows of spinules laterally and dorsally; last only with lateral spinules; ventrally, first four welts consisting of spinules; remaining six welts with two long rows of reclinate spines ventrally and multiple additional rows of spinules anterior and posterior to spines; first row of spines on fifth segment consisting of only denticles with multiple tips, remaining welts with 10–16 spines, not counting the denticle-size median ones; second row with 10–21 spines; no anteromedian spines, but some denticles in that area slightly enlarged. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 440, ventral view; fig. 442, lateral view; fig. 444: dorsal view; fig. 466): Not bulbous, with few hairs; anal plate very large with diagonal fold, as wide as last segment; spiny postanal protuberance; preanal protuberance very conspicuously bulbous, buttonlike, and composed of fused spines; small, hairy subanal tubercle, immediately lateral of tips with a subanal sensory organ; pair of well-developed, long ventral tubercles with a ventral sensory organ at each base; small, but deep depression at base of ventral tubercles; all spines on last segment very small, not much larger than denticles; anterior band of spines not well defined, not meeting ventrally; weakly developed posterior band of spines; numerous denticles between spines; however, none between bands; small lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings moderately long, with moderately large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of more or less regularly spaced spines on either side; no additional spines or hairs between grooves; sensory organs with short hairs.

POSTERIOR SPIRACULAR DISC (fig. 439): Has three openings and four processes of spiracular hairs, those associated with openings ("a–c") with 6–7 hairs, unassociated process ("d") with 3–4 hairs; weakly curved openings in rectangular arrangement with opening "B" only slightly displaced toward slit "C"; ecdysial scar halfway between spiracular plate and dorsal tubercle in median position (fig. 444).

BIOLOGY: Unknown.

DISTRIBUTION: Zuska and Pont (1984) reported Hungary and Romania as the only countries in which this species occurs, but Ozerov collected some specimens in the Caucasus Mountains (Georgia).

Themira superba (Haliday, 1833)

Locality: Caucasus, North Ossetia, near Alagir (Georgia), coll. Dr. A. L. Ozerov, Lomonosov University Moscow
Specimens examined: 5
Length: 4.69–5.25 mm ($\bar{x}$ = 4.99 0.21; n = 5)

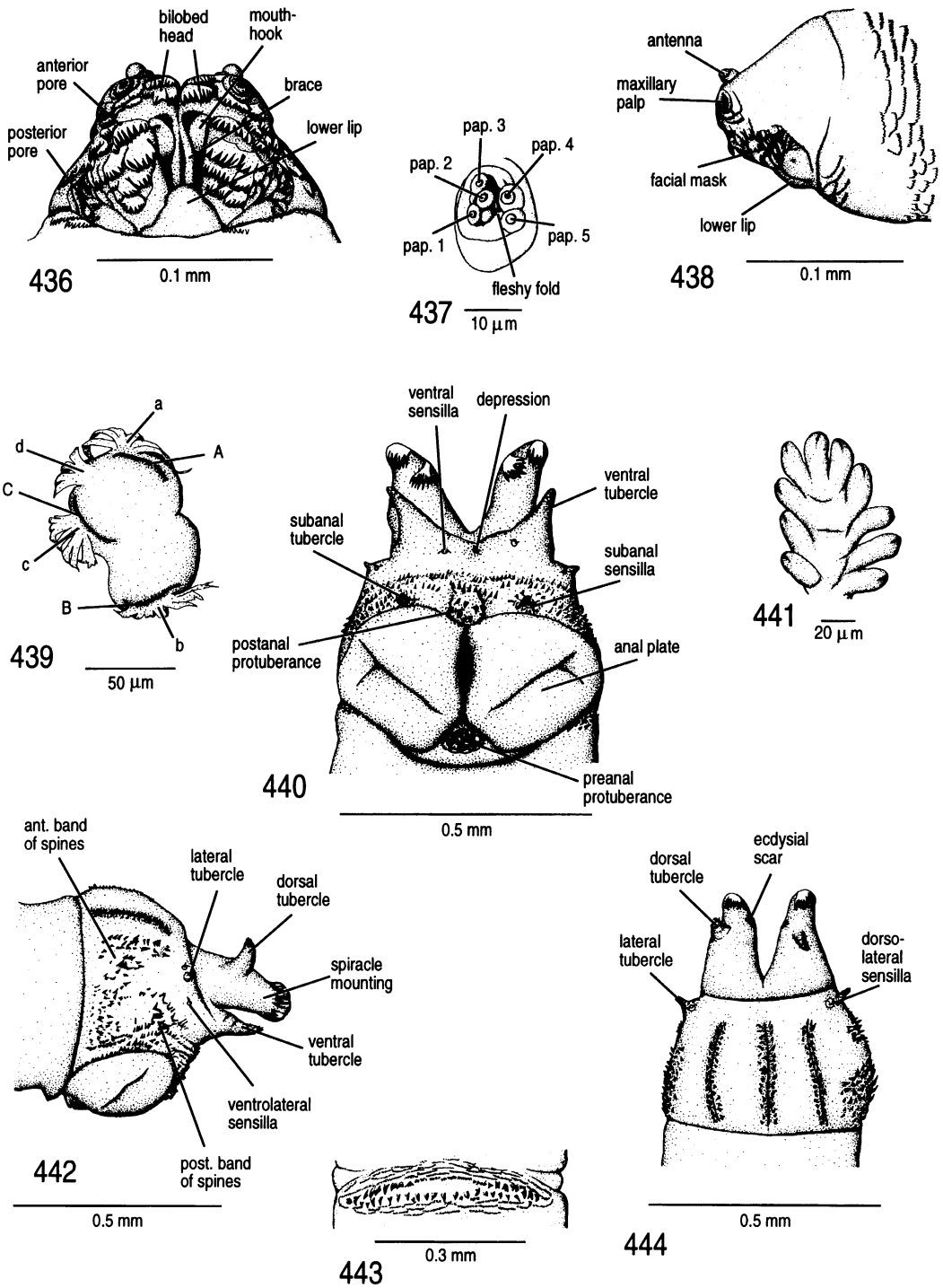


Fig. 436–444. *Themira simplicipes.* **Cephalic region:** 436: ventral, 438: lateral; **maxillary palp:** 437; **posterior spiracle:** 439: **last segment:** 440: ventral, 442: lateral, 444: dorsal; **anterior spiracle:** 441; **creeping welt:** 443.

Largest width of body segments: 0.61–0.87 mm ($\bar{x}$ = 0.7^ 0.10; n = 5)
Width of last segment: 0.69–0.85 mm ($\bar{x}$ = 0.77 0.08; n = 5)

CEPHALIC REGION (fig. 445, ventral view; fig. 447, lateral view): Wider than long, distinctly bilobed, small lower lip; anterior pore on one comb to either side of mouthhooks; posterior pore on both lower lobes; lower lobes surrounded by crescent-shaped ridge; brace consisting of two ridges adjacent and fused only at tip, tip not enlarged; combs not restricted to anterior section of cephalic lobes, also on facial mask posterior to pore-bearing combs, on the inner side of cephalic lobes, and around maxillae; combs about as wide as long with numerous fine teeth; large facial mask largely covered with combs, only a few ridges around lower lobe remain; rows of combs and ridges converging onto anteromedian corner of lower lobe.

MAXILLA (fig. 446): Composed of five compound papillae in two distinct groups of two and three; four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); gap between groups distinct with remnants of fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 450): 15–17 lobes arranged along central axis standing perpendicular to body axis.

CREEPING WELTS (fig. 452): First five segments with dorsal rows of spinules, first six with lateral spinules; ventrally, first four welts consisting of rows of spinules; fifth welt with few spines in one row; remaining six welts with two long rows of ventral reclinate spines and multiple additional rows of spinules anterior and posterior to spines; first row of spines with 15–31, median ones missing or reduced in size; second row with 19–30; no anteromedian spines. Body without hairs except for on last abdominal segment.

LAST ABDOMINAL SEGMENT (fig. 449, ventral view; fig. 451, lateral view; fig. 453, dorsal view): Slightly bulbous, with few denticlelike hairs; anal plate enlarged with diagonal fold and protuberant anterolateral and posteromedian corners; spiny postanal protuberance; preanal protuberance absent but with a few spines along anterior margin of anal plate; moderate-size, hairy subanal tubercles immediately lateral to tips with a subanal sensory organ; pair of well-developed ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; spines on last segment rather small; anterior band of spines well defined, not meeting ventrally; rather small number of spines forming a posterior band; denticles between spines; lateral tubercle associated with a dorso- and a ventrolateral sensory organ; spiracle mountings short, with large dorsal tubercle; dorsal side of segment without three longitudinal grooves, instead dorsal side of segment entirely covered with equally spaced spines; hairs of sensory organs short.

POSTERIOR SPIRACULAR DISC (fig. 448): Has three openings and four processes of spiracular hairs, those associated with openings ("a–c") with 5–8 hairs, unassociated process ("d") with three hairs; weakly curved openings in rectangular arrangement with opening "B" displaced toward "C"; ecdysial scar in dorsomedian position just below spiracular plate (fig. 453).

BIOLOGY: Duda (1925) collected *T. superba* on pastures along creeks and lake shores where the species was very common locally. Minder (1963) also found the species in cattlesheds and cited Shtakel'berg (1958) who reported it from water banks. The latter reference is in good agreement with Duda (1925) and F. Püchel's observation (personal commun.) that the species breeds on either duck- or goose dung. Van der Goot (1986a) observed visits of *Heracleum* flowers.

DISTRIBUTION: This species can be found in central, northern, and eastern Europe (Zuska and Pont, 1984).

