Beitr. Ent., Berlin 32 (1982) 2, S. 195–282

Slezské muzeum
Entomologické oddělení
Opava (ČSSR)

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A monograph and re-classification of the previous genus *Limosina* MACQUART (Diptera, Sphaeroceridae) of Europe

With 1098 text figures

Part I

Abstract

The European species belonging to the previous genus *Limosina* MACQUART (sensu HACKMAN 1969a) are monographed. This taxon was found to be polyphyletic and is divided using cladistic classification into 17 genera with a total of 81 European species. 11 genera and 11 subgenera are described as new: *Gigalimosina* gen. nov., *Herniosina* gen. nov., *Terrilimosina* gen. nov., *Minilimosina* gen. nov., *Minilimosina* (*Svarciella*) subgen. nov., *Minilimosina* (*Allolimosina*) subgen. nov., *Xenolimosina* gen. nov., *Paralimosina* (*Canarisina*) subgen. nov., *Spelobia* (*Eulimosina*) subgen. nov., *Spelobia* (*Bifronsina*) subgen. nov., *Pullimosina* gen. nov., *Pullimosina* (*Dahlimosina*) subgen. nov., *Spinilimosina* gen. nov., *Kimosina* gen. nov., *Kimosina* (*Collimosina*) subgen. nov., *Kimosina* (*Alimosina*) subgen. nov., *Telomerina* gen. nov., *Opalimosina* gen. nov., *Opalimosina* (*Pappiella*) subgen. nov., *Opalimosina* (*Hackmanina*) subgen. nov., *Opalimosina* (*Dentilimosina*) subgen. nov. and *Rudolfia* gen. nov. Other included genera (*Limosina* MACQUART, 1835; *Apteromyia* VIMMER, 1929 gen. restit.; *Paralimosina* PAPP, 1973; *Spelobia* SPULER, 1924 nom. restit., stat. nov.; *Chaetopodella* DUDA, 1920; *Halidayina* DUDA, 1918) are redescribed.

Descriptions of 14 new species are given (*Minilimosina* 4, *Spelobia* 6, *Kimosina* 1, *Telomerina* 3), other species are fully redescribed. 4 new synonyms are established; numerous species (besides those included in the monograph) are put in new combinations. All available type material of European species (including synonyms) was revised, number of lectotypes designated and in this way the status of particular species fixed. A description of each species is supplemented by numerous illustrations, data on the morphology of preimaginal stages, biology, distribution and by discussion of relationships.

Identification keys to all included taxa are given. The general part includes a summary of basic data dealing with history of investigations, morphology, biology, zoogeography and phylogeny (cladistic classification) of the groups under study.

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DOI: 10.21248/contrib.entomol.32.2.195-282

Dedication

I should like to dedicate this study to my dear late father, ANTONÍN ROHÁČEK (1925–1977) who, although a classical philologist, encouraged my interest in entomology and later promoted my dipterological research work.

Introduction

The genus *Limosina* MACQUART, 1835 (sensu HACKMAN, 1969a) is the largest and most diverse group of the Sphaeroceridae, differing from other genera of Limosininae merely in lacking the features by which these genera are diagnosed (RICHARDS, 1973). HACKMAN (1969a) considers it the "remaining body" of Limosininae left after separation of the various aberrant groups (genera) by apomorphic characters. Such an ill-defined genus, characterized only be plesiomorphic features, cannot be considered as a monophyletic group (HACKMAN, 1969a: 203) — the present investigation showed it to be of not only paraphyletic but also polyphyletic origin.

A possible way of finding the real relationships of particular groups of this genus is to study the male genitalia and female terminalia in all included species, carefully evaluating old as well as newly discovered diagnostic criteria regarding the variability, possible convergent evolution and functional adaptability of particular organs, and only then, on the basis of a detailed analysis, to characterize particular monophyletic groups. Although various authors (HACKMAN, 1969a, b; RICHARDS, 1973; ROHÁČEK, 1975c, 1977a) draw attention to the fact that it is necessary to undertake such work because the present status of the genus *Limosina* MACQUART is untenable, none has attempted to solve this difficult problem.

About 6 years ago I began work on a monograph of European species of *Limosina* MACQUART (sensu HACKMAN, 1969a) and having examined male genitalia and female terminalia in the majority of species from the area I conclude that it is inevitable that the previous genus *Limosina* be divided into a number of genera and subgenera. This solution might be considered as rather atomistic or even megalomaniac, but all other solutions (for instance the division of *Limosina* into subgenera and delimitation of the most aberrant

DOI: 10.21248/contrib.entomol.32.2.195-282

groups as genera) proved to be inconsistent and non-phylogenetic. The following main reasons substantiate the present solution of the generic classification of the previous genus *Limosina*.

(1) As the classification of Sphaeroceridae currently used (HACKMAN, 1969a) is based mainly on non-genital characters, it is not surprising that the genera are established on a very different level. The groups (now considered genera) were originally separated from *Limosina* MACQUART as taxa differing from other included species-groups by a few striking features without searching for the real relationships. However, examination of the post-abdominal structures of some of these genera clearly demonstrate their affinity to some groups of *Limosina* (sensu HACKMAN, 1969a). It is apparent that the groups associated with these genera should be considered as taxa on the same level, thus deserving generic rank, or these genera (e.g. *Chaetopodella* DUDA, *Poecilosomella* DUDA, *Paralimosina* PAPP, *Paraspelobia* DUDA) should be treated as synonyms of the genus *Limosina*, but the latter alternative is incorrect because it does not resolve the polyphylety of *Limosina*.

(2) On the contrary, in the previous genus *Limosina* there are some groups without distinct affinity to other of its groups or even to all known genera of Limosininae. These groups cannot be treated as less than genera and these groups caused the polyphylety of the genus *Limosina* sensu HACKMAN (1969a).

(3) All previous attempts to divide *Limosina* (sensu HACKMAN, 1969a) into more natural groups were not successful not only because of the ignorance of the genital characters but also because they were made "from above", by detaching the most strikingly aberrant species and/or groups. The present classification was elaborated from the specific level. On the basis of available criteria from detailed descriptions, species were grouped in the largest clear monophyletic groups. These groups were considered to be at least subgenera and were further classified by HENNIG's method of cladistic classification, using a raster of about 30 selected characters delimiting each group. The level of the generic rank was established on the basis of the cladograms obtained, but always with the principle that the group must be monophyletic and separated from corresponding groups by a distinct gap.

(4) The higher (suprageneric) supposed cladistic classification within the previous genus *Limosina* clearly showed the polyphylety of this taxon (see the chapter "Phylogeny").

(5) The present solution of the generic classification of the *Limosina* (sensu HACKMAN, 1969a) follows the general trend of the construction of more natural ("phylogenetic") systems and the decrease in the level of supraspecific taxa due to increased knowledge, so that the level of genera here established should be comparable with that in better known families of Diptera and other insects (for instance HIPPA 1978).

(6) The number of known species relegable to *Limosina* MACQUART (sensu HACKMAN, 1969a) is comparatively high (over 230 described species) and the number of existing ones is certainly at least three times higher; therefore this practical aspect may be considered a minor reason for the division of the genus *Limosina*. I hope the breakup of the previous genus *Limosina* into more genera will have a much more important practical result — the necessity to describe genitalia of new species.

The present paper is not limited to the establishment of a new generic classification of the previous genus *Limosina* MACQUART. Various problems connected with taxonomy, morphology, biology, zoogeography and relationships have been resolved in this work on the European species of this group.

The latest summary works (DUDA, 1918, 1925, 1938; RICHARDS, 1930) require further revision because many papers concerning the group were published after 1938, the date of DUDA's (1938) monograph of Palaearctic Sphaeroceridae. The revision of available type material (mostly neglected by previous authors) brought a number of essential changes at specific level and made it possible to discover some new species confused under single names. Many undiscovered diagnostic features facilitate the identification of particular species and were used in new keys to the West Palaearctic subfamilies of Sphaeroceridae, to genera of Limosininae and to species.

DOI: 10.21248/contrib.entomol.32.2.195-282

In morphology, special attention was paid to the elucidation of the terminology of all used features. In particular the morphology of the male and female terminalia (including their function) was studied extensively. Knowledge of the morphology of preimaginal stages was summarized and supplemented. Regarding the immature stages of particular species only references are given but the most diagnostic features or similarity to allied species are often also noted.

The biology in general was dealt with in a separate chapter comprising a discussion of biological phenomena known in the group. This part is not a compilation — its concept as well as contents are for a great part original and contain new data, theories and opinions.

The principles of zoogeographical classification are explained in the chapter "Zoogeography" and the distribution of particular species discussed in a separate paragraph under each species, as is the biology or preimaginal stages. Although the title refers only to Europe, all known species of the previous genus *Limosina* from the W. Palaearctic are dealt with here, including those from the Atlantic islands (Canary Is., Azores, Madeira). There is, however, a lack of faunistic data from many European countries and only the following countries may be considered comparatively well studied: Spain, England, FRG, GDR, Czechoslovakia, Hungary, Finland. Since some countries have been practically neglected by collectors up to the present (e.g. Portugal, Switzerland, The Netherlands, Norway, Albania, Marocco and especially the European part of USSR) further undescribed species will probably be discovered in Europe in the future.

The preimaginal stages and biology of the included species are even less well known and perhaps this monograph will encourage research in these relevant fields.

Acknowledgements

I wish to express my sincere gratitude to the following persons for the generous loan of type and/or comparative material, for provision of valuable data and information about the depository of type material and other help without which this work could hardly have been finished: Dr. H. ANDERSSON and Mr. R. DANIELSSON (ZIL[1]), Dr. P. H. ARNAUD, Jr. (CAF), Dr. V. BESHOVSKI (IZS), Mr. M. BAEZ (ULT), Mr. B. H. COGAN, Mr. J. P. DEAR and Mr. B. R. PITKIN (BML), Prof. CHRISTINE DAHL (ZIU), Dr. J. C. DEEMING (Institute for Agricultural Research, Zaria, Nigeria), Dr. G. DEMOULIN and Dr. P. VANSCHUYTBROECK (IRB), Dr. H. H. EVENHUIS (Instituut voor Plantenziektenkundig, Wageningen, The Netherlands), Dr. W. A. FOSTER (MZC), Mrs. PAMELA GILBERT (BML, library), Dr. M. W. R. DE V. GRAHAM (UMO), Prof. R. A. HARRISON (Dept. of Entomology, Lincoln College, Canterbury, N. Z.), Dr. J. JEŽEK (NMP), Dr. P. LAUTERER and Dr. J. STEHLÍK (MMB), Dr. C. LEONARDI (MCM), Dr. RUTH LICHTENBERG (NMW), Dr. B. LINDEBERG (ZMH), Mr. L. LYNEBORG (ZMK), Mr. S. MARSHALL (University of Guelph, Canada), Dr. SARAH MASCHERINI (MSF), Dr. L. MATILE (Museum National á Histoire Naturelle, Paris), Mr. B. MOCEK (MHK), Prof. Dr. G. MORGE, „IPF" (i. e. former DEI), Dr. J. P. O'CONNOR (NMI), Dr. I. OKÁLI (SMB), Dr. M. PAOLETTI (Noventa di Piave, Italy), Mr. P. POKORNÝ (RMM), Dr. L. PAPP (TMB), Dr. F. QUAGLIA (Istituto di Entomologia Agraria, Pisa), Dr. H. SCHUMANN (ZMB), Dr. H. STOCKNER and Dr. H. TROGER (IZI), Dr. J. VAŇHARA (Ústav ekologie lesa, Brno) and Dr. J. ZUSKA (VUP).

My particular thanks are due to Dr. J. W. ISMAY (UMO) who kindly improved the English of the entire manuscript and added a number of valuable comments, to Prof. Dr. G. MORGE (DEI) for his many-sided help with the publication to Mr. L. LYNEBORG (Z. M.K) for the arrangement of the scanning micrographs, to Dr. K. SAMŠINÁK (Parazitologický ústav ČSAV, Praha) for the identification of mites found on flies examined and to Dr. H. SCHUMANN (ZMB) for permission to use his figures of larval morphology of *Chaetopodella scutellaris*.