16. GENUS *XENOSEPSIS* MALLOCH, 1925

Xenosepsis fukuharai Iwasa, 1984

Locality: Berlin (Germany), coll. R. Meier
Specimens examined: 6
Length: 5.5–8.74 mm ($\bar{x}$ = 7.84 1.09; n = 6)
Largest width of body segments: 0.67–0.74 mm ($\bar{x}$ = 0.71 0.03; n = 6)
Width of last segment: 0.68–0.84 mm ($\bar{x}$ = 0.76 0.06; n = 6)

CEPHALIC REGION (fig. 454, ventral view; fig. 456, lateral view): Longer than wide, distinctly bilobed; small lower lip; posterior pore on both lower lobes and anterior pores on

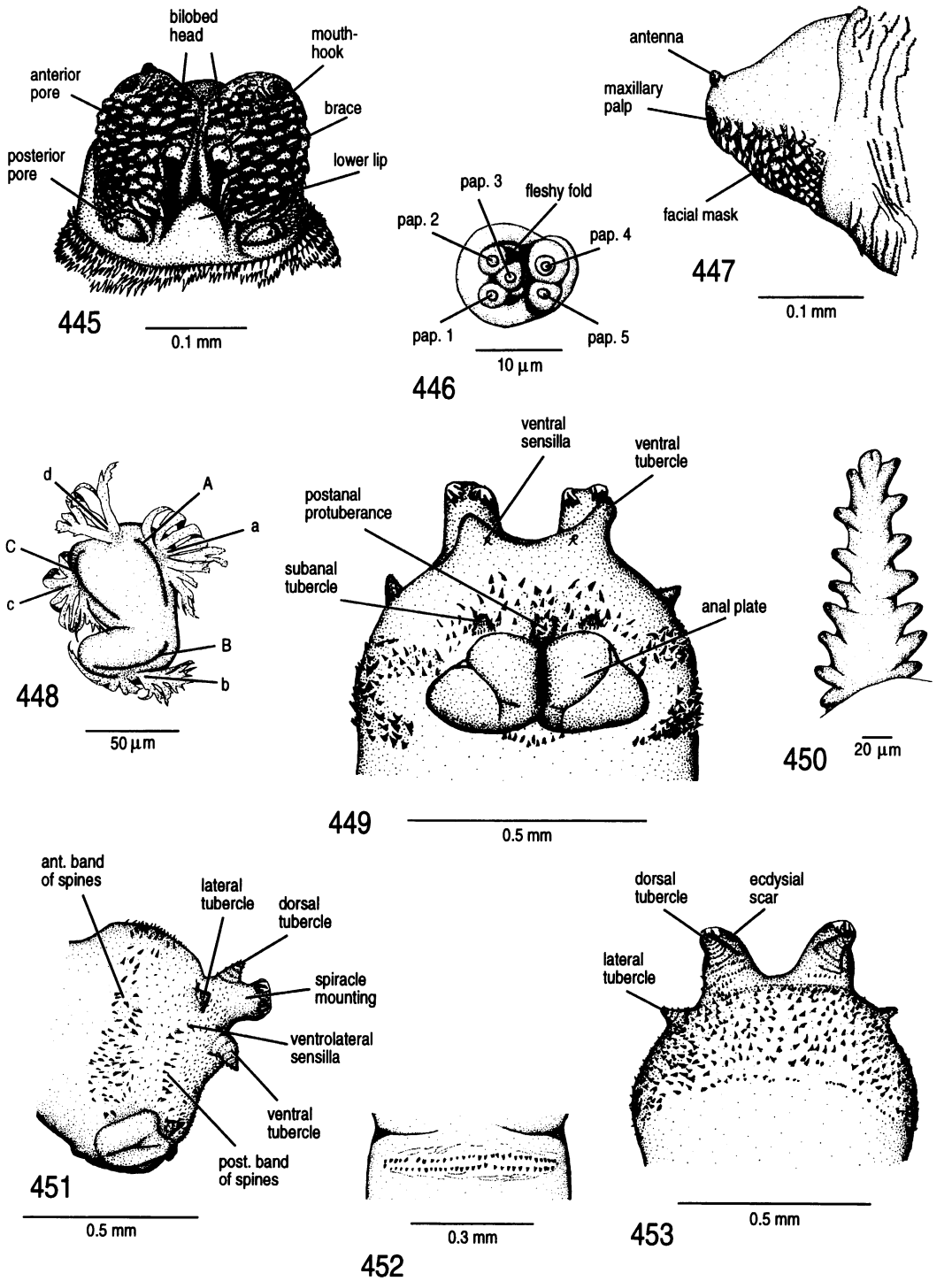


Fig. 445–453. *Themira superba.* **Cephalic region:** 445: ventral, 447: lateral; **maxillary palp:** 446; **posterior spiracle:** 448; **last segment:** 449: ventral, 451: lateral, 453: dorsal; **anterior spiracle:** 450; **creeping welt:** 452.

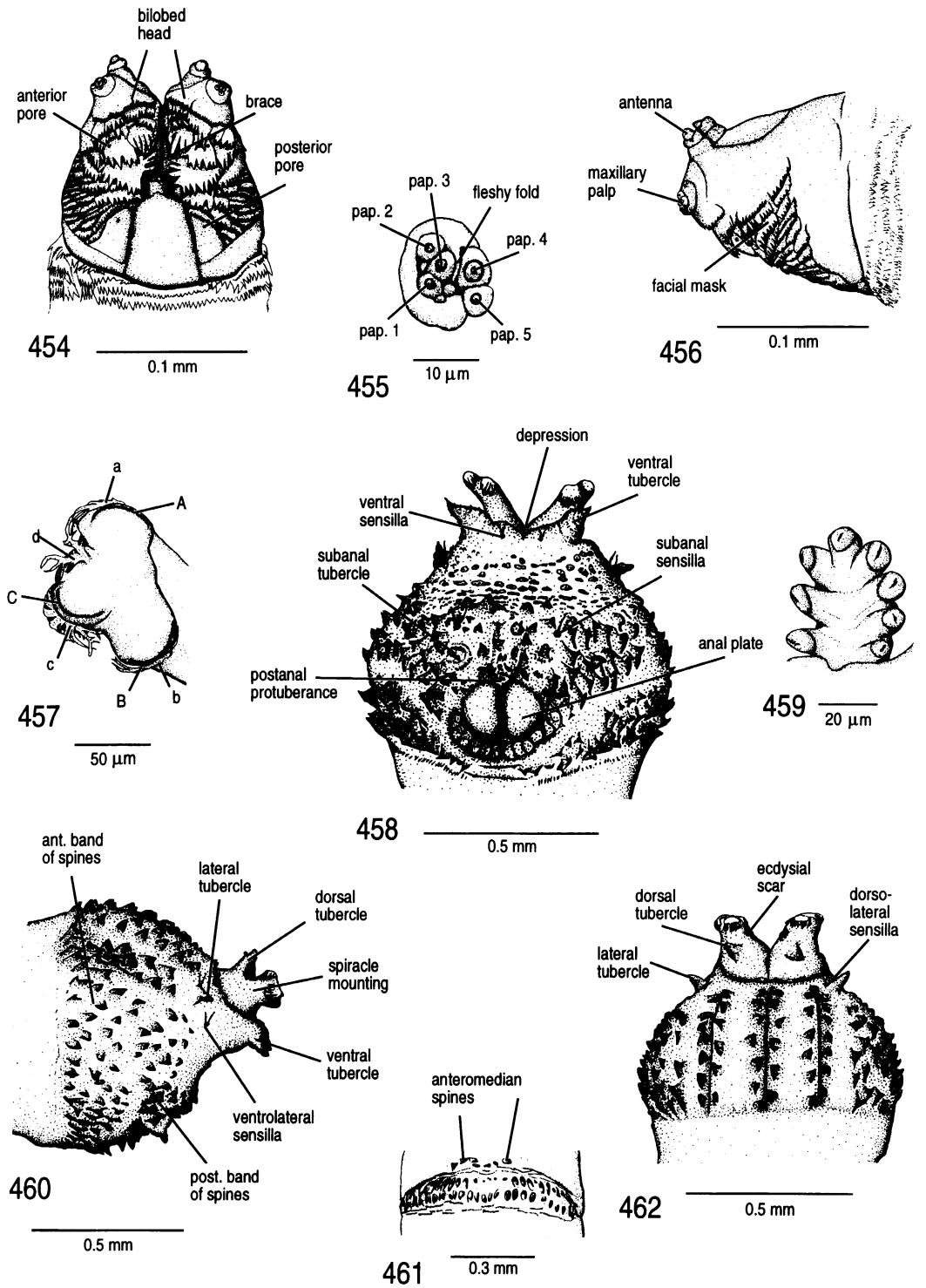


Fig. 454–462. *Xenosepsis fukuharai*. **Cephalic region:** 454: ventral, 456: lateral; **maxillary palp:** 455; **posterior spiracle:** 457; **last segment:** 458: ventral, 460: lateral, 462: dorsal; **anterior spiracle:** 459; **creeping welt:** 461.

one comb to either side of mouthhooks; brace gaping along full length, tips not distinctly enlarged; combs not restricted to anterior section of cephalic lobes but also on facial mask; combs on cephalic lobes much wider than long with multiple small teeth arranged in horizontal rows; no combs on the inner side of cephalic lobes and around maxillae; facial mask with ridges transformed into combs, with coarse, often bifurcated, tips converging onto anteromedian corner of lower lobe.

MAXILLAE (fig. 455): Composed of five compound papillae in two distinct groups of two (pap. 4, 5) and three (pap. 1–3); four papillae consisting of two superimposed lobes (pap. 1–3, 5), one composed of three superimposed lobes (pap. 4); distinct gap between groups, with an incomplete fleshy lobe separating them.

ANTERIOR SPIRACLE (fig. 459): 8–11 lobes arranged along a central axis.

CREEPING WELTS (fig. 461): First six segments with rows of spinules laterally and dorsally; first four welts consisting of ventral spinules; remaining six welts with two long rows of reclinate spines ventrally and additional rows of spinules anterior and posterior to spines; first row of spines with 22—29, median ones missing or reduced to denticle-size; second row with 22–24 spines; in addition to long rows, 3–7 anteromedian spines forming short anterior row. Except for last abdominal segment, integument without hairs.

LAST ABDOMINAL SEGMENT (fig. 458, ventral view; fig. 460, lateral view; fig. 462, dorsal view): Distinctly bulbous, not at all hairy, but with large warts between anal plate and ventral tubercles; anal plate simple, not enlarged and without diagonal fold, rounded laterally; postanal protuberance tongue-shaped, spiny; preanal row of spines along anterior margin of anal plate; weakly developed, bare subanal tubercle, posterior to tip with subanal sensory organ; pair of ventral tubercles with a ventral sensory organ at each base; depression between bases of tubercles; anterior band of spines well developed, but not well separated from posterior band; anterior band almost meeting ventrally at midline; spines large with wide base and somewhat blunt tip; lateral tubercle associated with a dorso- and ventrolateral sensory organ; spiracle mountings short, with large dorsal tubercle; dorsal side of segment with three longitudinal grooves, each bordered by a row of equally spaced, large spines on either side; no hairs between grooves; hairs of sensory organs long.

POSTERIOR SPIRACULAR DISC (fig. 457): Three openings and four processes of spiracular hairs on trifoliate plate, the processes ("a–c") associated with openings with 6–8 hairs, unassociated process ("d") with two hairs; hairs distinctly branched; weakly curved openings in a triangular arrangement; ecdysial scar in dorsomedian position halfway between dorsal tubercle and spiracular plate (fig. 461).

BIOLOGY: Iwasa (1984) who described *X. fukuharai* reported: "The adult flies are mainly found on the manure heap of pig dung." Ozerov (1989) found adults in vegetation at a refuse pit and collected larvae and imagines from vertebrate carcasses (see also Ozerov, 1991a). The development takes 12–14 days (Ozerov, 1991a). In Berlin, I collected and reared this species very successfully and in very large numbers on chicken dung. The development times were longer than the ones observed by Ozerov (at 24°C: 17 days). Under laboratory conditions, adults only reluctantly deposit eggs in cow dung, the larvae rarely completing development. *Xenosepsis fukuharai* belongs to the sepsids with precopulatory guarding.

DISTRIBUTION: This species was initially described from Japan, although in 1949 Hennig was aware of a specimen from China (Iwasa, 1984). It appears that the species has since spread westward. Ozerov (1991a) collected it in the Caucasus mountains (in litt.) and the Far East of Russia. I found the species in Berlin and recently it was reported from the Reserve Naturelle de Bruges in France (Gallis, 1994).