I am deeply indepted to the following specialists on the family Sphaeroceridae, Prof. W. HACKMAN (ZMH), Prof. K. C. KIM (Pennsylvania State University, USA), Dr. L. PAPP (TMB) and Prof. O. W. RICHARDS (London) for their valuable comments, helpful criticism and submission of many unpublished data. Finally I should like to thank Dr. R. ROZKOŠNÝ, my teacher in dipterology, for his advices, stimulation and promotion during my many-year's investigations in the family Sphaeroceridae.

Abbreviations

1. Abbreviations of morphological terms used in text and figures

a — anterior (bristle)
A — anal vein
ac — acrostichal bristle
ad — anterodorsal (bristle)
ads — additional setulae on orbit
AE — aedeagus
al — alula
AN — antenna
AP — aedeagal apodeme
ar — arista
AS — anus
ASC — additional sclerite(s)
ASP — anterior spiracular process
av — anteroventral (bristle)
C — costa
CA — carina
CE — cercus
C-index — costal index ($Cs_2 : Cs_3$)
CPS — cephalopharyngeal skeleton
Cs_1, Cs_2, Cs_3 — 1st, 2nd, 3rd costal sector
cx_1, cx_2, cx_3 — fore, mid, hind coxa
d — dorsal (bristle)
DB — dorsal bridge
dc — dorsocentral bristle
DC — dorsal cornu
DP — distiphallus
ds — discal cell
EAP — ejaculatory apodeme
ED — ejaculatory duct
EP — epiphallus
ES — epistomal sclerite
f_1, f_2, f_3 — fore, mid, hind femur
FA — face
FC — facial cavity
FT — frontal triangle
FTE — fore part of telomere
g — genal bristle
GE — gena

[1] For the abbreviations of institutions and museums see p. 199

DOI: 10.21248/contrib.entomol.32.2.195-282

GO – gonopore
h – humeral cross-vein
HA – haltere
HC – humeral callus
HPP – hypopleuron
HS – hypostomal sclerite
HTE – hind part of telomere
hu – humeral bristle
HY – hypandrium
if – interfrontal bristle
IP – intraperiandrial sclerite
IS – internal sclerite
ISP – interspiracular hairs
LB – labial sclerite
LS – ligulate sclerite
LU – frontal lunule
M_{1+2} – 1st medial vein
M_{3+4} – 2nd medial vein
MH – mouthhook
ML – mesolobus
MN – mesonotum
MP – micropyle
MSP – mesopleuron
MSS – mesothoracic spiracle
mt_1, mt_2, mt_3 – fore, mid, hind basitarsus
MT – medial tooth
MTP – metapleuron
MTS – metathoracic spiracle
npl – notopleural bristle
oc – ocellar bristle
occe – external occipital bristle
occi – internal occipital bristle
OR – orbitistle
ors – orbital bristle
OT – ocellar triangle
p – posterior (bristle)
P – periandrium
pa – prealar bristle
PB – parastomal bar
pd – posterodorsal (bristle)
PEP – pre-epiphallus
PG – postgonite
phu – posthumeral bristle
poc – postocular setae
PP – phallophore
PRP – propleuron
PS – pharyngeal sclerite
psa – postalar bristle
PSC – postscutellum
PSP – posterior spiracular process
PTP – pteropleuron
pv – posteroventral (bristle)
pvt – postvertical bristle
R_1 – 1st radial vein
R_{2+3} – 2nd radial vein
R_{4+5} – 3rd radial vein
S – abdominal sternum
sa – supraalar bristle
sc – scutellar bristle
Sc – subcosta
SCU – scutellum
SP – spectacles-shaped sclerite
SS – spiracular split
ST – spermatheca
STP – sternopleuron
stpl – sternopleural bristle
T – abdominal tergum
t_1, t_2, t_3 – fore, mid, hind tibia
t_a – anterior cross-vein
t_a–t_p – sector on M_{1+2} between t_a and t_p
TE – telomere
t_p – posterior cross-vein
v – ventral (bristle)
va – ventroapical bristle
VC – ventral cornu
VH – ventral hooklets
vi – vibrissa
vte – external vertical bristle
vti – internal vertical bristle
VW – ventral window

2. Abbreviations of museums and collections

BML – British Museum (Natural History), London (England)
CAF – California Academy of Sciences, San Francisco (USA)
DEI – Institut für Pflanzenschutzforschung der Akademie der Landwirtschaftswissenschaften (= IPF), Eberswalde (ehem. DEI) (GDR)
IRB – Institut Royal des Sciences Naturelles de Belgique, Bruxelles (Belgium)
IZI – Institut für Zoologie der Universität Innsbruck (Austria)
IZS – Institut Zoologique et Musée, Academie des Sciences de Bulgarie, Sofia (Bulgaria)
JRO – J. ROHÁČEK, Opava (Czechoslovakia)
JZP – J. ZUSKA, Praha (Czechoslovakia)
MCM – Museo Civico di Storia Naturale, Milano (Italy)
MCV – Museo Civico di Storia Naturale, Venezia (Italy)
MHK – Krajské muzeum východních Čech, Hradec Králové (Czechoslovakia)
MMB – Moravské muzeum, Brno (Czechoslovakia)
MSF – Museo Zoologico de „La Specola", Firenze (Italy)
MZC – University Museum of Zoology, Cambridge (England)
NMA – Naturhistorisches Museum der Benediktiner-Abtei, Admont (Austria)
NMI – National Museum of Ireland, Dublin (Ireland)
NMW – Národní muzeum, Praha (Czechoslovakia)
NME – Naturhistorisches Museum, Wien (Austria)
PFB – Přírodovědecká fakulta UJEP, Brno (Czechoslovakia)
RMM – Regionální muzeum, Mikulov na Mor. (Czechoslovakia)
SMB – Slovenské národné muzeum, Bratislava (Czechoslovakia)
SMO – Slezské múzeum, Opava (Czechoslovakia)
TMB – Természettudományi Múzeum Állattára, Budapest (Hungary)
ULT – Universidad de la Laguna, Departamento de Zoologia, Tenerife (Canary Is., Spain)
UMO – University Museum, Oxford (England)
VUP – Výzkumný ústav potravinářského průmyslu ČAZ, Praha (Czechoslovakia)
ZIL – Zoological Institute, Lund (Sweden)
ZIU – Zoological Institute, Uppsala (Sweden)
ZMB – Zoologisches Museum an der Humboldt-Universität zu Berlin (GDR)
ZMH – Zoological Museum of the University, Helsinki (Finland)
ZMK – Zoologisk Museum, København (Denmark)

3. Abbreviations of countries

FRG – Federal Republic of Germany
GB – Great Britain
GDR – German Democratic Republic
USA – United States of America
USSR – Union of Socialist Soviet Republics

Remarks: Abbreviations for the provinces of Fennoscandia and Denmark are those used in Fauna Entomologica Scandinavica (see e.g. ROZKOŠNÝ, 1973).

DOI: 10.21248/contrib.entomol.32.2.195-282

A. General part

Historical review of taxonomic investigations in the genus *Limosina* MACQUART

The history of taxonomic work in the genus *Limosina* MACQUART is very intricate but it is possible to delimit three distinct stages. The first stage began with the description of the genus *Limosina* by MACQUART (1835) and ended when DUDA's (1918) monograph appeared. MACQUART (1835) described the genus *Limosina* without designating the type species and included 9 species with reduced M_{1+2} and M_{3+4} and without basal and anal cells in the wing. The type species was subsequently established by WESTWOOD (1840) who designated the first species recorded by MACQUART (1835) in the genus *Limosina* — *Borborus silvaticus* MEIGEN, 1830. In this concept the genus *Limosina* contained the majority of species and genera of the present-day subfamily Limosininae (see e.g. HALIDAY, 1836; MEIGEN, 1838; ZETTERSTEDT, 1847, 1855, 1860; STENHAMMAR, 1854; RONDANI, 1880; VILLENEUVE, 1918a, 1918b). No authors during this period (1835—1918) attempted to divide this large taxon into groups.

Towards the end of the 19th century the situation with the genus *Limosina* became somewhat more complicated. MIK (1888) rediscovered the old paper of OLIVIER (1813) and discussed, among others, the genus *Leptocera* OLIVIER, 1813 as being obviously congeneric with *Limosina* MACQUART. Because of priority, *Leptocera* OLIVIER, 1813 was used (this concept was followed by MALLOCH, 1914 or VILLENEUVE, 1917 and also by authors from the next period — see below) and *Limosina* MACQUART, 1835 became a synonym.

DUDA's (1918) revision of the European species of *Limosina* is thought to be the dividing line between first and second stage of taxonomic research in the genus *Limosina*. DUDA (1918) was the first divider the genus *Limosina* (s. lat. = sensu MACQUART) into subgenera, redescribed all European species and constructed the first usable key to them. The high taxonomic value of DUDA's (1918) revision is not impaired by his nomenclatorical shortcomings, for example the fact that he did not include the subgenus *Limosina* s. str. and described the subgenus *Scotophilella* DUDA, 1918 instead. Later DUDA (1925), following his previous subgeneric classification of *Limosina* (s. lat.), used the name *Leptocera* OLIV. (s. lat.) but again without containing the nominate subgenus and described new subgenera and species from the tropics. SPULER (1925a) established some new subgenera of *Leptocera* (s. lat.) from North and Central America, and also revised the North American species of the subgenus *Scotophilella* DUDA (SPULER, 1925b).

RICHARDS (1930) monographed British Sphaeroceridae and included a valuable and comprehensive survey of all generic and subgeneric taxa proposed in the family up to 1929. He asserted the use of the name *Leptocera* OLIVIER (s. lat.), synonymized sg. *Paracollinella* DUDA, 1924 with its nominate subgenus *Leptocera* (s. str.) and restricted *Limosina* MACQUART, 1835 to a subgenus of the genus *Leptocera* (s. lat.) and reduced *Scotophilella* DUDA, 1918 to its synonym. However, DUDA's (1918, 1925) original concept of the sole giant genus *Leptocera* OLIVIER with many subgenera had been in essence followed by RICHARDS (1930 and almost all subsequent papers) and was generally in use even recently (RICHARDS, 1965, 1967, 1968, 1973, 1976; DEEMING, 1969; HACKMAN, 1967b; GAPASIN & KIM, 1972; HARRISON, 1976). DUDA (1938) resumed the use of the name *Limosina* (s. lat.) which has been accepted by some subsequent workers (e.g. RICHARDS, 1952a; VANSCHUYTBROECK, 1943a, b, 1950a, 1962b).

In 1950—60 the first papers appeared in which subgeneric names were given generic status[2] (e.g. VANSCHUYTBROECK, 1951, 1962a, 1970; HACKMAN, 1958, 1960, 1961, 1965a). These papers are thought to be transitory to the third stage, initiated by HACKMAN (1969a) who gave a new classification of Sphaeroceridae, with special regard to phylogeny and zoogeography. In this study, the majority of subgenera of *Leptocera* (s. lat.) are classified as genera and aggregated into groups considered to be more or less natural. The genus *Leptocera* OLIVIER is restricted to 4 subgenera (*Leptocera* s. str., *Rachispoda* LIOY, 1864, *Opacifrons* DUDA, 1918 and *Pteremis* RONDANI, 1856) and the previous subgenus *Limosina*

[2] VANSCHUYTBROECK (1942) presented the subgenera of earlier authors as genera, but probably only as a consequence of his misunderstanding DUDA's (1938) work. DUDA (1918, 1925, 1938) described the particular species using subgeneric names only but in the introductory text the genus to which they belong is always clearly stated.

DOI: 10.21248/contrib.entomol.32.2.195-282

MACQUART is treated as a genus, with *Halidayina* DUDA, 1918 included as a synonym. However, the genus *Limosina* MACQUART sensu HACKMAN (1969a) continued to be the largest, very heterogeneous and ill-defined group of Limosininae whose monophylety was questioned by HACKMAN (1969a). This classification was maintained by PAPP and ROHÁČEK (in all papers) with the exception that PAPP treats *Halidayina* DUDA, 1918 as an independent genus.

After HACKMAN's (1969a) study, the necessity of further subdivision of the redefined genus *Limosina* into more natural (monophyletic) groups was discussed (RICHARDS, 1973; PAPP, 1973a; ROHÁČEK, 1975c, 1977a) suggesting a comparative study of the genitalia as the only possible solution of this problem. More detailed data about male and female genitalia and relationships of some groups of *Limosina* MACQUART sensu HACKMAN (1969a) were published by ROHÁČEK (1977a, b, 1978a, c) — these papers are considered to be preparatory studies for the present monograph.

Morphology

Whilst the external adult morphology of the previous genus *Limosina* is relatively well known and extensively employed in its taxonomy (see below), the preimaginal stages have been hitherto very insufficiently studied. I include also some discussion of the morphology of immature stages in this chapter because of their potential importance in future research on the relationships and classification of particular taxa.

Although detailed investigation is outside the scope of this work, some material was studied, originally with the view of improving knowledge of at least the general morphology of particular stages, with special emphasis on structures of presumed taxonomic or diagnostic importance.

1. Egg (Figs. 2—6)

This stage is very little known. GODDARD (1938) described and illustrated the egg of *Limosina silvatica* and *Pullimosina heteroneura*. HAMMER (1941) superficially described the egg of *Spelobia clunipes* and *Pullimosina moesta* (the identification of the latter species is rather doubtful). TENORIO (1968) published descriptions and figures of eggs of 4 other species (*Spelobia bifrons*, *Spinilimosina rufifrons*, *S. pectinata* and *Opalimosina mirabilis*). Three further species are figured here.

The eggs are white to pale yellowish, elongate oval, usually dorsally flattened (the egg is usually buried in the larval food with only the dorsal or anterodorsal part uncovered). The chorion seems to be differently sculptured in particular taxa — for example in *Limosina silvatica*, the entire surface is covered by minute indentations, in *Pullimosina heteroneura* with about 13 longitudinal ridges extending the length of the egg (see GODDARD, 1938), in *Spelobia* spp. and *Opalimosina simplex* finely or more roughly pitted and/or tuberculate (Figs. 2—5). Various additional structures are often developed on the dorsal surface and especially round the micropyle (Figs. 2, 5, *MP*), e.g. two longitudinal band-like ledges (Figs. 2—4), a small anterior lip (in *Limosina silvatica* — GODDARD, 1938, Fig. 1F) or the peculiar anterior, somewhat fringed flat structure (Figs. 5, 6). The latter mentioned structure[3] probably has the same function as the respiratory horns described in eggs of *Coproica* species (cf. HAMMER, 1941; HAFEZ, 1939).

The known eggs of species of the previous genus *Limosina* are comparatively large (0.43—0.68 mm), especially in the smaller species. It is interesting that the egg of *Limosina silvatica* (length of female 3.0—3.7 mm) is only up 0.68 mm long, while in *Opalimosina simplex* (female body length 1.4—1.7 mm) the egg figured here (Figs. 5, 6) measured 0.56 mm.

2. Larva (Figs. 7—15)

Only SCHUMANN (1962) has described and illustrated in detail all three larval instars of a species (*Chaetopodella scutellaris*), also included in this work. GODDARD (1938) figured the cephalopharyngeal skeleton of *Limosina silvatica*, probably prepared from the puparium

[3] TENORIO (1968) described similar structure in *Opalimosina mirabilis*. She observed that this structure is exposed and lies parallel to the surface of the substrate. Possibly it plays some role in the hatching process of the young larva.

DOI: 10.21248/contrib.entomol.32.2.195-282

and TENORIO (1968) that of 3rd instar larva of *Opalimosina mirabilis* I have also examined the cephalopharyngeal skeleton from puparia (thus of 3rd instar larva) of two species, *Apteromyia claviventris* and *Spelobia palmata* and illustrated that of the latter species (Fig. 7). The general construction of the cephalopharyngeal skeleton of the 3rd larval instar essentially similar in all examined genera and therefore it is possible that this structure is also similar in 1st and 2nd instars of these genera to that of *Chaetopodella scutellaris*, described below.

a) First-instar larva (Fig. 8). Described by SCHUMANN (1962) for *Chaetopodella scutellaris*. Transparent white, about 1 mm long, of usual maggot-like apodous form, as in other Acalyptrata. The larva is amphipneustic but the anterior (prothoracic) spiracles of the 1st instar are very simple, each situated on the tongue-shaped rounded prolongation of the tracheal stock. The posterior (abdominal) spiracles are also simple, rounded, flat. 6th—11th segments with an anteroventral row of pale brown pigmented small spines; 2nd, 5th and 12th segments with minute non-pigmented rows of spines.

Cephalopharyngeal skeleton (Fig. 8) simple, with an unpaired medial tooth (*MT*); anteroventrally there are 2 minute sclerites considered to be labial sclerites (*LB*). Epistomal sclerite (*ES*), hypostomal sclerite (*HS*) and pharyngeal sclerite (*PS*) more or less coalesced together. Pharyngeal sclerite with simple but long dorsal bridge (*DB*) and short dorsal cornua (*DC*).

b) Second-instar larva (Fig. 9, 11). Described by SCHUMANN (1962) for *Chaetopodella scutellaris*. Colour transparent white, the anteroventral rows of spines on 2nd, 4th—12th segments colourless. Length of body about 2 mm. Anterior spiracles as in first instar, posterior spiracles somewhat better differentiated (Fig. 9).

Cephalopharyngeal skeleton (Fig. 11) already with paired mouth-hooks (*MH*); hypostomal sclerite (*HS*) and parastomal bars (*PB*) well developed. Ligulate sclerite (*LS*) rather weakly sclerotized, epistomal sclerite (*ES*) comparatively distinct. Dorsal bridge (*DB*), dorsal (*DC*) and ventral cornua (*VC*) of the pharyngeal sclerite similar to those in 3rd instar. Ectostomal sclerite absent.

c) Third-instar larva (Figs. 7, 10, 12—15). Described by SCHUMANN (1962) with some alterations regarding cephalopharyngeal skeleton. Colour white, partly transparent. Length about 3 mm (*Chaetopodella scutellaris*). Ventrally, on 2nd, 5th—12th segments with anterior row of short spines (hooklets) as usual. Anterior (prothoracic) spiracles elongate and with numerous finger-like lateral papillae (Fig. 12). Some other species have these spiracular processes shortly palmate (as found in puparia, see below). Posterior spiracles (Figs. 10, 15) roughly circular, situated on short cylindrical projections, each with 3 elongately oval spiracular splits (Fig. 10, *SS*) and usually 4 barely visible (not figured in Fig. 10) interspiracular palmately branched hairs (preserved also on puparium, Fig. 29, *ISP*).

Cephalopharyngeal skeleton (Fig. 7, 13, 14) heavily sclerotized, with somewhat reduced and membraneous ventral ligulate sclerite (*LS*) and dorsal epistomal sclerite (*ES*). Ectostomal sclerite always absent (probably in the whole subfamily Limosininae). Other sclerites well developed. Mouthhooks (*MH*) with simple pointed and ventrally bent apices, and without dorsal connective. Hypostomal sclerite (*HS*) H-shaped in dorsal view (Fig. 14), with posteriorly projecting arms articulating with parastomal bars (*PB*) of pharyngeal sclerite. Pharyngeal sclerite (*PS*) with long, slender dorsal cornua (*DC*), longer but wider, ventrally weakly sclerotized and pale pigmented ventral cornua (*VC*). Dorsal cornua connected by the anterodorsal perforated dorsal bridge (*DB*); ventral cornua only with incomplete ventral window (*VW*).

3. Puparium (Figs. 16—31)

The puparium is the best known preimaginal stage. Thanks to the studies of GODDARD (1938) TENORIO (1968) and OKELY (1974) puparia of 18 species of the previous genus *Limosina* were described and illustrated. Although the morphology of the puparium is comparatively well known, there is little precise evaluation of the variability of the characters used (cf. OKELY, 1974).

The vacant puparium is translucent white to brown, usually yellowish or golden brown; it is virtually a sclerotized skin of the 3rd-instar larva. The pupa lies in the posterior two-thirds to four-fifths of the puparium so that the anterior cleared part may be sometimes

DOI: 10.21248/contrib.entomol.32.2.195-282

characteristically bent (*Opalimosina mirabilis* — cf. OKELY, 1974: 50). The larval structures are comparatively well preserved in the puparium, even if modified by sclerotization and drying up. The size of the puparium ranges between 1.8 mm (*Minilimosina fungicola*) and 3.8 mm (*Limosina silvatica*).

The segments of the puparium, corresponding to those of 3rd instar larva, are labelled from I to XI (Figs. 16—18), the first being the prothoracic segment, the last (XI) is a fusion of the 11th and 12th segment of the larva. The puparium is more or less elongate cylindrical with a tapered anterior end flattened dorsoventrally, and tapered but truncate posterior end. The segmentation is more or less distinct, at least ventrally. There are often shallow longitudinal foveae on laterodorsal and/or lateroventral margins of segments II(III)—X. Dorsal and ventral surface of puparium is covered with numerous very fine transverse lines. Segments IV—X carry anteroventral rows of larger hooklets (Figs. 17, 18, *VH*) and minute spines (see detail in Fig. 24).

Segments I—II are dorsally intensively, but rather variably wrinkled. The first (prothoracic) segment carries 2 anterior spiracular processes (*ASP*) which vary in shape in different taxa, either shortly palmate (*Limosina silvatica, Herniosina bequaerti, Minilimosina fungicola* — see GODDARD, 1938, Figs. 1—3) or spine-like, with pale tubercles and papillae. The spine-like process may be long (Figs. 16, 25, 28) or short (Fig. 20). Although the length and direction of the anterior spiracular processes (especially when spine-like) shows great intraspecific variability because they are formed from soft larval spiracular processes (cf. Fig. 12) whose form depends on the surrounding substrate, the shape and position (distance between processes) of the anterior spiracular processes are comparatively good diagnostic criteria, used by GODDARD (1938) and OKELY (1974).

The ventral surface of segments I—II is also wrinkled and segment I bears 2 flat, roughly circular impressions (Figs. 22, 26). The cephalopharyngeal skeleton (Fig. 18, *CPS*) is preserved, adhering internally to the ventral surface of segments I—III in the empty part of the puparium (the pupa lies more posteriorly).

The posterior truncate segment (XI) is intensively wrinkled on the dorsal and ventral surface. It carries a pair of terminal processes which bear the posterior spiracles. The posterior spiracular processes (Figs. 16, *PSP*, 21, 27, 29) are of some diagnostic value, especially regarding their length, shape and the orientation of the spiracular plates. Each spiracle (Figs. 23, 29) has 3 spiracular splits (*SS*) and the relics of interspiracular palmately branched hairs (*ISP*); the latter are well preserved especially in some species with longer posterior spiracular processes (*Opalimosina mirabilis* — see OKELY, 1974). The anus (Fig. 31, *AS*) is situated subterminally on the ventral surface of the posterior segment (see also Fig. 18).

The sculptural features of puparium discussed above should prove to be good diagnostic characters, especially when their variability is measured; scanning electron microscopy might be a useful method for this (see Figs. 19—31).

4. Imago (Figs. 1, 32—50)

The morphology of adult Sphaeroceridae was thoroughly dealt with by KIM & COOK (1966), but their study is based only on selected species of some genera (*Sphaerocera, Copromyza, Leptocera*) of which only the genus *Leptocera* is somewhat related to the groups under study.

The major aim of the following pages is to explain and define the morphological terms which are important in taxonomy and are used in this work. Some parts of the adult morphology are therefore wholly or partly omitted (e.g. mouthparts, prothorax, metathorax, wing base) and conversely some taxonomically significant structures are considered in detail (chaetotaxy, wing venation, postabdomen in both sexes). The terminology used as a rule is that of a taxonomist's and not that of a morphologist's, but the correct morphological terms (according to KIM & COOK, 1966) are also mentioned. For the postabdomen and genitalia, GRIFFITHS' (1972) and MATSUDA's (1976) terminology is followed with some alterations (see also ROHÁČEK, 1978c).