CLADISTIC ANALYSIS

The cladistic analysis was carried out using Hennig86 (Farris, 1988) in conjunction with DADA (Nixon, 1995). The data set comprised 85 characters and 57 taxa (including outgroups). Some of the taxa had identical character combinations or differed only by autapomorphies and could be eliminated for the computation of the parsimonious cladograms. The data set that was ultimately analyzed comprised 36 taxa. The cladistic analysis was carried out using approximate algorithms as implemented in Hennig86 (mh*; bb*). Because a single run may not find all parsimonious trees (Maddison, 1991), the sequence of taxon input was randomly modified 100 times using the "autospin" option of DADA (Nixon, 1995). Using **ie-**, an option of Hennig86 that is guaranteed to find one of the parsimonious cladograms, I was able to verify that the cladograms found during the approximate searches belonged to the set of parsimonious solutions.

Most characters in this cladistic analysis come from immatures. They are discussed in detail in a separate paper (Meier, 1995) and are only briefly summarized here. Additional characters of imagines were taken from the literature and in a few cases from my own studies. A more comprehensive sampling of the adult morphology will be undertaken shortly.

CHARACTERS FOR CLADISTIC ANALYSIS

The exact character distribution can be read from the data matrix (table 3). Some information on the distribution and the character-state codes is indicated in parentheses following the descriptions. Characters marked by an asterisk (*) were coded additively.

Cephalic Region

1) Sensory organ to either side of mouthhooks ("anterior sensory organ" on figures): papilliform (0, outgroups, *Orygma*, *Ortalischema*; fig. 463); integrated into a comb at approximately same position (1, fig. 464 remaining sepsids)

2) Without pore posterior to facial mask (0, outgroups, *Orygma*, *Ortalischema*); pore behind facial mask, usually on lower lobe (1; remaining sepsids)

3) Head consisting of two distinct cephalic lobes (0, most taxa); cephalic lobes fused (1, *Sepsis* spp. in the *flavimana* species group and *Australosepsis*)

4) Facial mask with combs on anteromedian corner posterior to anterior sensory organ (0, coelopids, *Orygma*, *Ortalischema*, *Paratoxopoda*, *Themira*); no combs on facial mask posterior to pore-bearing comb (1, remaining sepsids, ropalomerids and *Neuroctena*)

5) Facial combs more or less adnate to body wall (0, all sepsids and *Neuroctena*); each comb placed on little stalks and protruding (1, Coelopidae); "combs" consisting of bundles of hairs (2, Ropalomeridae)

6*) Facial mask consisting of a combination of ridges and combs (0, most sepsids); ridges largely transformed into combs, only a few ridges remain close to the mouth opening (1, *Themira putris*); facial mask composed exclusively of combs (2, *Themira superba*, *lucida*, *leachi*)

7) Facial mask of normal size (0; most sepsids); facial mask largely reduced with few combs and very few ridges (1, *Themira annulipes*, *simplicipes*)

8) Facial mask large and consisting of ridges with smooth edges (0, most sepsids); reduced facial mask consisting of ridges with bifurcated fringes (1, *Meroplius*). The reduction of the facial mask is independent of the previous characters because a facial mask of ancestral size, however, with bifurcated fringes is found in *Xenosepsis* (for a more detailed discussion, see Meier, 1995).

9) Numerous combs on inner side of cephalic lobes and around antenna and maxilla (0, Coelopidae, *Orygma*, *Ortalischema*, *Paratoxopoda*, *Themira*); combs restricted to area posterior to maxilla and antenna (1, Ropalomeridae, *Neuroctena*, remaining sepsids)

10) Facial mask without lower lobe, thus ridges parallel (0, outgroups, *Orygma*, *Ortalischema*, *Nemopoda*); facial mask with lower lobe, divided into anterior and posterior sections, ridges converging onto a midfurrow separating the sections (1, remaining sepsids)

TABLE 3

Data Matrix for Cladistic Analysis (- = nonapplicable character; ? = missing data)

	0	1	2	3	4	5	6	7	8
	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345	67890	12345
1) outgroup representatives:															
Neuroctena caucasica	0?010	00010	000?0	0?000	0000-	-1011	100-0	-1---	--0--	-----	---0-	0-000	00000	0000?	00010	00000	00000
Ropalomera sp.	0?012	00010	000?0	000??	00010	00010	100?0	-1001	0-0--	-----	-000-	0-000	10100	10010	00000	00000	00001
Willistoniella pleuropunctata	0?012	00010	000?0	000??	00010	00010	100?0	-1001	0-0--	-----	-000-	0-000	10100	10010	00000	00000	00001
Coelopa frigida	00001	00000	000-0	01000	0000-	-0001	00001	-0000	0-0-0	-----	-000-	0-000	00000	0000?	00000	00000	00000
Chaetocoelopa sydneyensis	00001	00000	000-0	01000	0000-	-0001	00001	-0000	0-0-0	-----	-000-	0-000	00000	0000?	00000	00000	00000
2) Sepsidae:															
Australosepsis niveipennis	11110	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10111	1011?	01111	11000	00001
Decachaetophora aeneipes	110?0	00011	01001	00001	10012	10113	10220	01111	10001	-0202	11110	1-011	10110	10110	00111	11001	00001
Dicranosepsis bicolor	11010	00011	01101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	00111	11000	00001
Lasiohirsuta hirsuta	11010	00011	01001	10011	10012	10013	10230	-1111	11001	-1?02	11110	1-011	10110	10110	00111	11000	00001
Meroplius minutus	110-0	00111	01000	00011	10012	10113	10210	-1121	11001	-0112	11110	1-011	10110	10110	00111	11001	00101
Meroplius vittatus	110-0	00111	01000	00011	10012	10113	10210	-1121	11001	-0112	11110	1-011	10110	10110	00111	11001	00101
Nemopoda nitidula	11010	00010	00001	1-011	10012	11013	10230	-1011	11001	-0102	11111	1-111	10110	10110	00111	11010	00001
Nemopoda pectinulata	1?010	0?010	?0??1	1??11	10012	11013	10230	-1011	11001	-0102	11111	1-111	10110	10110	00111	11010	00001
Nemopoda speiseri	?????	?????	?????	???11	10012	11013	10230	-1011	11001	-0102	11111	1-111	11110	10110	00111	11010	00001
Ortalischema albitarse	00000	00000	00000	10010	00012	00013	00120	00000	000-0	--001	00000	0-011	10110	10110	00011	10?00	00001
Orygma luctuosum	00000	00000	00000	01000	00011	00003	00100	-0001	000?0	--000	00010	0-000	10110	0001?	00011	11000	00001
Palaeosepsis diversiformis	11010	00011	00001	10111	10012	10113	10230	-1121	11011	00102	11110	10011	10110	10111	00111	11000	00001
Palaeosepsis mitis	11010	00011	01001	10011	10012	10113	10230	-1121	11011	00202	11110	10011	10110	10111	00111	11000	00001
Palaeosepsis polychaeta	11010	00011	00001	10111	10012	10113	10230	-1121	11011	00102	11110	10011	10110	10111	00111	11000	00001
Palaeosepsis pusio	11010	00011	00001	10011	10012	10113	10230	-1121	11011	00102	11110	10011	10110	10111	00111	11000	00001
Parapalaeosepsis compressa	11010	00011	01001	10011	10012	10114	10230	-1121	11011	00202	11110	11011	10110	10111	00111	11000	10001
Parapalaeosepsis plebeia	11010	00011	01001	10011	10012	10114	10230	-1121	11011	00202	11110	11011	10110	10111	00111	11000	10001
Paratoxopoda amonane	11000	00000	00000	10001	00012	00012	00120	00111	10000	---0-	01110	0-011	10100	10110	00-11	11000	00001
Saltella nigripes	11010	00011	00001	01011	11012	10013	10220	01112	11001	-0202	11110	1-011	10111	1011?	10111	11001	00001
Saltella sphondylii	11010	00011	00011	01011	11012	10013	10220	01112	11001	-0202	11110	1-011	10111	10110	10111	11001	00001
Sepsis biflexuosa	11110	00011	10111	10011	10012	10114	10230	-1121	11011	01202	11110	10011	10110	10111	01111	11100	00001
Sepsis cynipsea	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis defensa	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10110	01111	11000	00011
Sepsis dissimilis	11110	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10111	10111	01111	11000	00001
Sepsis duplicata	11110	00011	10111	10011	10012	10114	11230	-1121	11011	11202	11110	10011	10110	10111	01111	11100	00001
Sepsis flavimana	11110	00011	10111	10011	10012	10114	11230	-1121	11011	11202	11110	10011	10110	10111	01111	11100	00001
Sepsis fulgens	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00011
Sepsis helvetica	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00011

TABLE 3—(*Continued*)

Sepsis indica	11010	00011	10101	10011	10012	10114	11220	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis kaszabi	11110	00011	10111	10011	10012	10114	10230	-1121	11011	01202	11110	10011	10110	10111	01111	11100	00001
Sepsis lateralis	11010	00011	10101	10011	10012	10114	10230	-1121	11001	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis latiforceps	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10110	01111	11000	00011
Sepsis monostigma	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10110	01111	11000	00011
Sepsis neglecta	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis neocynipsea	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis orthocnemis	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis punctum	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	1011?	01111	11000	00011
Sepsis secunda	11110	00011	10111	10011	10012	10114	11230	-1121	11011	11202	11110	10011	10110	10111	01111	11100	00001
Sepsis thoracica	11010	00011	10101	10011	10012	10114	10230	-1121	11011	00202	11110	10011	10110	10111	01111	11000	00001
Sepsis violacea	11010	00011	10101	10011	10012	10014	10230	-1121	11001	00202	11110	10011	10110	10111	01111	11000	00011
Susanomira caucasica	11010	00011	00001	01011	11011	10013	10220	01111	100-1	-0202	11110	1-011	10110	10110	00111	11010	00001
Themira annulipes	11000	01001	00001	00001	10012	00013	10220	01111	101-1	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira flavicoxa	11000	00001	01001	00001	10112	10013	10110	01011	100-1	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira leachi	110-0	2000-	--001	00001	10012	00013	10120	11011	10001	-0002	11110	1-011	11110	11110	00111	10011	01001
Themira lucida	110-0	2000-	--001	00001	10012	00013	10120	01011	10001	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira lutulenta	11000	00001	01001	00001	10112	10013	10110	01011	100-1	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira minor	11000	00001	00001	00001	10012	00013	10120	01011	10001	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira nigricornis	11000	00001	01001	00001	10112	10013	10110	01011	100-1	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira putris	11000	10001	0-001	00001	11012	10013	10120	01011	10001	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira simplicipes	11000	01001	00001	00001	10012	00013	10220	01111	101-1	-0202	11110	1-011	11110	11110	00111	10011	01001
Themira superba	110-0	2000-	--001	00001	10012	00013	10120	11011	10001	-0202	11110	1-011	11110	11110	00111	10011	01001
Xenosepsis fukuharai	110-0	0001-	-1000	00011	10012	10113	10210	-1121	11021	-0112	11110	1-011	10110	10110	00111	11001	00101