The European species of the previous genus *Limosina* are small (0.8—3.7 mm), brown to black coloured flies. In some species the head is partly or wholly yellow or reddish. The body is shiny to dull but usually more or less (mainly brown) dusted.

DOI: 10.21248/contrib.entomol.32.2.195-282

a) Head (Figs. 32—34). The head is rather short and high, especially in some groups (*Telomerina*, *Opalimosina*). Frons (postfrons of KIM & COOK, 1966) is wide, anteriorly limited by ptilinal suture, posteriorly by occiput (behind ocellar triangle). The most conspicuous structures of frons are: (1) the orbit (*OR*) bordering the eye and carrying 2 orbital bristles (*ors*), a number of small additional setulae (*ads*) and posteriorly the internal (*vti*) and external (*vte*) vertical bristles; (2) the frontal triangle (*FT*) — more or less distinctly defined bare triangular area in front of ocellar triangle between interfrontalia; (3) the interfrontalia (frontalia of KIM & COOK, 1966) — narrow stripes between orbits and frontal triangle carrying the interfrontal bristles (*if*); (4) the ocellar triangle (*OT*) — a distinctly protruding triangular flat tubercle on top of head and carrying 3 ocelli, 2 ocellar bristles (*oc*) and some small setulae (interocellar and postocellar setae of KIM & COOK, 1966). Externally to the most anterior *if* is an additional small (nameless) seta. Behind the ocellar triangle in the uppermost part of occiput are situated: (1) postvertical bristles (*pvt*) — small, the most medial setae, sometimes (*Halidayina*, *Chaetopodella*, *Spinilimosina*, *Spelobia*) in two pairs (Fig. 34, 803), but the small anterior pair are probably not true *pvt*; (2) internal occipital bristles (*occi*) — larger bristles between *pvt* and *occe*; (3) external occipital bristles (*occe*) arising laterally to *occi*. All these bristles are inclinate, the *pvt* may sometimes be absent. Behind the eye and on posterior margin of gena there is a row of postocular setae (*poc*) (postorbital of KIM & COOK, 1966).

Eyes are always dichoptic, without sexual dimorphism, bare, in some species distinctly reduced. The eye is anteriorly separated from the facial cavity by narrow face (*FA*) which also may bear some minute setulae and is continued by wide gena below eye. Gena (*GE*) may be enlarged in species with reduced eyes; it carries a distinct genal bristle (*g*), some smaller setae behind it and a number of small peristomal setulae on its ventral margin. Anteriorly to gena is an elevated ridge — the vibrissal angle (facial ridge of KIM & COOK, 1966) with a stout and long vibrissa (*vi*) and often 1—2 additional setae. The facial cavity (*FC*) is the concavity in prefrons (of KIM & COOK, 1966) below antenna, in which the antenna rests. The facial cavities are separated by a more or less protruding medial keel — the carina (*CA*). Between antennae, above the carina but below the ptilinal suture there is a well developed frontal lunule (*LU*).

Antennae (*AN*) are inserted below ptilinal suture, laterally to carina and have 3 segments and the distinctly pubescent arista (*ar*). The basal segment (scape) is short, forming a small ring; the second segment (pedicel) is truncated, conical, widened distally, with a crown of distal setulae; the third segment (postpedicel) is homologous with the basal segment of flagellum in Nematocera. It is the largest antennal segment, of oval, somewhat laterally flattened form, finely pubescent. Arista (*ar*) is composed of 2 segments and form a long and thin filament with distinct ciliation (Figs. 834—837).

The mouthparts, which are of the non-piercing muscoid type, are not considered here; detailed information about them in the genus *Leptocera* OLIVIER are in KIM & COOK (1966).

b) Thorax (Figs. 38, 39). The thorax is short and high. Prothorax is reduced; the most significant structures are: the humeral callus (*HC*) (postpronotum of KIM & COOK, 1966) usually carrying 2 humeral bristles (*hu*), the internal often reduced to a microseta; the propleuron (*PRP*) (episternum I of KIM & COOK, 1966) which supports the first leg and the ventral prosternum (basisternum I of KIM & COOK, 1966) which is very narrow, linear, at most posteriorly somewhat extended. The shape of the latter structure is considered to be of great taxonomic importance in some genera (RICHARDS, 1973) not dealt with here.

Mesothorax is the largest part of thorax. Its dorsal part — mesonotum (*MN*) may be divided into four areas — prescutum, scutum, scutellum and postnotum. The prescutum is separated from scutum by an incomplete (intrascutal) suture before wing bases; the scutellum (*SCU*) from scutum by the deep scutoscutellar suture. The postnotum is situated posteroventrally to scutellum and consists of metapleuron (*MTP*) (laterotergite of KIM & COOK, 1966) and postscutellum (*PSC*) (mediotergite of KIM & COOK, 1966).

The chaetotaxy of the mesonotum (Fig. 39) is very important in taxonomy. In the group considered the following setae are recognized: 2 posthumerals (*phu*), 1 notopleural (*npl*), 1 prealar (*pa*), 1 large supraalar (*sa*), 1 postalar (*psa*), 1—5 dorsocentrals (*dc*) some of which may be situated in front of (intrascutal) suture and then called presutural in contrast to

DOI: 10.21248/contrib.entomol.32.2.195-282

the remaining postsutural *dc*. The entire scutum and prescutum is covered by microsetae — those arranged in more or less regular rows between dorsocentrals are the acrostichal microsetae (*ac*). The number of rows of *ac* hairs just in front of the suture (or between the anterior postsutural *dc*) is an important character; more posteriorly the number of *ac* rows is reduced. The medial prescutellar *ac* pair is often enlarged, sometimes very distinctly (some *Spelobia*, *Rudolfia*). Scutellum carries 2 marginal scutellar bristles (*sc*), the shorter lateral and the longer apical. Some additional minute marginal setulae may be present on scutellum (*Pullimosina* sg. *Dahlimosina*, *Opalimosina* sg. *Dentilimosina*).

The pleural part of the mesothorax (Fig. 38) is composed of large sclerites — the bare mesopleuron (*MSP*) (anepisternum II of Kim & Cook, 1966), pteropleuron (*PTP*) (anepimeron II), hypopleuron (*HPP*) (katepimeron II) and the sternopleuron (*STP*) (preepisternum II) carrying usually 2 sternopleural bristles (*stpl*), the anterior of which may be reduced or absent. The mesothoracic spiracle (*MSS*) is situated at anterior margin of mesopleuron, the metathoracic spiracle (*MTS*) above the dorsal margin of hypopleuron, in the foramen of insertion of the haltere.

The metathorax is strongly reduced, the major visible part — anepisternum III — is fused to hypopleuron; for details see Kim & Cook (1966).

c) Legs. Each leg has a coxa, trochanter, femur, tibia and tarsus. The tarsus is composed of 5 segments, the first of which — the basitarsus — is most significant in taxonomy. The last tarsal segment ends in a pair of claws, 2 small pulvilli and a medial hair-like empodium. Fore coxa (cx_1) is large, the mid (cx_2) and hind coxa (cx_3) are smaller. Femora, especially the fore (f_1) and hind (f_3) ones of some species may be thickened in the male (*Gigalimosina*, *Paralimosina*). The chaetotaxy of fore femur, although previously commonly used in taxonomy is found to vary greatly within species and is not used here. On the contrary, the ventral chaetotaxy of male mid femur (f_2) is sometimes distinctive (see Figs. 69, 89, 213). f_2 also carries an anterior row of bristles terminated by stronger preapical seta. Fore tibia (t_1) is always simply haired but it may be clavately incrassate (Figs. 35, 437) and with an internal impression or incision in the male (some *Spelobia*). Mid tibia (t_2) bears a number of distinctive and important bristles; also hind tibia (t_3) may be armed by one, rarely more bristles (Fig. 68). Mid basitarsus (mt_2) is sometimes strikingly elongate and may also carry a ventral or anteroventral bristle, or row of short (mostly posteroventral) spines. Hind basitarsus (mt_3, Fig. 438) is always short, thickened or incrassate (the autapomorphic feature of the family Sphaeroceridae).

The terminology of the pedal chaetotaxy is based on Kim & Cook (1966). Particular bristles on femora, tibiae or metatarsi (= basitarsi) are termed according to their position in the 8 imaginary parts in which can be divided the periphery of cross section of any part of leg. The legs are assumed to be stretched horizontally. The bristles are thus dorsal (*d*), posterodorsal (*pd*), posterior (*p*), posteroventral (*pv*), ventral (*v*), anteroventral (*av*), anterior (*a*) or anterodorsal (*ad*) (Kim & Cook, 1966, Fig. 18). The position of the bristle is also specified in longitudinal direction (e.g. *ad* in distal two-fifths). Complicated and tedious description of the pedal (particularly t_2) chaetotaxy in the present work is replaced by more instructive figures.

d) Wing and haltere. The wing base, not discussed here, is referred in Kim & Cook (1966). The wing venation (Fig. 40) is very significant. Costa (*C*) is broken twice — distally to humeral cross-vein (*h*) and at termination of R_1. It reaches to or overpasses beyond R_{4+5}. Subcosta (*Sc*) is reduced to thin fold not reaching costa. Costa may be divided into 3 sectors — Cs_1 (from wing base to R_1), Cs_2 (from R_1 to R_{2+3}) and Cs_3 (from R_{2+3} to R_{4+5}). The ratio Cs_2: Cs_3, called the costal index (C-index) is a very important characteristic. First radial vein (R_1) is short, curved to *C*; the second radial vein (R_{2+3}) is longer and its shape, especially in apical part, is often a useful feature. The third radial vein (R_{4+5}) is the longest vein and its shape is commonly used in the taxonomy. The first (M_{1+2}) and the second medial vein (M_{3+4}) are greatly reduced, hardly extending beyond the posterior cross-vein. R_{4+5} and M_{1+2} are connected by the anterior cross-vein (t_a) (*r—m* of Kim & Cook, 1966); M_{1+2} and M_{3+4} by the posterior cross-vein (t_p) (*m* of Kim & Cook, 1966). The ratio of distance between t_a and t_p to length of t_p (t_a—t_p: t_p) is used to characterize the discal cell (*ds*) (M_2 of Kim & Cook, 1966). Basal and anal cells not developed. Anal vein (*A*) (Cu_2A_1 of Kim & Cook, 1966) is reduced, sinuate, apically modified to a colourless venal fold not reaching

DOI: 10.21248/contrib.entomol.32.2.195-282

the wing margin. Basally the wing has a well developed alula (alar lobe of KIM & COOK, 1966), whose shape is also of some taxonomic importance. All veins are bare, except for the costa which basally carries a pair of strong bristles (in some genera, e.g. *Halidayina*, *Rudolfia* one of these bristles is very enlarged and the second absent) and is finely haired along its entire length (on Cs_1 the hairs are stronger but not as long as in *Leptocera* or *Thoracochaeta*).

Haltere (Fig. 38, *HA*) is borne on the metathorax, in a foramen behind metathoracic spiracle. It is composed of basal stem (scabellum + pedicel of KIM & COOK, 1966) and enlarged apical knob (capitellum of KIM & COOK, 1966). Its colouring is relatively constant within species and is therefore useful for diagnostical purpose.

e) Abdomen (Figs. 41—46). The abdomen is relatively short and broad, cylindrical or rather dorsoventrally flattened. It is generally composed of 9 segments and the cerci which represent the 11th segment (see MATSUDA, 1976) as in other Cyclorrhapha. The postabdomen of the male is strongly modified (because of rotation) and many sclerites (especially terga) are lacking. In the female, on the contrary, all 9 segments usually have well preserved terga and sterna; sometimes some postabdominal sterna may be reduced or absent (see below).