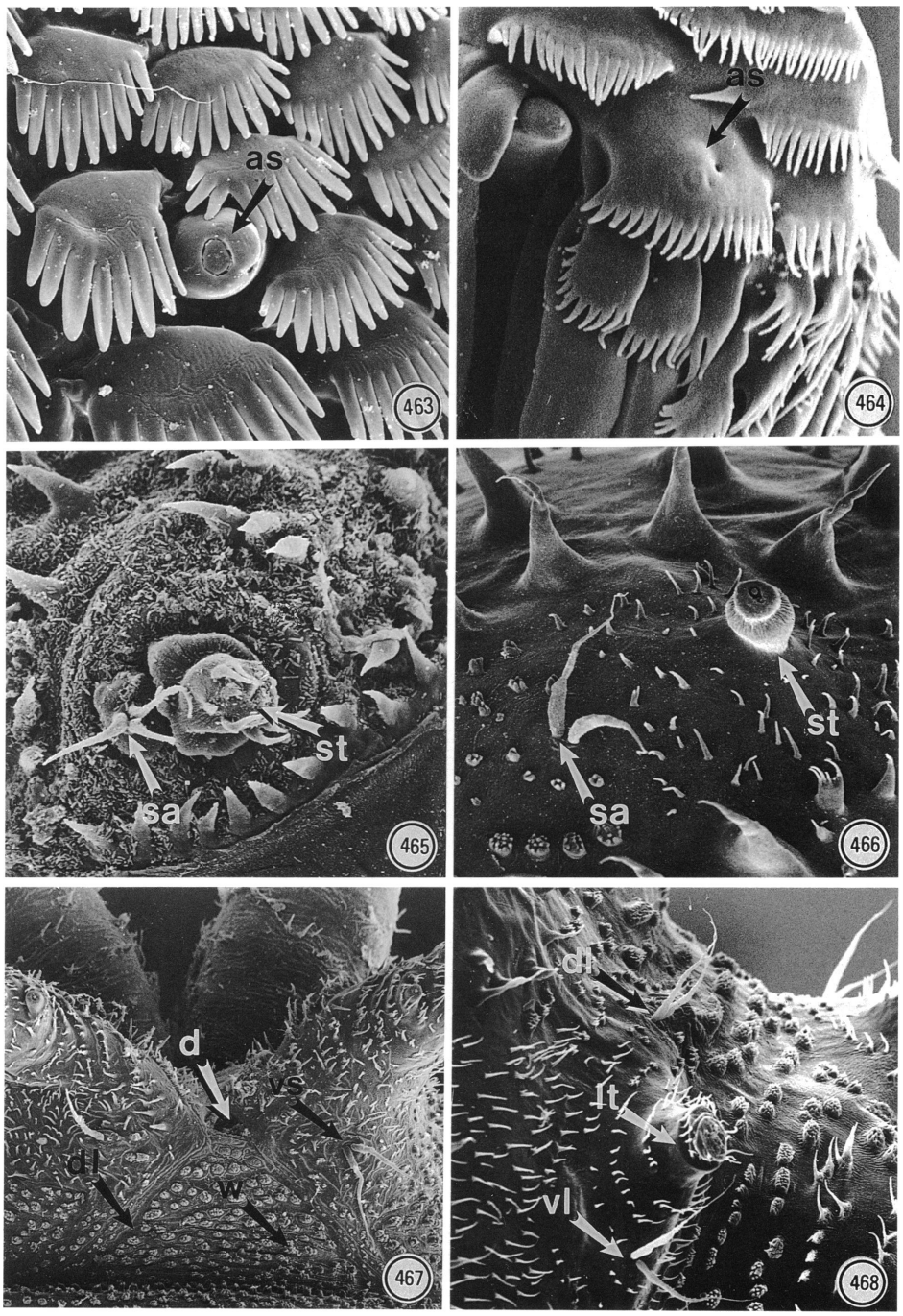


Fig. 463–468. **463:** Combs and papilliform anterior sensory organ of *Orygma luctuosum*; **464:** combs and anterior pore of *Parapalaeosepsis compressa*, note shape of papilla still visible underneath comb; **465:** subanal tubercle of *Themira simplicipes*; **466:** subanal tubercle of *Australosepsis niveipennis*; **467:** base of ventral tubercles of *Sepsis orthocnemis*; **468:** lateral tubercle of *Australosepsis niveipennis*. **as:** anterior sensory organ; **d:** depression; **dl:** dorsolateral sensory organ; **lt:** lateral tubercle; **sa:** subanal sensory organ; **st:** subanal tubercle; **vl:** ventrolateral sensory organ; **vs:** ventral sensory organ; **w:** warts.

11) Ridges not arranged into "blocks" (0, most sepsids); ridges arranged into blocks (1, *Sepsis*, less distinct in some species of the *flavimana* species group)

12) All ridges of facial mask with smooth edges (0, most sepsids); posterior edges of ridges on facial mask with fringes (1, *Themira lutulenta, flavicoxa, nigricornis, Decachaetophora, Lasionemopoda, Palaeosepsis, Parapalaeosepsis mitis, Dicranosepsis*)

13) Two ridges bordering oral cavity on either side parallel, but not fusing at tip (0, most sepsids, e.g., *Decachaetophora, Palaeosepsis*); ridges fused at tip (1, *Dicranosepsis, Sepsis*)

14) Lower lobe on either side of lower lip round and about as wide as long (0, most sepsids); lower lobe strongly elongated (1, *Saltella sphondylii*, some species in the *flavimana* species group)

15) Fleshy ridges dividing oral cavity in half ("brace" on figs.) gaping (0, outgroups, *Orygma, Ortalischema, Paratoxopoda, Xenosepsis, Meroplius*); ridges at least partly adjacent or fused (1, remaining sepsids)

16) Anterior tip of brace unmodified (0, many sepsids); tip enlarged into hooklike projections (1, *Ortalischema, Paratoxopoda, Nemopoda, Palaeosepsis, Parapalaeosepsis, Dicranosepsis, Sepsis*)

17) Fold indicating border between cephalic region and prothorax with spinules on either side (0, most outgroups and sepsids); spinules restricted to anterior side (1, coelopids, *Orygma, Saltella, Susanomira*)

18) Cephalic region without posterior constriction ("neck") (0, most species); elongated with "neck" (1, *Palaeosepsis polychaeta, diversiformis*)

19) Head wider than long (0, most outgroups, *Orygma, Paratoxopoda, Themira, Decachaetophora*); longer than wide (1, remaining sepsids)

Maxillary Palp

20) Maxillary palp consisting of five compound papillae divided into two groups separated by wide fleshy lobe (0, outgroups, *Orygma, Ortalischema*); all papillae grouped together, at most with narrow fleshy lobe or gap separating groups (1, remaining sepsids)

Anterior Spiracle

21) Anterior spiracle consisting of transverse row of lobes on body wall (0, outgroups, *Orygma, Ortalischema, Paratoxopoda*); lobes arranged along a central axis protruding from body wall (1, remaining sepsids)

22) All lobes arranged along the central axis (0, most sepsids with treelike spiracle); with some lobes around base of central axis (1, *Themira putris, Saltella, Susanomira*)

23) Spiracle lobes with smooth surface (0, most species); lobes with secondary annulations (1, *Themira flavicoxa, lutulenta, nigricornis*)

Creeping Welts and Body Segments

24) Creeping welts consisting of spinules only (0, coelopids and *Neuroctena*); welts with strong spines arranged in rows and short rows of spinules (1, all sepsids and ropalomerids)

25*) Spines arranged in numerous rows (0, ropalomerids); spines in three long rows (1, *Orygma, Susanomira*); spines in two long rows (2, remaining sepsids)

26) No anteromedian spines (0, *Orygma, Ortalischema, Paratoxopoda*, most *Themira*); additional anteromedian spines forming short anterior row (1, *Themira flavicoxa, lutulenta, nigricornis, putris, Decachaetophora, Susanomira, Saltella, Nemopoda, Lasionemopoda, Meroplius, Xenosepsis, Palaeosepsis, Parapalaeosepsis, Dicranosepsis, Sepsis*)

27) Body outside creeping welts not covered with hairs (0, most species); body segments densely hirsute (1, *Neuroctena, Nemopoda*)

Posterior Spiracle

28) Extra spiracular process ("d") with numerous wide hairs (0, most sepsids); process consisting of two short, narrow hairs (1, *Meroplius, Xenosepsis, Palaeosepsis, Parapalaeosepsis, Dicranosepsis, Sepsis* except *S. violacea*)

29) Spiracular hairs arranged around rim of spiracular plate (0, coelopids, *Orygma*); spiracular processes "a-d" each originating in a "root" (1, remaining species)

30) All three openings parallel (0, ropalomerids); openings radiating from ecdysial scar on spiracular plate (1, *Neuroctena*); spiracle

openings on three separate elevations (2, *Paratoxopoda*); two openings parallel to each other, third in 90° angle to former two (3, most genera); openings in a whirllike arrangement with two openings leaving spiracular plate and third being bent toward process "d" (4, *Parapalaeosepsis*, *Dicranosepsis*, *Sepsis*)

31) Spiracular slits strongly bent (0, coelopids, *Orygma*, *Ortalischema*, *Paratoxopoda*); spiracular slits straight or slightly curved (1, remaining species)

32) Spiracular plate almost flat or slightly bulging (0, most species); spiracular plate strongly bulging (1, *Sepsis flavimana*, *secunda*, *duplicata*, *indica*)

33*) Ecdysial scar positioned on spiracular plate (0, all outgroups); scar on spiracular mounting just below spiracular plate (1, *Orygma*, *Ortalischema*, *Paratoxopoda*, most *Themira*); scar halfway between plate and dorsal tubercle on spiracle mounting (2, *Themira annulipes*, *simplicipes*, *Decachaetophora*, *Susanomira*, *Saltella*, *Nemopoda*, *Lasionemopoda*, *Meroplius*, *Xenosepsis*, *Palaeosepsis*, *Parapalaeosepsis*, *Dicranosepsis*, *Sepsis*)

Last Abdominal Segment

34) Anal plate reduced and replaced by subanal tubercles (0, coelopids, *Orygma*); anal plate consisting of single small lobe without folds (1, *Themira flavicoxa*, *lutulenta*, *nigricornis*, *Meroplius*, *Xenosepsis*); anal plate enlarged with diagonal fold (2, *Ortalischema*, *Paratoxopoda*, most *Themira*, *Decachaetophora*, *Susanomira*, *Saltella*, *Sepsis indica*); anal plate wing-shaped (3: *Nemopoda*, *Lasionemopoda*, *Palaeosepsis*, *Parapalaeosepsis*, *Dicranosepsis*, most *Sepsis*)

35) Subanal tubercle without star-shaped structure (0, most sepsis); star-shaped structure on subanal tubercle (1, coelopids)

36) Anal plate laterally rounded (0, most species with enlarged anal plate); anal plate with angular edges (1, *Themira leachi*, *superba*)