The abdomen is traditionally divided into the preabdomen (1st to 5th segment) and postabdomen (6th to 9th segment). The preabdomen has well developed terga (*T*); sterna (*S*) are usually narrower (especially narrower, for example, in *Minilimosina*). First and second terga are coalesced intosynterg um ($T1+2$); similarly the synsternum ($S1+2$) is thought to be a fusion of first and second sternum, but in contrast to $T1+2$ where the part originating from *T1* is more or less distinct, in $S1+2$ the part which might be ascribed to *S1* is indistinct, probably due to reduction. $T1+2$ is the largest dorsal sclerite of preabdomen, while $S1+2$ is usually smaller than the following sterna. $T1+2$, rarely also other terga, may be partly membraneous and pale pigmented which is often a good diagnostic feature. Female preabdominal sterna are usually simple, unmodified, but the male 5th sternum (*S5*, pregenital sternum) is almost always distinctive in shape and armature because it has a function in copulation (see below). Rarely *S4* (*Apteromyia*) or all preabdominal sterna of the male (e.g. *Gigalimosina*, *Herniosina*) are also modified.

f) Male postabdomen and genitalia. The terminology used in the male postabdomen has been unstable and complicated. Even in recent taxonomic studies various "neutral" terms were introduced (e.g. RICHARDS, 1973; PAPP, 1973a, 1978a) since the homology of structures of the male postabdomen was not reliably understood. The study of KIM & COOK (1966) only brought further confusion to this problem and in particular the morphology of the male postabdomen of *Leptocera* as described by them is apparently incorrect. In my opinion GRIFFITHS' (1972) study is the most probable, except for his homologization of certain genital structures (HENNIG, 1976; MATSUDA, 1976).

The male postabdomen (Figs. 41—43, 95, 106) is asymmetrical; all terga from *T6* are absent with the possible exception of *T9* if we accept HENNIG's (1976) supposition that the terminal genital segment is the epandrium (homologous with *T9*). As a consequence of the rotation which more or less effects all postabdominal segments, *S6* has become asymmetrical and displaced ventrolaterally to the left side; *S7* is also asymmetrical and moved laterodorsally and *S8*, being situated dorsally, is fused with the epandrium (of HENNIG, 1976 = periandrium of GRIFFITHS, 1972) forming the terminal segment. This fused complex is called here the "periandrium". It should also be pointed out that the 6th right spiracle is enlarged and displaced ventrally. *S7* usually has a distinct fissure in the sclerotization.

The asymmetry of the postabdominal sterna has apparently been produced by torsion of the postabdomen. The hypopygium of Sphaeroceridae is of the "circumverted" type, but only the 9th segment rotates through 360°; the rotation of the 8th segment is about 180° (*S8* is situated dorsally and is a little asymmetrical) and that of 7th and 6th segments is less and the asymmetry of *S7* and *S6* more extensive. According to GRIFFITHS (1972), the hypandrium (= *S9*) is the only remaining sclerite of 9th segment in Sphaeroceridae. The homology of the periandrium sensu GRIFFITHS (1972) with the basimeres of lower Brachycera is not certain and was not confirmed by recent studies (HENNIG, 1976; MATSUDA, 1976). On the other hand, the predication of GRIFFITHS (1972) that the terminal

DOI: 10.21248/contrib.entomol.32.2.195-282

segment of Limosininae is a fusion of his periandrium and *S8*, is clearly demonstrated by the intermediate condition of *Copromyza* (*Crumomyia*) where a lateral slot is still visible between *S8* and epandrium (see TROGER & ROHÁČEK, 1980). To summarize, the whole terminal segment (dorsal sclerite) is for practical reasons called the periandrium (*P*) here, but it is recognized that it is not equivalent to GRIFFITHS' (1972) original term.

The hypandrium (*HY*, Figs. 52, 75, 141) is usually reduced to a Y-shaped, anteriorly rod-like sclerite situated ventrally to the periandrium. It has a very important function. Its lateral arms are connected with the periandrial corpus as well as with the basal anterior corners of the telomeres. These lateral parts of hypandrium are called by GRIFFITHS (1972) the "vertical section". The medial hypandrial part between the arms carries 2 small sclerites (genital rod of KIM & COOK, 1966) by means of which the aedeagal complex is suspended in the hypandrial arch.

Telomeres (Fig. 53, *TE*; surstyli of HENNIG, 1976 and authors) are the ventral appendages of the periandrium. Each telomere is anteriorly connected with the hypandrial arm, posteriorly with the internal structure called here "intraperiandrial sclerite" (= intraepandrial sclerite of ANDERSSON, 1976). This posterior connection is sometimes very distinctive — it may be formed by long band-like arms (*Kimosina*, see Fig. 883, 884). The shape of the telomere greatly varies, from a simple, lobe-shaped form to complex structures with various keels, lobes, projections etc. (*Kimosina*, *Chaetopodella*, *Rudolfia* etc.). Regarding the homology of the telomere, the same argument applies as to the periandrium. GRIFFITHS (1972) erected the term "telomere" because he considered this appendage to be homologous with the distimere of lower Brachycera. This assertion was criticized by HENNIG (1976) and MATSUDA (1976), but GRIFFITHS' term is used here since the homology of this appendage with the surstylus in the sense of HENNIG (1976) is meantime also dubious.

Cerci (*CE*, Figs. 52, 861, 862) are situated below the anal fissure and fused with the periandrium, but they usually carry some peculiar bristles and sometimes may be characteristically modified (*Herniosina*, *Apteromyia*, *Rudolfia* etc.). The cerci also probably produced the intraperiandrial sclerite (Fig. 52, *IP*) which in the extreme case (*Kimosina*) forms a peculiar ventromedial projection — the mesolobus (*ML*, see Figs. 862, 908). The cerci are normally medially connected by the so-called subanal plate, but it may be also absent (*Telomerina*) or replaced by mesolobus (*Kimosina*).

The aedeagal complex (Figs. 52, 74, 728) is suspended in the hypandrium by means of 2 small sclerites, each attached to the anteroproximal part of the relevant postgonite, and is composed of the aedeagal apodeme (*AP*), aedeagus (*AE*), paired postgonites (*PG*) and ejaculatory apodeme (*EAP*). The aedeagus is distinctly divided into 2 parts — the basal phallophore (*PP*) which may sometimes (*Opalimosina*) project posteroventrally forming the epiphallus (*EP*, Figs. 990, 1030) or more anteriorly forming the pre-epiphallus (*PEP*, Fig. 322) (term of ROHÁČEK, 1976) — and the apical and usually larger distiphallus (*DP*). Apart from the postgonite, the distiphallus is the most variable part of the internal genitalia, often of complex form with various processes and teeth, but it may be membraneous, finely spinulate or haired etc. The paired postgonites (*PG*) are always symmetrical, usually laterally flattened and carrying some minute setulae on their surface. The aedeagal apodeme (*AP*) is a simple, rod-like sclerite, often with enlarged dorsal keel (for attachment of muscles). The ejaculatory duct (Fig. 52, *ED*) emptying into the posterior aperture of phallophore may be reinforced by the ejaculatory apodeme (*EAP*, Fig. 54, 96, 322). However, this sclerite is often reduced or absent. The function and taxonomic importance of the above described structures are discussed below. A comparison of some terms of the male genitalia used by recent authors is presented in Tab. 1.

g) Female postabdomen and genitalia. As mentioned by ROHÁČEK (1978c), the female terminalia of the species of the previous genus *Limosina* are very poorly known. The female postabdomen (Figs. 47—49) is traditionally considered to be composed of the 6th to 9th segments and the cerci representing the 11th segment. All segments are usually easily recognizable but some additional (secondary) sclerites may be developed which might cause confusion. Two main types of formation of the postabdomen were found within the previous genus *Limosina*. The more primitive telescopic, retractile postabdomen is usually long and narrower than preabdomen (see Fig. 186) and resembles the type occurring in the

DOI: 10.21248/contrib.entomol.32.2.195-282

subfamilies Copromyzinae and Ceropterinae. The more advanced type of postabdomen is short, non-telescopic, wide at the 6th segment and gradually tapering terminally. It has apparently evolved from the telescopic type.

The 6th and 7th segments usually have normally developed terga and sterna, though *T7* may sometimes be modified (some *Opalimosina*) and *S7* prolonged or shortened. The 8th segment is much more variable in formation of its sclerites because of its involvement in copulation. The gonopore (Fig. 734, *GO*) lies on the 8th segment. *T8* is often membraneous dorsomedially or divided into 2 lateral parts which are usually enlarged. *S8* is the most variable sclerite of the postabdomen. The cause of this great variety is that *S8* is situated anteroventrally to the gonopore. *S8* may be strongly reduced (*Kimosina, Rudolfia, Minilimosina* s. str.) or absent (*Minilimosina* sg. *Allolimosina*) or conversely there may be evolved further sclerites additional to *S8* (*Spelobia* genera-group). I consider these additional sclerites (see Figs. 753, 817, 830, *ASC*) to be secondary sclerotizations round the gonopore. They are situated between *S8* and *S9*, connected by ligaments to *S9* and the spectacles-shaped sclerite. The spectacles-shaped sclerite (*SP*, see ROHÁČEK, 1978c) is a specialized internal genital structure, probably a secondary sclerotization of the vagina since the spermathecal opening into the common oviduct (cf. MATSUDA, 1976) lies in the anterior part of the spectacles-shaped sclerite (Figs. 54, 350, 737).

The spermathecae (Fig. 54, *SP*) are further genital structures of taxonomic importance. Three spermathecae are present, two borne on the common duct and one single (as in the whole subfamily Limosininae). They are of simple oval or ball shape to peculiar tyre-shaped form with protrusible internal sac (*Spelobia, Pullimosina* etc.). The short terminal part of the spermathecal ducts (to conjoinment of ducts in double spermathecae) is sclerotized, the rest of the ducts is membraneous.

The 9th segment is small. Both *T9* and *S9* are usually distinctly developed; *T9* is a simple plate, sometimes medially membraneous, rarely divided, reduced or even fused with cerci (*Opalimosina, Rudolfia*) and carrying 2 or more dorsal setulae as a rule. *S9* is more variable, large and broad or reduced to a short horseshoe-shaped sclerite, often with anterior incisions or projections. The anus (*AS*, Fig. 734) is situated between and posteriorly to *T9* and *S9*; 1—2 very minute sclerites, sometimes visible near the anus, probably evolved by secondary sclerotization (see Figs. 190, 308, 316, 687).

The one-segmented cerci (Figs. 47, 48, *CE*), attached to the posterolateral margin of *T9*, are considered to be appendages of the lost 11th segment (MATSUDA, 1976). They were probably originally relatively long, slender and with long wavy hairs (e.g. *Minilimosina*); in more progressive and advanced groups they are shortened, with thickened terminal bristles, fused with *T9* (*Opalimosina*) or even modified to distinctive spines (*Rudolfia*).

5. Mechanism of copulation and its influence upon the formation of the male and female postabdominal structures

In the literature there is a lack of data concerning the functional morphology of the postabdominal structures in the Acalyptratae Diptera. In my opinion it is important to know the function of the genital structures involved in copulation. On the basis of such knowledge it may be possible to evaluate better the variability of features of the genitalia and their usefulness in taxonomy, to determine cases of convergence of some structures and eventually also to find the decisive characters for considering the phylogenetical relationships of taxa.

I have studied the copulation in *Spelobia clunipes* (MEIGEN), one of the commonest species of the previous genus *Limosina*. In this species (and also in other Sphaerocerids) flies often persist in copula after being killed. This make it possible to examine the coupled postabdomina (their sclerotized structures) by the same methods as used in the study of genitalia.

The most useful informations about copulation in Diptera was found in HARDY (1944) and its criticism by GRIFFITHS (1972). The developmental morphology of the abdomen by MATSUDA (1976) was also helpful.

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The Sphaeroceridae copulate in the so-called "superimposed position" (HARDY 1944) in which the male lies above the female (Fig. 723). In *Spelobia clunipes*, the male holds the female by its specialized (anteriorly incised) fore tibiae and dilated fore tarsi. The postabdomina of a pair of this species in copula are shown in Fig. 53, but they lie closer and more parallel to each other in life. The following facts were found in the present study (Figs. 51—54):

(1) The 9th female segment with its cerci is bent up and placed into the genital pouch (term of HARDY, 1944) below male *S5* where the distiphallus is normally positioned (when at rest) (see Fig. 53).