37) No postanal protuberance behind anal opening (0, coelopids, *Orygma*, *Ortalischema*, *Paratoxopoda*); postanal protuberance behind anal openings (1, most outgroups and sepsids)

38) Large, hairy subanal tubercle (0, coelopids, *Orygma*, *Ortalischema*, *Themira*, *Nemopoda*; fig. 465); small spine-size naked subanal tubercle (1, most outgroups and sepsids; fig. 466)

39*) No subanal sensory organ immediately below tip of subanal tubercle (0, outgroups, *Orygma*, *Ortalischema*); subanal sensory organ just below tip of tubercle (1, *Paratoxopoda*, *Themira*, *Decachaetophora*, *Susanomira*, *Saltella*, *Nemopoda*, *Lasionemopoda*, *Meroplius*, *Xenosepsis*; fig. 465); sensory organ posterolateral to subanal tubercle (2, *Palaeosepsis*, *Parapalaeosepsis*, *Dicranosepsis*, *Sepsis*; fig. 466)

40*) No ventral tubercles (0, outgroups, *Ortalischema*); one pair of ventral tubercles (1, most sepsids); two pairs of ventral tubercles (2, *Saltella*)

41) No ventral sensory organ at base of ventral tubercles (0, outgroups, *Orygma*, *Ortalischema*); ventral sensory organ at base of ventral tubercle (1, remaining sepsids; fig. 467)

42) Hairs of sensory organs short (0, *Paratoxopoda*, *Themira*, *Decachaetophora*, *Susanomira*); long sensory hairs (1: *Saltella*, *Nemopoda*, *Lasionemopoda*, *Meroplius*, *Xenosepsis*, *Palaeosepsis*, *Parapalaeosepsis*, *Dicranosepsis*, *Sepsis*)

43) Preanal row of spines along anal plate (0, most species); spines fused into buttonlike structure immediately anterior to anal opening (1, *Themira annulipes*, *simplicipes*)

44) Ventral side of last segment with hairs between anal plate and ventral tubercles (0, many species); hairs transformed into warts (1, fig. 467–468; *Palaeosepsis*, *Parapalaeosepsis*, *Dicranosepsis*, *Sepsis* except for *lateralis* and *violacea*); large wartlike protrusions (2: *Xenosepsis*)

45) No depression between bases of ventral tubercles (0, outgroups, *Orygma*, *Ortalischema*, *Paratoxopoda*); depression at this position (1, remaining sepsids; fig. 467)

46) Warts in vicinity of depression not enlarged (0, most species with warts); warts strongly enlarged (1, *Sepsis flavimana*, *duplicata*, *secunda*)

47) Depression at base of ventral tubercles (0, most species); area posterior to depression strongly elongated, thus depression at more anterior position (1, *Lasionemopoda*, *Sepsis biflexuosa*, *kaszabi*, *flavimana*, *duplicata*, *secunda*)

48*) Creeping welts of last segment con-

sisting of two rows of spines (0, *Orygma*, *Ortalischema*, *Themira leachi*); creeping welt of last abdominal segment reduced to a single, complete, or almost complete row of spines (1, *Nemopoda*, *Meroplius*, *Xenosepsis*, *Palaeosepsis* except for *mitis*); row incomplete ventrally (2, remaining sepsids)

49) No rows of spinules anterior to creeping welt of last segment (0, most species); multiple rows of spinules (1, *Xenosepsis*, *Meroplius*)

50*) Creeping welt of last segment restricted to ventral side (0, *Orygma*); creeping welt extends halfway up lateral side (1, *Ortalischema*); creeping welt covers entire lateral aspect of last segment (2, remaining sepsids)

51) No posterior band of spines on last segment (0, outgroups, *Orygma*, *Ortalischema*, *Paratoxopoda*); posterior band present (1, remaining sepsids)

52) No lateral tubercle (0, *Orygma*, *Ortalischema*); with lateral tubercle (1, remaining sepsids; fig. 468)

53) No dorso- and ventrolateral sensory organs dorsal and ventral of lateral tubercle (0, *Orygma*, *Ortalischema*); sensory organs present (1, remaining sepsids; fig. 468)

54) Dorsal tubercle on spiracular mounting (0, most sepsids); no dorsal tubercle on spiracle mounting (1, *Ortalischema*, outgroups)

55) Single anterior band of spines laterally (0, see character 49; most sepsids); anterior band divided into two diagonal rows (1, *Nemopoda*)

56) Three lines or grooves on dorsal aspect of last segment lacking spines (0, *Orygma*, *Ortalischema*, *Paratoxopoda*); one row of spines on either side of grooves (1, remaining sepsids, except for *Themira superba* where the spines are not arranged in rows)

57) Hairs on dorsal aspect of last segment and between lateral bands of spines (0, most sepsids); hairs between bands of spines and on dorsal surface of last segment transformed into warts (1, *Parapalaeosepsis*)

58) No dorsal transverse row of spines (0, most sepsids); dorsal transverse row present (1, *Nemopoda*)

ADULT CHARACTERS: The following characters are largely taken from the literature. For some characters published as apomorphies that support the sister-group relationship between the Sepsidae and Ropalomeridae or the monophyly of the Sepsidae, it is assumed that they are present in all sepsids although they have not been studied for all the species in the data set.

59) Largest width of head at posterior end and head more or less adnate to prothorax (0, fig. 469); head bead-shaped and not adnate the anterior margin of prothorax (1, fig. 470)

60) Palpi of normal size (0, fig. 469); palpi reduced in size (1, fig. 470)

61) No enlarged subvibrissae (0); one or more subvibrissal setae enlarged and vibrissalike (fig. 469, 470)

62) Outer vertical setae on head (0, figs. 469, 470); no outer vertical (1) (see Hennig, 1949)

63) A_2 vein present (0); A_2 absent (1) (see fig. 470; McAlpine, 1989)

64) A_1 vein reaching wing margin at least as a fold (0); A_1 not reaching margin (1) (see fig. 470; McAlpine, 1989)

65) Wing cells br and bm separate (0, fig. 470); wing cells br and bm fused (1) (see Hennig, 1949)

66) Two postalar setae (0, fig. 469); one postalar seta or second extremely small (1, fig. 470)

67) Supra-alar bristle (0); without or with minute supra-alar bristle (1) (see Duda 1925, 1926)

68) Katepisternum setulose (0, fig. 469); katepisternum bare (1, fig. 470) (see McAlpine, 1989)

69) Posterior margin of metathoracic spiracle without seta (0); one or more distinct setae present (1) (figs. 469, 470; see McAlpine, 1989)

70) One pair of dorsocentral bristles (0, fig. 469); two pairs (1, fig. 470)

71) Scutellum twice as wide as long (0); scutellum longer than wide and enlarged (1) (Hennig, 1949)

72) Abdomen of males without macrochaetae (0, fig. 469); abdomen of males with macrochaeta (1, fig. 470) (Hennig, 1949)

73) Separate tergite 6 in males (0); tergite 6 very small and fused to the 8th sternite (1) (Pont, in litt.)

74) 6th and 7th abdominal spiracles of females in pleural membrane (0); embedded within respective tergites (McAlpine, 1989)

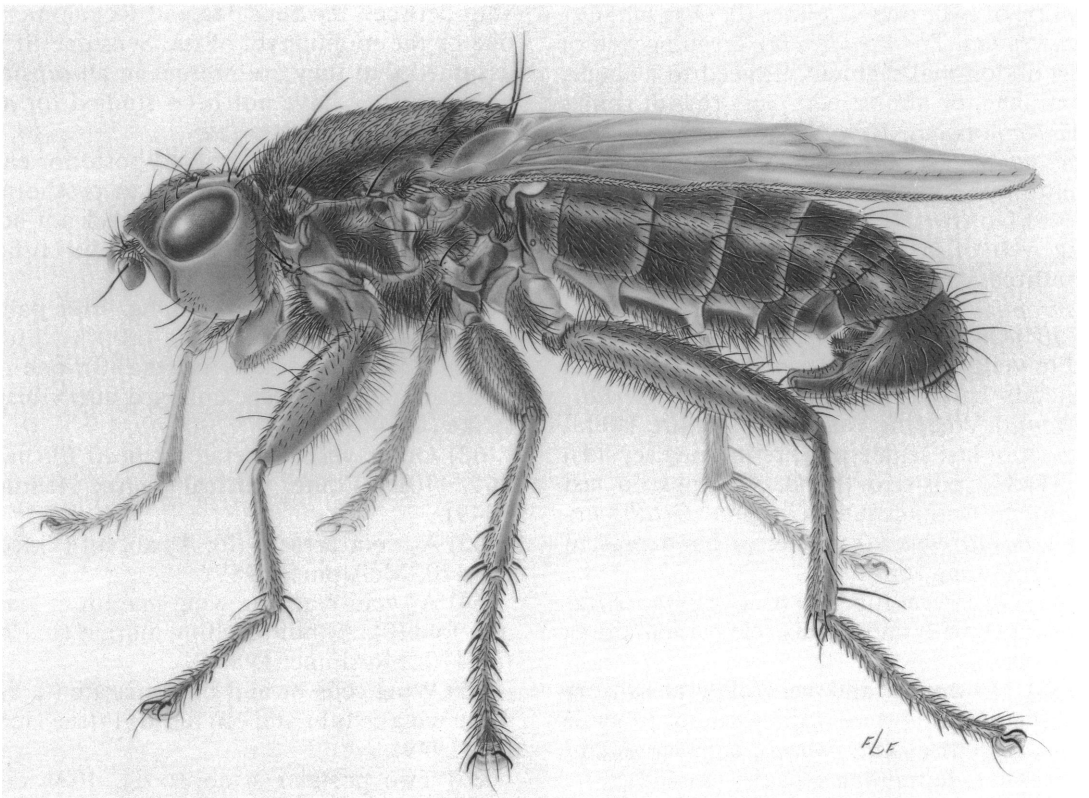


Fig. 469. Habitus drawing of *Orygma luctuosum*.

75) 6th abdominal spiracles of males within membranes (0); within tergites (1; McAlpine, 1989)

76) 7th sternite of males present, visibly fused or separate (0); lost or completely fused to 8th sternite without visible suture (1) (McAlpine, 1989)

77) Surstylus and epandrium not fused (0); fused without visible suture (1, figs. 469, 470) (see comments in introduction)

78) Surstylus straight (0, figs. 469, 470); surstylus with approximately 90° bend (1) (Hennig, 1949)

79) 4th sternite of males unmodified (0, figs. 469, 470); brushes of hairs on 4th sternite (for fig., see Hennig, 1949)

80) Fieldlike osmeterium (0); with or without ribbon-shaped osmeterium (1, figs. 469, 470) (see Hennig, 1949)

81) Hind coxa with or without bristle but bristle never modified (0, figs. 469, 470); strong ventral bristle bent backwards (see Zuska, 1970)

82) Forefemora with various modifications but without cuticular elevation in the middle (0); forelegs with cuticular elevation (1) (see Hennig, 1949 for figures.)

83) Forefemora unmodified or with different morphology (0); forefemur with two flattened or otherwise strongly modified bristle (1) (see Zuska, 1972, for figs.)

84) Forefemora without cuticular elevation in distal fourth (0, fig. 469); special cuticular elevation and two short setae (1, fig. 470) (see Hennig, 1949, for additional figures)

85) Aedeagal apodeme not fused to hypandrium (0); aedeagal apodeme fused to hypandrium, i.e. cuneiform (1) (see Griffiths, 1972)

RESULTS

The 100 cladistic analyses using "mh*; bb*;" found 40 trees at 157 steps (CI = 0.63; RI = 0.90; reduced data set RI = 0.82). With the aid of **ie-**, it was confirmed that these trees belong to the set of parsimonious cladograms. Upon closer inspection and removal

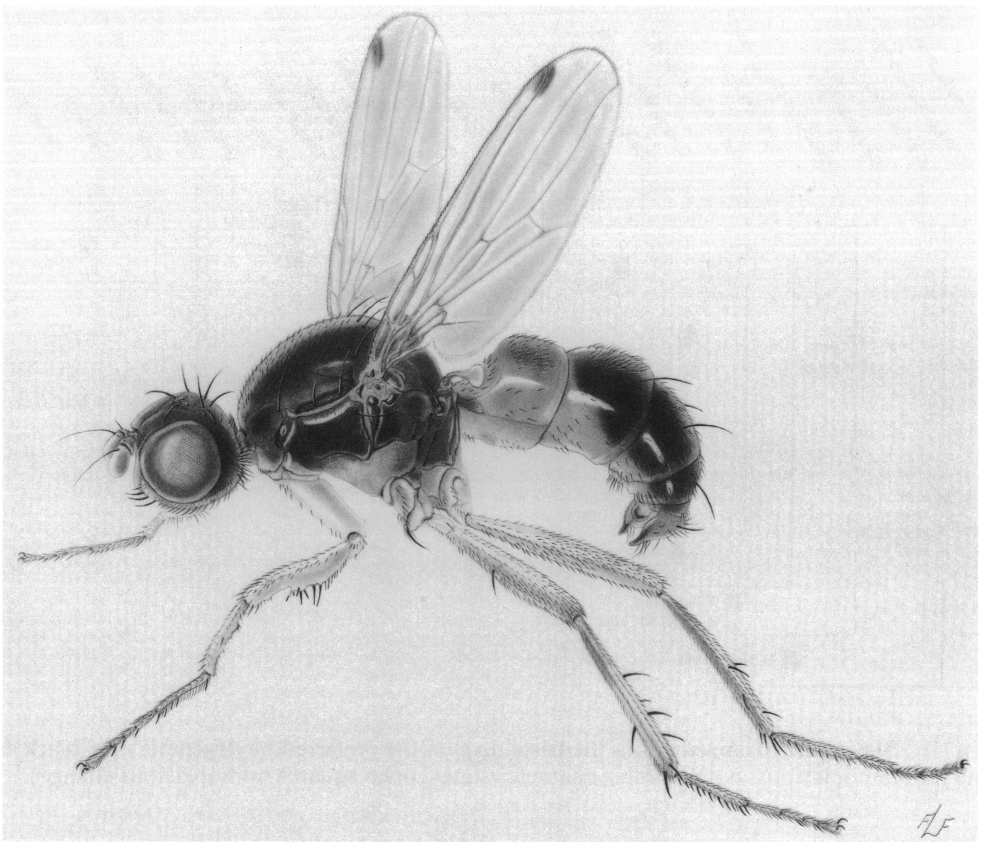


Fig. 470. Habitus drawing of *Sepsis punctum*.

of all unsupported branches with the aid of CLADOS (Nixon, 1994), 16 different cladograms remained. Their topology differed with respect to three areas. One involved the arrangement of species within *Sepsis* (four different arrangements; figs. 472, 476, 477, 478), another concerned the hypothesized relationships within *Themira* (two different arrangements; figs. 471, 474), and the last, the relationships between *Nemopoda*, *Lasionemopoda*, *Decachaetophora*, *Meroplius* and *Xenosepsis* (two different arrangements; figs. 471, 472, 475). All combinations of the different arrangements were parsimonious, explaining the total of 16 parsimonious cladograms. In figures 471—472 a preferred tree is depicted that was chosen based on criteria outlined in the discussion section. Figure 473 depicts the consensus tree and on figures 474–478, the different arrangements for the areas of uncertainty are shown. When successive weighting, as implemented in Hennig86, was applied to the data set, the parsimonious solutions only included two trees. Both trees were two steps longer than the parsimonious trees that were found for the data set with all characters weighted equally.

DISCUSSION

The cladistic analysis found 16 cladograms (variable regions depicted in figs. 474–478). I prefer the one in figures 471–472 based on the following arguments. Within *Sepsis* the trees differed with respect to the placement of *S. lateralis*. On two of the equally parsimonious topologies (figs. 476; 478), it appears as a sister group of *Sepsis violacea*. This

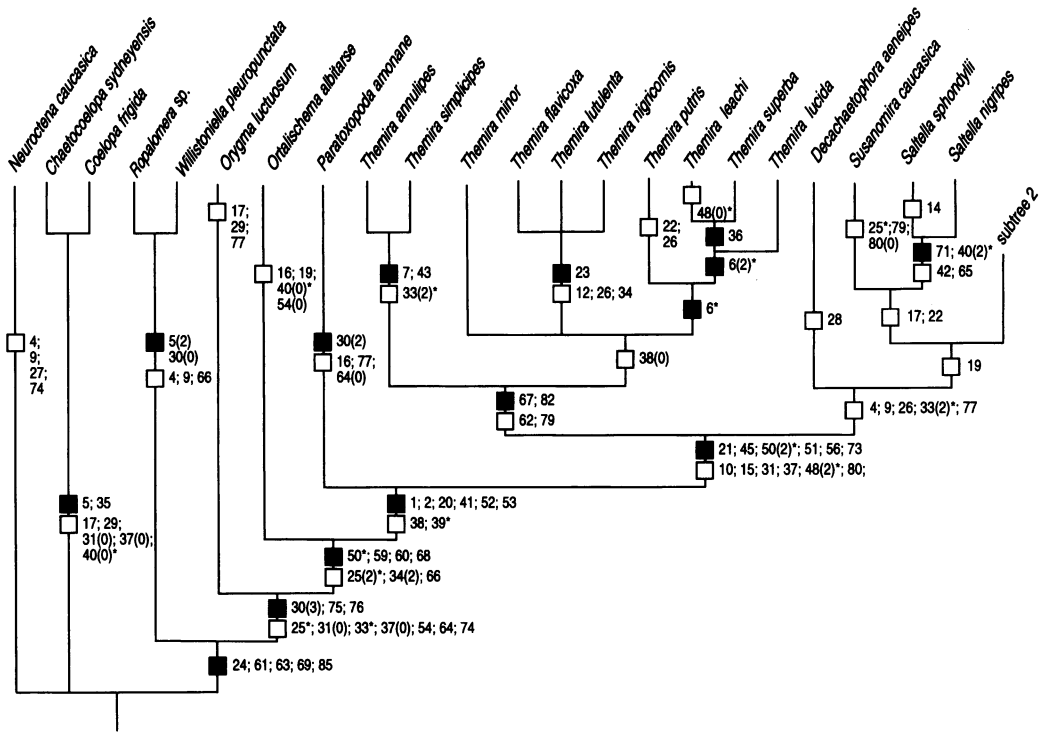
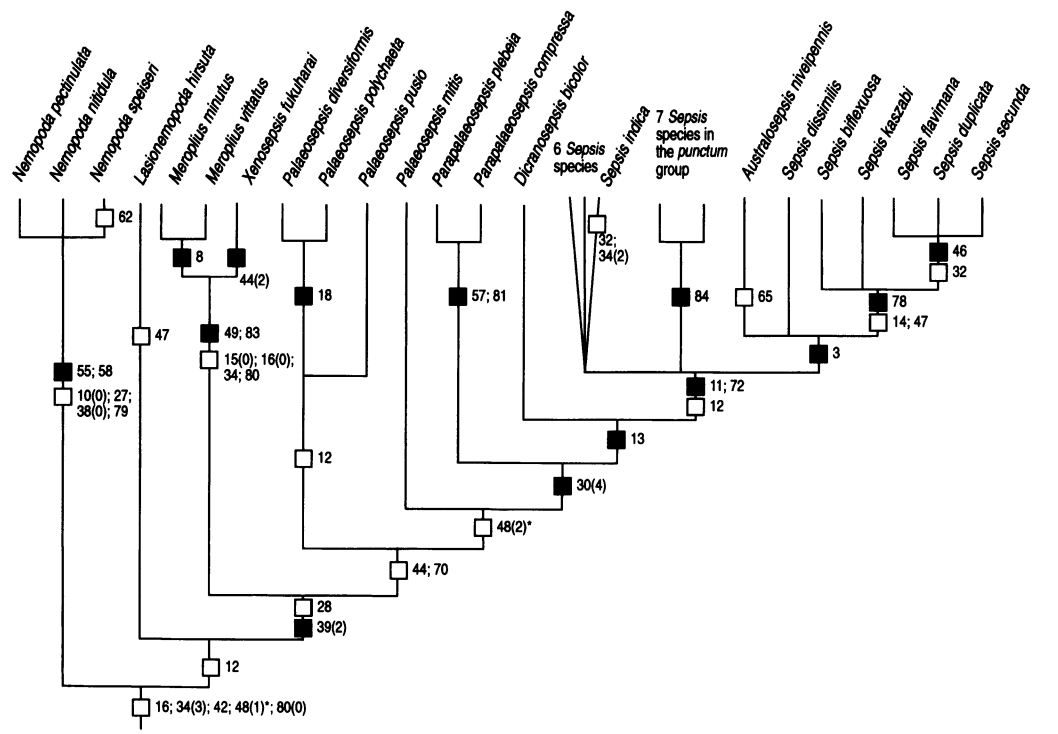


Fig. 471. **Subtree 1:** Arrangement of the basal taxa on the preferred phylogenetic tree; black squares indicate nonhomoplasious, nonreversing character states, open squares homoplasious changes.



placement is based on a reversal (warts on the last segment of larvae replaced by hairs which I consider weak support for the clade). A study of early instars of *Sepsis* revealed that all second instars have hairs on the last segment. Apparently, ontogeny recapitulates phylogeny for this character i.e., the direction of character change on the tree (hairs to warts) is also found within ontogeny (hairs in second instars to warts in third instars). A slow-down (paedomorphosis) of development will necessarily result in hairs being present on the last segment. Furthermore, there is adult evidence beyond the characters used in this cladistic analysis against placing *lateralis* as the sister group of *violacea*. *Sepsis lateralis* belongs to a section of the genus *Sepsis* without a wing spot. This character, although discrete in *Sepsis*, is unfortunately continuous outside the genus, so that it could not be included in the data set. However, I believe that it should be considered when choosing among equally parsimonious trees. Among the remaining two arrangements of *Sepsis*, I opted for the more conservative one that does not place *lateralis* as the sister group of the *punctum* species group (fig. 472).