(2) The greatest contact and strain is on the male *S5* and female *T8*. Both these sclerites are thus modified for their function. The female *T8* is medially membraneous or divided (evolved in parallel in a number of species) or rarely has further structures facilitating contact with the male *S5* (e.g. the medial tubercle in *T9* of female *Pullimosina meijerei* corresponding with the medial incision of male *S5*); sometimes the female *T7* may also be adapted for this purpose (*Apteromyia*, *Opalimosina* sg. *Pappiella* and *Dentilimosina*). It should be noted that in the telescopic type of postabdomen (see above) other terga (*T6*, *T7*) are in contact with the male *S5* and may also be membraneous or incised.

Various structures have also evolved in the male *S5*; the most frequent is the medial comb of spines on the posterior margin. This structure developed by convergent evolution in different groups (for example *Minilimosina*, *Spelobia*, *Pullimosina*, *Spinilimosina*, *Halidayina*) as in other taxa has the membraneous, finely spinose, semicircular posteromedial area (some *Opalimosina*, *Telomerina*, *Halidayina*). Although these structures are strongly affected by convergence, detailed construction indicates some differences and consequently they may be usable in lower (subgeneric or species-group) classification. Similarly or in addition to *S5*, *S4* and *S6* may serve the same function and are then adapted (some *Terrilimosina*, *Apteromyia*, some *Minilimosina*).

(3) By curving up the 9th female segment, the posterior part of the 8th female segment (and the gonopore) is exposed. The internal spectacles-shaped sclerite (see Fig. 54, *SP*) is connected by ligaments (or by additional sclerites in some genera) with *S9* and shifts (in consequence of the movement of the 9th segment) to the posterior margin of the 8th segment. The medial part of the spectacles-shaped sclerite is apparently a secondary sclerotization of the vagina as the spermathecal ducts lead into its anterior part. The lateral circles of the spectacles-shaped sclerite serve as auxiliary structures for the attachment of the telomeres. The spectacles-shaped sclerite is a highly specialized structure occurring only in some genera (*Spelobia* genera-group). A more primitive form of this structure is found in some *Minilimosina* (Figs. 285, 286), which indicates the possible origin of the *Spelobia* genera-group.

The female *S8* may be greatly modified under the influence of its function in copulation and due to its position near the gonopore. Besides the above particular cases where some additional sclerites are developed, it often becomes reduced in various ways (*Minilimosina*, *Herniosina*, *Kimosina*, *Opalimosina*).

(4) The telomeres are the main organs used in holding the female postabdomen; they are applied internally to the 8th female segment (Fig. 53). This attachment may be facilitated by the spectacles-shaped sclerite. The telomere is very variable in shape, but its intraspecific variability is small and even such details as the position of particular bristles, their length, thickness, the position and the extent of micropubescence etc. are highly constant. Thus the telomere is a very important structure in taxonomy, especially at specific level, but its general appearence may be useful for characterization of higher categories.

There is probably a correlation between the formation of the telomeres and internal genitalia, especially the phallophore. I have found that many taxa with large and complicated telomeres (e.g. *Minilimosina*, *Terrilimosina*, *Kimosina*, *Telomerina*, *Rudolfia*) usually have a simple aedeagal complex, often a reduced phallophore without epiphallus and sometimes even a reduced intraperiandrial sclerite. On the other hand taxa with a complicated aedeagal complex with the phallophore provided with an epiphallus or similar structures (e.g. *Herniosina*, *Apteromyia*, *Xenolimosina*, *Opalimosina*) have small and plain telomeres.

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(5) During copulation the aedeagal complex is held in a different position than when resting. The distiphallus is taken out of the genital pouch and "erected" ventrally (see Fig. 52). The postgonites are attached by their apices to each other and to the ventral surface of the distiphallus. It seems (Fig. 54) that both distiphallus and postgonites enter the female gonopore and the postgonites may facilitate this process. From examining the differences in the rest and erected position of the aedeagal complex (cf. Figs. 51, 52) I conclude that the "hypopygium circumversum" of the type studied has developed as a rest condition for protecting the internal genitalia, as GRIFFITHS (1972) suggests. When at rest, the aedeagal complex is loosely hinged in the hypandrium by means of small sclerites, ligaments and musculature between the postgonites and hypandrial arms; the distiphallus is directed anteriorly and hidden in the genital pouch. When erected for copulation (Fig. 52), the phallophore is fixed between the specialized intraperiandrial sclerite and the hypandrial arch and the distiphallus is directed ventrally. Thus, an additional structure (the intraperiandrial sclerite) has developed for the erected position of the aedeagus, which confirms the opinion of GRIFFITHS (1972) concerning the circumverted hypopygium and the rest condition.

All structures of the aedeagal complex are of great importance in taxonomy judging from their stabilized general formation among particular groups — especially some apomorphic structures of the phallophore (epiphallus, reduction to frame-shaped structure), distiphallus or intraperiandrial sclerite (mesolobus in *Kimosina*) are thought to be of importance for the cladistic classification of higher taxa.

(6) The hypandrium, furnished with a strong musculature, is probably the main element influencing movement of the aedeagal complex (through the mediation of ligaments and connecting sclerites between it and postgonites) and the telomere. On the other hand, the aedeagal apodeme (*AP*) and its robust musculature attached to the dorsal keel seems to have a rather static function — it probably makes it impossible to push the fixed phallophore into the periandrial hollow during copulation. Both the above structures show rather great intraspecific variability, especially in their prominent keels where the muscle bands are attached.

(7) The ejaculatory apodeme (*EAP*) is usually small and reinforces the ejaculatory duct (*ED*, see Fig. 52). Its function as the sperm pump is rather doubtful due to its minute size. In a number of species, the ejaculatory apodeme is not developed at all, or it is present only in some specimens. A larger ejaculatory apodeme occurs much more rarely (some *Minilimosina*) and then its shape may be a usable feature for identification.

Biology (general)

1. Feeding

All species of Sphaeroceridae are generally saprophagous, i.e. their larvae develop in decaying organic matter of various kinds. No species are known to be phytophagous, carnivorous or parasitic. The few records of Sphaeroceridae on flowers (e.g. KNOLL, 1926; LYNEBORG, 1968) are apparently due to their scent attracting adults (see below).

The classification of Sphaeroceridae according to the food of larvae and imagines is not always easy. It is true that breeding records represent sufficient evidence for the correct recognition of larval food, but such data are very scattered and available only for some commoner species. In most cases, our knowledge is limited to the collecting data of the adults which, however, may also occur on substrates unsuitable for larval development. This is usually caused by a scent being attractive to the imagines. On the other hand, it was found that adults occur most abundantly on the larval food and consequently the occurrence of imagoes on particular substrates is an indication of the larval food.

Although it is definitely known that Sphaeroceridae feed on various types of decayed organic matter, there are still doubts as to the real food of larvae and adults. They could consume decomposing, dead or decaying remains of plant and animal bodies directly or only the microorganisms causing decay. The first alternative, at least, seems to be demonstrated by GODDARD's (1938) and OKELY's (1974) experiments with rearing some species

DOI: 10.21248/contrib.entomol.32.2.195-282

on boiled (sterilized) grass cuttings. The second has not been experimentally confirmed, but probably the larvae eat both above components of decaying matter. The species can be classified according to the feeding substrate of the larvae and adults as follows:

a) Phytosaprophagous species. Larvae and adults feed on decaying plant matter. This group is composed of species living in leaf litter, decayed grass, hay, moss, in compost heaps etc., e.g. *Limosina silvatica*, *Gigalimosina flaviceps*, *Spelobia ochripes*, *Pullimosina antennata*, *P. moesta*, *P. pullula*, *P. meijerei*, *Terrilimosina schmitzi*. Papp (1976a) states that some of these species are mycelium feeders and calls them micromycophagous. Two species living exclusively in Sphagnum on peat-bog meadows are probably also phytosaprophagous — *Spelobia pappi* spec. nov. and *Pullimosina dahli*.

b) Fungivorous species (= macromycophagous or mushroom feeders of Papp, 1976a). The food of larvae is decaying fruit bodies of macrofungi. It is interesting that some fungivorous species are attracted by carrion and some necrophagous species were often collected on rotten fungi; for example *Telomerina flavipes*, a predominantly necrophagous species, has even been bred from fungi (Duda, 1938; Papp, 1972). The explanation is probably the similarity of proteins and their decomposing products in both fungal and animal bodies. There are two typical fungivorous species in the group examined — *Spelobia parapusio* and *Opalimosina czernyi*. *Minilimosina parvula* and the very rare *Xenolimosina setaria* may also belong to this category (cf. Richards, 1930).

c) Necrophagous species (= zoosaprophagous; carrion feeders of Papp, 1976a). Larvae develop in decaying meat, on carrion of vertebrates and dead invertebrates. There are some species preferring this substrate (demonstrated be breeding records) but all were also found rarely in another situations, e.g. *Kimosina empirica*, *Spelobia palmata*, *Telomerina flavipes*. Fungivorous species (see above) show some affinity to this substrate.

d) Coprophagous species. Larvae live in the excrement of various animals. It should be noted that there are relatively few purely coprophagous species in the group examined, e.g. *Chaetopodella scutellaris*, *Telomerina pseudoleucoptera*, *Opalimosina denticulata*, *O. collini*, *Rudolfia rozkosnyi*. Many other species, though bred from excrement and preferring this substrate for larval development, are polysaphrophagous (see below). Excrement often attracts adults of species developing in different substrates e.g. some phytosaprophagous and necrophagous species.

e) Polysaprophagous species. Non-specialized species whose larvae can develop in a diversity of decaying organic matter. These species are often very common and ubiquitous. They usually prefer some substrate but can successfully develop in others, e.g. *Spelobia clunipes*; *S. luteilabris*, *Opalimosina mirabilis* and *Halidayina spinipennis* prefer excrement of large animals but develop also in decaying herbaceous material and was also found on carrion; *Spelobia pseudosetaria*, *Pullimosina heteroneura* and *Opalimosina liliputana* prefer decayed vegetation but live also on excrement; *Apteromyia claviventris* develops in decayed plants but was also bred from rotten fungi (see Hackman & Meinander, 1979) etc. Many macrocavernicolous and microcavernicolous species are polysaprophagous (*Herniosina bequaerti*, *Terrilimosina racovitzai*, *Spelobia talparum*, *S. czizeki*). It is noteworthy that almost all these non-specialized species belong to phylogenetically progressive and ecologically successful species-groups. In the case of cavernicolous species this non-specialization is an evident adaptation for survival in space-limited biotopes, poor in food.

2. Movement

The type of movement of Sphaeroceridae is very characteristic (especially skipping — see below) and is of great phylogenetic importance. There are also modifications of the movement of particular species apparently depending on their habitat. Three types of movement were recognized in the group examined:

a) Running. Known in all species. It is the slowest movement often combined with the following type. The species run in very small steps.

b) Skipping. Typical of the whole family. Species make short, low jumps (the length of the jumps may be prolonged by short flight), faster than the normal run. Jumps are also

DOI: 10.21248/contrib.entomol.32.2.195-282

used at the start of flight. This peculiar movement is reflected in the modification of hind legs which have a strongly thickened basitarsus (an apomorphic feature of the family). Thus, in skipping Sphaerocerids use only the hind pair of legs.

c) Flight. Species of the previous genus *Limosina* fly rather infrequently. Many species seems to be incapable of flight despite being fully winged (cf. PAPP, 1976a; PAPP & PLACHTER, 1976). This inability to fly was chiefly noticed in terricolous and microcavernicolous species, some of which are brachypterous or wing-polymorphic (*Spelobia pseudonivalis*, *Pullimosina meijerei*, *Terrilimosina sudetica*) but also in the fully winged *Pullimosina pullula* or in the cave-dwelling species *Terrilimosina racovitzai* and *Herniosina bequaerti* (see PAPP & PLACHTER, 1976). The majority of species fly for short distances and combine this with skipping. Some species may fly at night as RICHARDS (1930) suggests although I have not found them in light-traps (which attract mainly *Leptocera*-species) but this may be partly affected by negative phototaxy, which is rather common in the species considered.