There is also disagreement among the parsimonious cladograms with regard to the relationships among *Nemopoda*, *Lasionemopoda*, *Decachaetophora*, *Meroplius*, and *Xenosepsis*. There is currently only very weak evidence from either adult- or larval characters that would favor one arrangement over the other. My main reason for choosing the topology on the proposed tree (figs. 471–472) is a recent study of sepsid eggs that revealed characters supporting a derived position of *Lasionemopoda* over a sister-group relationship between this genus and *Nemopoda* (Meier, in press).

There are two arrangements within *Themira* (figs. 471, 474). Since I have currently no reason to favor one over the other, I decided to choose the solution that was also consistently supported by the trees found by using successive weighing.

My cladistic analysis of the Sepsidae furnishes further evidence for the monophyly of the family. I point out in the introduction that some of the adult characters considered autapomorphic in the literature may not be considered valid evidence. Some apparently evolved within the Sepsidae, others potentially support a sister-group relationship between this family and various other remaining families within the Sciomyzoidea. Additional support from larval characters is thus welcome to restore the confidence that the Sepsidae are monophyletic. Most of the new evidence is associated with the posterior spiracles. The ecdysial scar is always moved off the spiracular plate. It may be argued that this shift of position is associated with the evolution of a long spiracle mounting. However, this is not the case since one species of the Coelopidae has been described (*Coelopa nigrifrons*), which has a long spiracle mounting and at the same time an ecdysial scar that remains on the spiracular plate. The "rectangular" arrangement of the spiracular slits on this spiracular plate is also a derived condition for the Sepsidae that has probably already been present in the sepsid ancestor. However, the value of this character has to be questioned since its expression differs somewhat in the basal sepsids, especially in *Orygma* with its strongly curved slits and *Ortalischema* where the shape of the spiracular plate has been autapomorphically changed. A further probable larval synapomorphy for the Sepsidae is the dorsal tubercle on the spiracle mounting. It is only missing in *Ortalischema* where I assume it has been secondarily lost when the spiracular plate and the spiracle mountings were modified.

←

Fig. 472. **Subtree 2:** Arrangement of the derived taxa on the preferred phylogenetic tree; black squares indicate nonhomoplasious, nonreversing character states, open squares homoplasious changes. The six *Sepsis* species mentioned on the tree are: *S. cynipsea*, *lateralis*, *neglecta*, *neocynipsea*, *orthocnemis*, and *thoracica*. The seven species in the *punctum* species group are: *S. defensa*, *fulgens*, *latiforceps*, *monostigma*, *punctum*, *helvetica*, and *violacea*. The following changes pertaining to *Sepsis* are not mapped: *Sepsis violacea*: 28: 1→0 and 44: 1→0; *Sepsis lateralis*: 44: 1→0; The following species within the *punctum* species group may form a monophyletic group based on the character change 70: 1→0: *S. latiforceps*, *defensa*, *monostigma*.

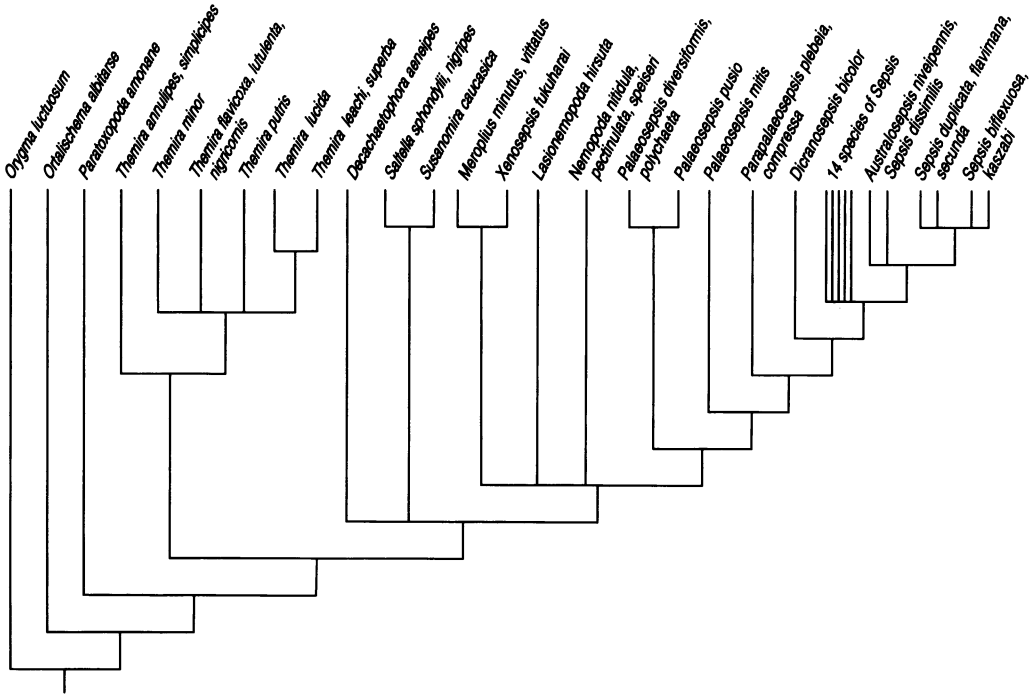
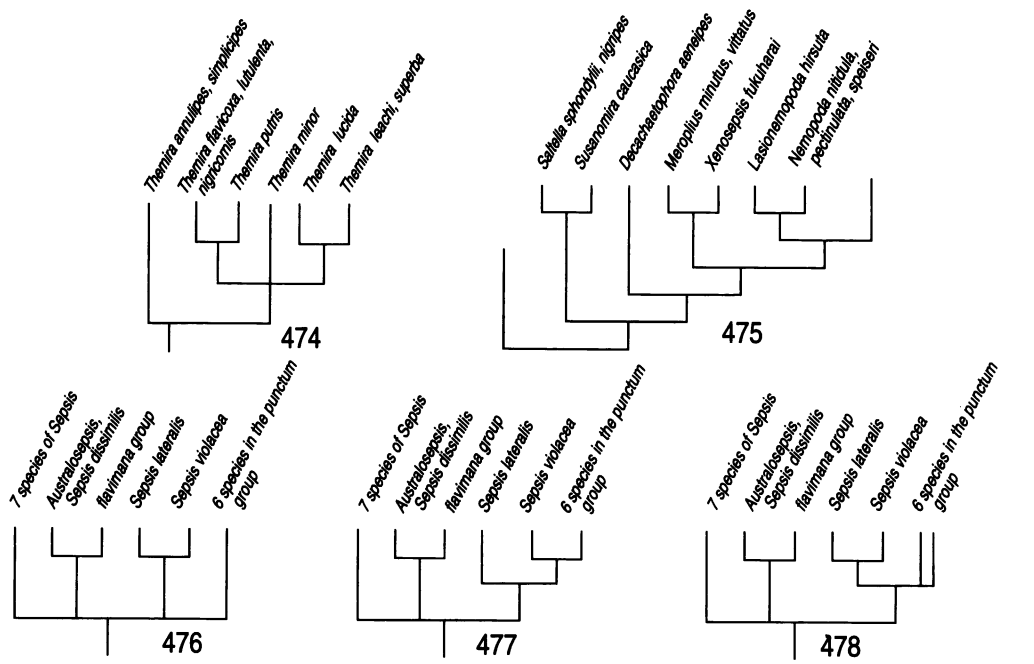


Fig. 473. Strict consensus tree.



Figs. 474–478. **474.** Equally parsimonious arrangement for the species within *Themira*. **475.** Equally parsimonious arrangement for *Decachaetophora*, *Saltella*, *Susanomira*, *Nemopoda*, *Lasionemopoda*, *Meroplius* and *Xenosepsis*. Tree connects at upper node to the *Sepsis* group. **476–478.** Equally parsimonious arrangements for some taxa within *Sepsis*. The six species of *Sepsis* mentioned on the tree are: *S. cynipsea*, *neglecta*, *neocynipsea*, *orthocnemis*, and *thoracica*. The six species in the *punctum* species group are: *S. defensa*, *fulgens*, *latiforceps*, *monostigma*, *punctum*, and *helvetica*.

The basalmost dichotomies of the trees are particularly well supported which indicates the conservative nature of most larval characters (fig. 471). The sister-group relationship between *Orygma* and the remaining sepsids comes as no surprise and has been consistently proposed by previous authors (Griffiths, 1972; Hennig, 1965; Steyskal, 1987; see also figs. 469–470). However, the basal position of *Ortalischema* has never been suggested in the literature, and this genus had previously been assumed to be a close relative of *Themira*. Since these proposals were not based on characters, the different results of my cladistic analysis is not surprising. The position of *Ortalischema* as sister group of all remaining Sepsinae is well supported by larval as well as adult characters. Here I point only to the morphology of the anterior spiracle and the large separated sixth tergite, which is very small and fused with a sternite in all more derived sepsids.

Only a single species belonging to Hennig's *Toxopoda* group (Zuska's *Toxopodini*) was included in the present cladistic analysis. It is therefore of interest to address the question whether the Toxopodini are monophyletic. If so, the single species (*Paratoxopoda amonane*) may indicate the position of the entire *Toxopoda* group. Its monophyly can preliminarily be supported by two adult characters. At least in the vast majority of all species, the halters are dark-brown to black. Halters are whitish in almost all other sepsids (somewhat darker in *Saltella*). Also, the midfemur is s-shaped in all species that I studied for this character. Thus, *Paratoxopoda amonane* may in fact indicate the position of the entire *Toxopoda* group on the phylogenetic tree of the Sepsidae. A basal position of the *Toxopoda* group had not been explicitly discussed in the literature. Hennig (1949) did not comment on the position of this group, and Zuska's (1980) classification does not allow conclusions with regard to the relationships among the tribes of his system. However, Duda (1925) proposed a basal position of taxa like *Saltella* and *Toxopoda*. Also, on his linear classification table that was intended to loosely reflect phylogeny, the *Toxopoda* group occupies a basal position. Again, his opinion was not supported by any characters.

The most surprising result of my cladistic analysis is the relatively derived position of *Saltella*. This genus has been unanimously surmised to constitute the most basal living sepsid apart from *Orygma*. This view can be traced back to Duda (1925) or even Frey (1921) but was maintained by Zuska (1980) and Hennig (1949). Apparently, all previous workers accepted this position without checking the character support. There are very few characters that point to such a basal position. They are all setal characters of questionable value: (1) strong basal scutellar bristles: I consider the secondary increase in size of the basal scutellar as probably associated with the increased size of the scutellum in *Saltella*, (2) presence of a proepisternal bristle: a normally developed proepisternal bristle is also known from other putatively "derived" genera like *Xenosepsis* and *Susanomira*, and this character appears thus prone to homoplasy, which is not surprising since the proepisternal bristle is reduced in size in most sepsids and not entirely lost. Frey (1921), who may have been the first author to propose the basal placement of *Saltella*, also mentioned that the mouthparts are somewhat more primitive. Unfortunately he fails to specify in what respect.

CONFLICT BETWEEN LARVAL AND ADULT DATA

When the larval characters are evaluated separately from the adult characters, two important hypotheses of relationship conflict. According to larval characters, Coelopidae and not Ropalomeridae is the sister group of Sepsidae. However, this result is based mainly on characters shared by the most basal sepsid (*Orygma*) and Coelopidae. The spiracular hairs are arranged along the rim of the spiracular plate and do not originate in four separate "roots," as in all other species, and the anal plate is largely reduced and replaced by large subanal tubercles. These character states are undoubtedly derived, but whether they are homologous is questionable. The larvae of both Coelopidae and *Orygma* live on decaying sea wrack, and the anal organ underlying the anal plate may be related to life on sea shores, suggesting that this character may have evolved twice convergently. Apparently the anal organ is responsible for osmoregulation (Stoffolano, 1970), and both *Orygma* and Coelopidae larvae ex-

perience similar osmoregulatory problems. The only character linking the Coelopidae to a number of sepsids besides *Orygma* are the strongly curved spiracular slits of the posterior spiracle.

The only larval character that may support the traditional hypothesis of a sister-group relationship between the Sepsidae and the Ropalomeridae comes from the creeping welts that consist not only of spinules (as in the Coelopidae) but also of several rows of strong spines. However, the distribution of the creeping welts across the body segments differs among the two families. In the Sepsidae they are plesiomorphically found on the first through last abdominal segment. In the Ropalomeridae they are restricted to the metathoracic segment and the first six abdominal segments. Therefore, one may have to doubt the homology of spinose creeping welts in the two families. Further study of adult morphology is needed in order to decide whether Ropalomeridae or Coelopidae is the sister group of Sepsidae.

The second important issue of conflict between larval and adult characters is the monophyly of the second largest genus within the Sepsidae, *Themira*. According to adult characters, it is monophyletic, supported by the morphology of the males' foreleg and two setal characters. It is paraphyletic according to larval data. The two species of *Themira* traditionally placed in the subgenus *Enicita* may be more closely related to the more advanced sepsids than to the remaining species of *Themira*. This hypothesis is based on the position of the ecdysial scar on the spiracle mounting. Since there is more support for a monophyletic than a paraphyletic *Themira*, and it is more conservative to maintain the genus with its present composition, I am not proposing a formal recognition of a genus *Enicita*. However, future studies on adults might consider the possibility that *Themira* may not be monophyletic.

Most genera of the Sepsidae are supported by both larval and adult characters. The one exception is *Palaeosepsis*. There is one larval character indicating that *P. mitis* is more closely related to the remaining genera in the *Sepsis* group than to its congeners. The creeping welt of the last abdominal segment is ventrally incomplete while it is complete in all other species of *Palaeosepsis*. Again, at this point it is premature to suggest taxonomic changes, but this finding should be kept in mind in future revisions of the notoriously difficult genera with affinities to *Palaeosepsis*. One adult character that could potentially support the monophyly of *Palaeosepsis* is the bifurcated surstyli, but I decided not to include this character in the data set since bifurcated surstyli of a somewhat different kind are also known from other closely related genera (e.g., *Meroplius minutus*, *Dicranosepsis*) and further study needs to reveal whether those surstyli are homologous with what is found in *Palaeosepsis*.

COMPARISON WITH TRADITIONAL CLASSIFICATIONS

In Duda's classification (1925) a number of genera were obviously misplaced. Hennig (1949) therefore removed *Australosepsis* from the Saltellinae. The fusion of the wing cells "bm" and "br" was obviously a convergent character linking *Australosepsis* and *Saltella*. Similarly, Hennig (1949) transferred *Sepsidimorpha* from the Nemopodinae to his *Sepsis* group. The species in Duda's Nemopodinae have males with largely unmodified forefemora (with at most a row of spinules). In the species of the subgenus *Sepsidimorpha*, similar forelegs are found, but here the comparatively simple morphology is a secondary condition associated with the small size of the species. Hennig (1949) recognized the secondary nature of the simple legs and considered *Sepsidimorpha* a subgenus of *Sepsis*. The placement of both *Australosepsis* and *Sepsidimorpha* within *Sepsis* is confirmed by my cladistic analysis.

All classifications agree with respect to the placement of *Orygma* as the sister group of all remaining sepsids (table 1; figs. 469–470). However, in most classifications *Saltella* is either considered to be the next basal taxon (Zuska, 1980; Steyskal, 1987; Duda, 1925) or considered basal within a taxon like Hennig's *Themira* group. As already pointed out, there is good evidence that *Saltella* occupies a more derived position on the phylogenetic tree of the Sepsidae. As a consequence, Zuska's Sepsini cannot be monophyletic. It could only be monophyletic if his Saltellini and his Tox-

opodini were included in the Sepsini (table 1). However, under these circumstances the Sepsini would include all sepsids except for *Orygma*, i.e., they would be identical to the Sepsinae. A similar situation is encountered, if one would attempt to make Hennig's *Themira* group monophyletic which, in its present composition, is polyphyletic. The next more comprehensive monophyletic taxon would be the Sepsinae. When Hennig (1949) proposed his *Themira* group, it was not supported by any convincing autapomorphy present throughout all component genera. It is therefore not very surprising that the *Themira* group is demonstrated herein to be polyphyletic.

In contrast to the *Themira* group, Hennig's *Sepsis* group is monophyletic and will almost certainly be a component of a future phylogenetic system of the Sepsidae. The same is true for the taxon that Hennig (1949) called the *Toxopoda* group and Zuska (1980) the Toxopodini. I have already pointed out that there is evidence for its monophyly.

Other monophyletic taxa that I consider firmly established by my cladistic analysis include all sepsids except for *Orygma* and *Ortalischema* and all genera except for *Orygma*, *Ortalischema*, and the species in the Toxopodini. Since formal names for these taxa are rarely needed, I refrain from proposing them. However, I would like to revive a synonym that Hennig (1949) proposed and that has been largely neglected in the literature. He synonymized *Australosepsis* with *Sepsis* and I certainly agree. If his proposal is not adopted, the largest genus of the Sepsidae (*Sepsis*) would have to be dissolved. I would also like to formally propose that *Xenosepsis* be synonymized with *Meroplius* (syn. nov.). The minute setal differences do not justify maintaining two very small genera.

For the following traditionally accepted genera, larvae were not available: *Lasiosepsis*, *Leptomerosepsis*, *Meropliosepsis*, *Platytoxopoda*, *Toxopoda*, *Perochaeta*, and *Zuskamira*. I will attempt an approximate placement of these genera based on adult characters. I have already mentioned that there is adult evidence for a monophyletic *Toxopoda* group, and will thus comment no further on the position of *Toxopoda* and *Platytoxopoda*. I am convinced that, combined with *Paratoxopoda*, they constitute a monophyletic lineage.

Lasiosepsis melanota is most likely just an aberrant *Sepsis* that received generic recognition based on the reduced postpronotal bristle and a very pubescent integument. It carries the only adult autapomorphy of *Sepsis*—macrochaetae on the abdomen of the males—and is thus probably nested within that genus. Also nested within *Sepsis* is the genus *Leptomerosepsis*, which was erected for a group of species distinguished from other *Sepsis* by, for example, a darkened wing base, the lack of a wing spot and large antennae. As already recognized by Hennig (1949), *Lasiosepsis* and *Leptomerosepsis* should be synonymized with *Sepsis* in order to create a monophyletic genus.

More difficult is the placement of *Meropliosepsis*, *Perochaeta*, and *Zuskamira*. The surstyli of the monotypic *Zuskamira* are not fused to the epandrium, and the fourth sternite is strongly modified to carry hair tufts. According to my interpretation, the articulated surstyli are plesiomorphic within the family but restricted to the mostbasal branches below the node where *Themira* branches off. However, the presence of a modified sternite is apomorphic and restricted to the branches above the *Toxopoda* node so that *Zuskamira* presumably falls within this section of the tree. Interestingly, the hind tibiae of the males do not bear an osmeterium like *Themira*, which could indicate that *Zuskamira* represents a separate branch on the phylogenetic tree of the Sepsidae which splits off above the *Toxopoda* node but below the *Themira* node. In any case, the genus differs markedly from *Themira* since the outer vertical bristle is present. *Zuskamira* also has several dorsocentrals, a supra-alar, a bare prosternum, and a long anepisternal bristle.

Very little is known about the genus *Perochaeta*. According to Duda (1925) and a recently described new species (Ozerov, 1992), the fourth sternite bears the tufts that I already mentioned. Duda also commented on a small flat bump on the hind tibiae which may indicate the presence of an osmeterium. At the same time the surstylus is fused to the epandrium, which would position the species above the node where *Decachaetophora* branches off. Duda (1925) placed the genus

next to *Nemopoda* since the forefemur of the males is unmodified. Such placement is consistent with my proposal, but the position of *Perochaeta* in the phylogenetic system of the Sepsidae remains uncertain.

The position of *Meropliosepsis* within a phylogenetic classification of the Sepsidae is even more difficult to infer. The only adult support for the monophyly of Hennig's *Sepsis* group currently comes from the presence of two pairs of dorsocentrals (plesiomorphic = 1 pair). Unfortunately, *Meropliosepsis* has three pairs, so that not even this weak autapomorphy applies unambiguously unless the character was coded additively. Nevertheless, it is likely that *Meropliosepsis* is a member of the *Sepsis* group since all previous authors have suggested a close affinity to *Palaeosepsis*. In *Meropliosepsis*, the base of the wings is blackened as in *Parapalaeosepsis*, which may indicate a sister-group relationship between these genera. Hennig (1949) considered it more likely that *Meropliosepsis* is nested within *Palaeosepsis* since both share conspicuously bifurcated surstyli and are restricted to the Neotropics. However, bifurcated surstyli are also found in various other genera (e.g., *Dicranosepsis*, *Meroplius*, *Nemopoda*, *Perochaeta*), so that this condition may have been present on the ancestor lineage of the *Sepsis* group. A detailed study of the surstyli is urgently needed in order to reveal homologies. Most experts on the Sepsidae believe that the bifurcated surstyli evolved several times independently (Pont, Zuska in litt.).

The results of this cladistic analysis shed interesting light on the evolution of the ecology and behavior of the Sepsidae. If the Coelopidae are the sister group of the sepsids, the occurrence of *Orygma* on sea wrack would constitute an ancestral trait suggesting that the ancestor of the Sepsidae was a seashore-inhabiting fly. If the Ropalomeridae are considered the sister group of the Sepsidae, the ecology of *Orygma* is derived since all other sepsids and all ropalomerids live inland on a variety of decaying organic matter (the Ropalomeridae appear to be specialized on tree saps). In any case, there is now good evidence that the ancestor of the Sepsinae deposited eggs on mammal feces. *Ortalischema* is specialized on horse dung, and the few species belonging to the *Toxopoda* group for which the breeding substrate is known utilize cow dung. The diet of *Themira* and *Nemopoda*, which have much less specialized needs than the more basal sepsids, is considerably more varied. Precopulatory guarding evolved several times but is apparently restricted to rather derived sepsids.

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