3. Reproduction and ontogenetical development

a) Bisexual reproduction (zoogamy). This normal type of reproduction is connected with the following phenomena:

Swarming. As far as is known no special swarming behaviour was discovered in Sphaeroceridae (the observation of swarming in *Copromyza* spec. — GRUHL, 1924 — I consider to be doubtful), but there are some records of occurrence of some species in large numbers (including *Limosina silvatica*) in limited areas (RICHARDS, 1930). I have several times found similar "swarms" of this species and that of *Gigalimosina flaviceps* and *Spelobia clunipes* on wet, rotten leaves in woods. Although these "swarms" include pairs in copula I do not consider it to be swarming behaviour preceding mating but only flies concentrating on a suitable substrate for oviposition or flies that have emerged from the substrate in large numbers, thus quite a similar situation to the mass-occurrence of Sphaeroceridae on manure or excrement.

Mating. Species of the previous genus *Limosina* mate in the superimposed position (HARDY, 1944). I have studied the copulation of *Spelobia clunipes* more thoroughly mainly in relation to the morphology of the male and female terminalia (see p. 208). Besides modifications of the postabdomina of both sexes, there are also secondary morphological adaptations of the male (and more rarely in the female) which facilitate coupling. RICHARDS (1930) described the modified male t_2 and f_2 which are ventrally armed with rows of short spines or tufts of bristles, apparently forming an apparatus for holding the female wings during mating. This is a very common feature of males of various groups (*Limosina*, *Gigalimosina*, *Herniosina*, *Apteromyia*, some *Terrilimosina*, some *Minilimosina*, some *Paralimosina*, some *Spelobia*, *Kimosina*, *Rudolfia*). *Kimosina empirica* not only has these specialized male mid legs but also has modified Cs_2 in the female so that the wings are sexually dimorphic. Cs_2 is strikingly concave. This is due to the fact that the male holds the female's wings just at Cs_2. Some species of *Spelobia* (*S. clunipes*, *S. manicata*, *S. palmata*, *S. talparum*) have clavate and anteriorly incised male t_1 with specially modified attaching setae (see Figs. 35—37) and dilated fore tarsi; this adaptation serves the same purpose but position at which the female is held is obviously different. Similarly the bulbously dilated f_1 and f_3 of some males are connected with mating (*Gigalimosina flaviceps*, *Paralimosina* s. str. species).

Oviposition. The oviposition behaviour has only been observed in several species which were bred under laboratory conditions. GODDARD (1938) found that in *Pullimosina heteroneura* the female begins ovipositing 5—12 days after copulation and eggs were laid up to 32 days. One female laid about 60—70 eggs, scattered on the surface of the breeding substrate (decayed lawn-mowings). HAMMER (1941) described oviposition in *Spelobia clunipes* and *Chaetopodella scutellaris*. Females of these species laid eggs in small holes in a cow pat and covered them with their own excrement. Likewise *Limosina silvatica* buries its eggs in decaying grass except for the dorsal surface (GODDARD, 1938).

Two parthenogenetic species (see below) were experimentally reared and their oviposition studied by OKELY (1974). The female of the fungivorous *Spelobia parapusio* laid a large

DOI: 10.21248/contrib.entomol.32.2.195-282

number (40—100) of eggs in regular lines along the gills of the mushroom cap, rarely irregularly scattered. The oviposition began on the 5th day after emergence and the eggs were laid over a 5 day period. Similarly the female of *Pullimosina pullula* began egg-laying on the 4th day after emergence and laid up to 80 eggs during a 20 day period.

b) Parthenogenetic reproduction. This has been discovered only recently and is known in two species. Already RICHARDS (1930) referred to the great disproportion between the numbers of males and females of *Spelobia parapusio* and *Pullimosina pullula*, but only PAPP (1972) has attempted to explain this phenomenon (in *S. parapusio*), suggesting two possibilities: (1) the viability of males is less than females due to their genetics; (2) as well as zoogamy there is parthenogenesis and specimens multiplying by parthenogenesis predominate. While the first theory is not acceptable (since the less viable males should have survived in breeding experiments), the second one was experimentally demonstrated by OKELY (1974) who bred a number of parthenogenetic generations of *Spelobia parapusio* and *Pullimosina pullula*. In both these species males are known but are extremely rare. There are thus parthenogenetic and normal populations of which the first are more common (see below).

c) Sex-ratio. RICHARDS (1930: 321) computed the sex-ratio (= M♂/N♀ · 100) for some Sphaeroceridae including several *Limosina*. He found a distinct preponderance of one sex (usually the female) in a number of species and attempted to explain this by differences in the length of life of particular sexes. This theory is certainly correct and applies to the majority of species. However, there are some species (*Spelobia parapusio*, *Pullimosina pullula*) in which the sex-ratio is too low to be explained in the above way. Probably the principal shortcoming of RICHARDS (1930) was that he used all records instead of computing the sex-ratio for particular populations. Both the above mentioned species have much rarer bisexual populations besides the usual parthenogenetic ones but RICHARDS (1930) did not discover this because he evaluated a mixed series containing specimens from various populations.

LAURENCE (1955) found that males of *Chaetopodella scutellaris* require a higher humidity than the females — this then strongly influences the sex-ratio in sites with the critical degree of moisture. It is possible that some other species of the group examined show sexual differences in their sensibility to humidity. Consequently we have to suppose that a number of other mechanisms affect the sex-ratio because the preponderance of males in some species (e.g. *Terrilimosina schmitzi*) has not been satisfactorily explained.

d) Ontogenetical development. The course and duration of the life-history of Sphaeroceridae is strongly dependent on abiotic ecological factors, chiefly temperature and humidity. Generally the development time is accelerated at higher temperatures (and optimum humidity). Thus the duration of the life-history (from egg to imago) of *Limosina silvatica* ranges between 76—205 days, in *Spelobia clunipes* 18—100 days etc. (LAURENCE, 1955) depending on the mean temperature during development. The length of ontogenetical development is more stabile only in macrocavernicolous species, which develop under relatively constant conditions (cf. PAPP & PLACHTER, 1976). The stages develop as follows:

Egg. The embryologic development within the egg is unknown. There are only three records of the duration of this stage. Larvae of *Pullimosina heteroneura* emerged from the egg after 2 days (GODDARD, 1938). The duration of the egg stage in *Spelobia parapusio* (see OKELY, 1974) and *Chaetopodella scutellaris* (see SCHUMANN, 1962) was found to be 24 hours.

Larva. Few data on duration of the larval stage and particularly its instars have been published. OKELY (1974) found that larvae of *Spelobia parapusio* pupated after 4 days; of the 3 recognized instars the first lasted 1—2 days. The larval development of *Pullimosina pullula* was 12 days (length of particular instars not specified). The larval stage of *Chaetopodella scutellaris* lasted 5 days under laboratory conditions (1st instar — 1 day, 2nd instar — 1 day, 3rd instar — 3 days) (SCHUMANN, 1962).

Pupa. The duration of this stage is very variable and may apparently be prolonged in unfavourable circumstances. For example, the pupa of *Spelobia talparum* emerged after 5—18 days, *Herniosina bequaerti* after 16—18 days (GODDARD, 1938), *Pullimosina pullula* after 4—12 days (OKELY, 1974).

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Imago. Some details of the biology of the imago were mentioned above. Flies probably copulate very soon after emergence and oviposition begins 5—12 days later; parthenogenetic species (see above) oviposite 4—5 days after emergence (cf. GODDARD, 1938; OKELY, 1974). The length of life of the imago is known only in *Herniosina bequaerti* and *Terrilimosina racovitzai* — 38—62 days (PAPP & PLACHTER, 1976).

There are more records of the total duration of the life-history, especially from LAURENCE's (1955) breeding experiments with coprophagous species. According to this author, *Limosina silvatica* develops in 76—205 days, *Spelobia clunipes* 18—100 days, *Chaetopodella scutellaris* 20—64 days, *Telomerina pseudoleucoptera* 35—60 days, *Opalimosina denticulata* 32—45 days, *O. collini* 32—50 days and *Halidayina spinipennis* 28—34 days under natural conditions. OKELY (1974) determined the duration of the life-history of *Pullimosina pullula* (22—36 days) and PAPP & PLACHTER (1976) of *Terrilimosina racovitzai* and *Herniosina bequaerti* (70—90 days).

4. Diurnal rhythm of activity

There is no doubt that besides the activity in daytime many species are also active during the night (RICHARDS, 1930). According to my experiences the activity of the majority of species seems to be mainly influenced by temperature and humidity. Although HAMMER (1941) states that *Spelobia clunipes* is not active at night, I have observed on several occasions increased activity in *Limosina silvatica*, *Spelobia clunipes* and *Terrilimosina schmitzi* on warm evenings after rain. However, more exact observations from extensive breeding are needed to explain all the dependencies of activity of particular species on ecological factors including light periodicity.

5. Seasonal variation (dynamics) and seasonal periodicity (voltinism)

The species of Limosininae are mainly characterized by relatively rapid development in suitable circumstances. The majority of species occur as adults during the whole vegetation period, usually with one peak of occurrence in summer or early autumn. These species are apparently polyvoltine (often with 4 or more generations yearly) and their seasonal variation can best be theoretically explained by Fig. 55, showing eight generation-lines of *Spelobia clunipes*, each consisting of 5 generations. Although the diagram is greatly simplified by the assumption that the filial population is equal in numbers to the parental one, it shows clearly that the number of imagoes may increase merely by a shortening of the preimaginal development in the warmest season. The data of duration of the life-history of *S. clunipes* were taken from LAURENCE (1955).

There are some species which, despite their occurrence throughout the year, have two peaks (in spring and late summer or early autumn) in their seasonal dynamics, e.g. *Pullimosina pullula* and *P. antennata* (cf. ROHÁČEK, 1975a). This cannot be explained by their having only 2 generations during the year as these species have rather short development times (*P. pullula* 22—26 days — OKELY, 1974). In my opinion, the spring peak may be caused by mass-emergence of flies from hibernating pupae (not experimentally demonstrated!) while the early autumn one is the normal peak occurrence corresponding with that of non-hibernating species overwintering as adults.

On the other hand, LAURENCE (1955) found that adults of *Opalimosina collini* and *Telomerina pseudoleucoptera* occur only in summertime (V—IX). *Opalimosina collini* has only one peak occurrence during this period and has approximately 3 generations (my calculation), the first overwintering as larvae or pupae. The second typical summer species, *Telomerina pseudoleucoptera*, is apparently only bivoltine, as LAURENCE (1955) discovered two peaks of occurrence and it was entirely absent in the middle of the summer. The development of the second generation is rapid (during summer), the first generation develops very slowly and probably hibernates during winter.

The seasonal variation and periodicity of Limosininae is strongly affected by the weather and mesoclimate and the course of the seasonal dynamics is dependent on the availability of feeding substrate. It is well-known that fungivorous species (e.g. *Spelobia parapusio*) occur rarely in spring and summer but are very abundant in late summer and autumn when numerous fungi are available. This ability to multiply quickly under suitable

DOI: 10.21248/contrib.entomol.32.2.195-282

conditions is a typical feature of Sphaeroceridae. Manure, dump heaps and other accumulated decaying matter are the most convenient substrates making possible large populations of some dominant species.

6. Predators and parasites

RICHARDS (1930) discussed some possible predators and parasites of Sphaeroceridae including those of several species of the previous genus *Limosina*. It is known that some large species of *Sphaerocera* and *Copromyza* are eaten by birds, but in a series of specimens obtained during investigations on the food of *Delichon urbica* and *Hirundo rustica*, I found *Coproica* species and *Spelobia clunipes*. These species are probably too small to be regular food of birds and may become an important food component only occasionally, during population explosions of certain species e.g. on manure.

On the contrary, it seems very probable that some small Empididae are predatory on Sphaeroceridae, especially on smaller species of the subfamily Limosininae. RICHARDS (1930) reports two genera of Empididae as possible predators of Sphaeroceridae. Species of *Drapetis* MEIGEN occur on several kinds of dung and other decaying material and are thought to be predators of coprophagous and polysaprophagous species of Sphaeroceridae while species of *Stilpon* LOEW live at the roots of grass and in moss and may be predators of *Spelobia ochripes*, *S. nana*, *Pullimosina pullula*, *Leptocera fenestralis* and other Limosininae preferring this habitat.

There are no records of parasitic Hymenoptera bred from the species of the group examined, but they surely exist since some such species are known to parasitise other genera of Limosininae (cf. RICHARDS, 1930; GODDARD, 1938).

Sphaeroceridae including Limosininae often have various mites attached but only RICHARDS (1930) recorded acari from these flies, including 4 species from *Spelobia clunipes*. These records are available partly due to a revision of the material in the VITZTHUM's collection made by Dr. SAMŠIŇÁK (Praha). When studying the species of the previous genus *Limosina*, I also found a number of specimens with mites attached. Dr. K. SAMŠIŇÁK kindly identified these and submitted available biological data. All data (including those of RICHARDS, 1930 and EVANS, 1980) are summarized in Tab. 2.

The relation of mites to flies is of a varying nature. RICHARDS (1930) states that the attachment is in many cases only for locomotion (phoresy). This is certainly correct because the majority of mites found attached to Sphaeroceridae (as well as other Diptera) are stages specially adapted for phoresy — e.g. hypopi of Anoetidae or phoretomorphs of *Pediculaster* (= *Siteroptes*) spp. (see SAMŠIŇÁK, 1979).

Hypopi of Anoetidae (*Bonomoia sphaerocerae*, *Myianoetus rohaceki*, *M. virgatus* — Fig. 59, *Glyphanoetus phyllotrichus*) are rather common on various Limosininae, especially on species living on excrement and forming symbovilous or hemisynanthropic populations (see Tab. 2). They are mostly attached to the abdomen of the host fly (Fig. 58). However, some clearly coprophagous species (e.g. from genera *Opalimosina*, *Rudolfia*, *Halidayina*) never seem to have these mites.

Besides the phoretomorphs (Fig. 57) normal females of *Pediculaster* species commonly occur on various flies. Judging from analogy with related species, these females may be considered as tending towards parasitism. The position of attachment of the mites on the soft intersegmental membranes (Fig. 56) indicates possible parasitism but direct evidence is not available. It is interesting that the majority of host species of *Pediculaster* spp. recorded here are asynanthropic and phytosaprophagous (see Tab. 2).

Mesostigmata found on the species under study (*Gamasodes spiniger*, *Cornigamasus lunaris*, *Crassicheles holsaticus*, *Eviphis* ?, *Dendrolaelaps* spec.) are probably predators; their deutonymphs live free in soil and prey on minute arthropods and occasionally also attack flies. They are more frequent on terricolous species living in decayed leaf litter (especially *Crassicheles holsaticus*). It is possible that the comparatively large deutonymphs of above Mesostigmata prey on minute phoretic stages of Anoetidae and Pyemotidae attached to flies.

The percentage of infestation was calculated for some species (Tab. 2). However, these values are to be considered as an indication because they were computed from series

DOI: 10.21248/contrib.entomol.32.2.195-282

containing infested specimens while specimens of the same species from different localities or habitats were not attacked by mites at all.

7. Habitat

An early attempt to construct a classification of habitats of Limosininae is that of DAHL (1909). Besides this classification being limited to habitats in the peat-bog and its environment, his results are not significant (RICHARDS, 1930: 322) and a classification based on ordinary edaphic factors is inconvenient for Sphaeroceridae.

Another classification was proposed by RICHARDS (1930). This was found to be useful and is adopted with some alterations in the present work. PAPP (1976a) added valuable knowledge concerning terricolous species. The habitats are classified as follows:

a) Decayed vegetable refuse (grass, moss) in meadows and fields. Many species are known to occur in this habitat but only the following are characteristic: *Pullimosina pullula*, *Spelobia ochripes*, *S. nana*, *Kimosina longisetosa*, *K. plumosula*, *K. spinosa*. The species occurring in moss can be called "muscicolous". Further non-specialized terricolous species e.g. *Pullimosina antennata* and *P. moesta* are also common here.

b) Decayed vegetable refuse (Sphagnum, grass, moss) in peat-bogs and peat-bog meadows. Two specialized "sphagnicolous" or "tyrphophilous" species were found — *Pullimosina dahli* and *Spelobia pappi* spec. nov. Some other species, referred to the above group, occur here commonly — *Pullimosina pullula*, *P. antennata*, rarely *Kimosina spinosa*, *Spelobia ochripes*, *S. nana*.

c) Decayed vegetable refuse (leaves, moss) in woods. Many terricolous species are confined to this habitat, especially *Limosina silvatica*, *Gigalimosina flaviceps*, *Paralimosina fucata*, *P. trichopyga*, *P. subcribrata*, *Terrilimosina schmitzi*, *T. sudetica*, *Pullimosina meijerei*. There are a number of features in the morphology and bionomics of terricolous species (cf. RICHARDS, 1930; PAPP, 1976a) evolved as adaptations to a terricolous habitat, the most striking of which are: reduction of wing musculature, inability to fly and tendency to brachyptery, reduction of eyes, shortening of bristles on legs, heavy sclerotization of the body etc. (see PAPP, 1976a).

d) Decayed sphorophores of fungi. The most common and truly fungivorous species is *Spelobia parapusio* (cf. PAPP, 1972; HACKMAN & MEINANDER, 1979). *Opalimosina czernyi*, *Xenolimosina setaria* and *Minilimosina parvula* are also known almost exclusively from this habitat. Other species occurring more frequently on decaying fungi: *Apteromyia claviventris*, *Telomerina flavipes*, *Pullimosina moesta*, *Spelobia cambrica* etc.

e) Burrows of mammals and birds. There is rather a rich literature on microcavernicolous Sphaeroceridae (FALCOZ, 1921; RICHARDS, 1930; HACKMAN, 1963a, b, 1965b, 1967a). Eucoenic for this habitat are *Spelobia talparum* and *S. pseudonivalis*, while *S. manicata* is rather common. Other species mainly known from different habitats occur here, e.g. *Herniosina bequaerti*, *Spelobia czizeki* (both macrocavernicolous), *Pullimosina meijerei*, *Terrilimosina schmitzi*, *T. sudetica* (all terricolous), *Spelobia palmata*, *Telomerina flavipes* (both necrophagous), *Apteromyia claviventris* etc. Modifications of the adult morphology similar to those of terricolous species have developed in true microcavernicolous species but in contrast the legs and arista are prolonged, as in cave-dwelling species.

f) Nests of insects. This habitat is scarcely inhabited by Sphaeroceridae (RICHARDS, 1930). Only several common terricolous, cavernicolous, necrophagous and ubiquitous species (*Apteromyia claviventris*, *Terrilimosina racovitzai*, *Spelobia palmata*, *S. clunipes*, *Minilimosina fungicola*) were recorded from nests of wasps, humble-bees and ants.

g) Caves, cellars and mine-galleries. The cave-dwelling (macrocavernicolous) species have been dealt with by numerous authors (BEZZI, 1903, 1907, 1911, 1914; CZIŽEK, 1916; ARNDT, 1921; DUDA, 1928; RICHARDS, 1930; PAPP & PLACHTER, 1976; PAPP, 1978a). For cellars and mine-galleries, there is only paper by PAX & MASCHKE (1935) although their fauna of Limosininae is quite similar to that of caves. There is no true troglobiont (eucoenic for caves) species among European Limosininae (PAPP & PLACHTER, 1976), only 3 troglophilous species — *Herniosina bequaerti*, *Terrilimosina racovitzai* and *Spelobia czizeki*.

DOI: 10.21248/contrib.entomol.32.2.195-282

Besides reduction of eyes, lengthening of legs and inability to flight they have no special morphological modifications. The "physogastry" considered a typical feature of macrocavernicolous insects and described in some species of Limosininae (Bezzi, 1911; Duda, 1918; Venturi, 1965) is not limited to these species. I have found that many clearly non-cavernicolous species (e.g. *Spelobia luteilabris*, *S. parapusio*, *S. clunipes*, *Halidayina spinipennis*) have "physogastric" gravid females with swollen abdomina. This "physogastry" was even misinterpreted as a taxonomically useful feature and the cave-dwelling specimens described as different species (*Limosina jeanneli* Bezzi = *Pullimosina heteroneura*; *Limosina ventruosella* Venturi = probably *Telomerina flavipes* and conversely non-physogastric *Limosina mikrops* Duda = *Terrilimosina racovitzai*). However, there are some biological adaptations characteristic of macrocavernicolous species, e.g. the polysaprophagity of larvae and strong negative phototaxy.

Further species inhabiting caves (hemitroglophilous of Papp & Plachter, 1976): *Apteromyia claviventris*, *Limosina silvatica*, *Spelobia pseudosetaria*; the rather frequent occurrence of *Telomerina flavipes* and *Pullimosina heteroneura* in caves is due to the presence of feeding substrate attractive to these species. All the above species (except for *Spelobia czizeki*) were also found in cellars. These cellar populations are to be considered hemisynanthropic (see below).

h) The excrement of various mammals and birds. The excrement and manure is not only a habitat for adults but also a feeding substrate of larvae of a number of species. Apart from a relatively small number of purely coprophagous species within the group studied, dung is attractive to a many polysaprophagous species. It was noted that the fauna of dung is different in woods and pasture or fields. The species associated with the dung of large domestic mammals (horse, cow, sheep, goat, pig etc.) are secondarily synanthropic (Gregor & Povolný, 1958) and are called "symbovilous" (see below). The most characteristic inhabitants of this habitat are *Opalimosina collini*, *O. denticulata* (both associated with cow dung), *O. simplex*, *Chaetopodella scutellaris*, *Telomerina pseudoleucoptera* and *Rudolfia rozkosnyi*. Other species often very common are: *Spelobia bifrons* (mainly on manure), *S. clunipes* (ubiquitous but preferring excrement), *S. luteilabris* (on rabbit dung and in henhouses), *Opalimosina mirabilis*, *Halidayina spinipennis* etc. In woods excrement often attracts several woodland terricolous species, such as *Paralimosina fucata*, *Minilimosina splendens*, *Gigalimosina flaviceps* or *Spelobia rufilabris*.

i) Carrion of vertebrates and invertebrates. The typical necrophagous species (confirmed by breeding) seem to be *Spelobia palmata*, *Telomerina flavipes* and *Kimosina empirica*. The latter is confined to human settlements (hemisynanthropic species — see below). The fungivorous *Spelobia parapusio*, coprophagous *Chaetopodella scutellaris* and polysaprophagous *Halidayina spinipennis*, *Spelobia luteilabris* and *Minilimosina fungicola* were also found on carrion (Richards, 1930). Other species occur occasionally.

j) Refuse and compost heaps. These habitats are characterized by heterogeneous decaying matter of plant and animal origin. Therefore the species composition of Sphaeroceridae and especially Limosininae is comparatively rich. In particular some polysaprophagous species have very successfully colonized these secondary habitats created by man. These species, often abundant or even in vast populations, are considered synanthropic (see below). The most typical species on refuse and compost heaps are: *Halidayina spinipennis*, *Opalimosina liliputana*, *Pullimosina heteroneura*, *Spelobia luteilabris*.

k) Ubiquitous species. These species, although usually with some preference of certain feeding substrates, occur and develop in different habitats. Many polysaprophagous species belong here, e.g. *Spelobia clunipes*, *Apteromyia claviventris*, *Pullimosina heteroneura*, *Halidayina spinipennis*, also perhaps *Opalimosina liliputana*, *O. mirabilis*, *Spelobia pseudosetaria*, *S. luteilabris* and *Minilimosina fungicola*.

8. Synanthropy

The concept of synanthropy in Diptera has been best defined by Laštovka & Zuska (1978): "To demonstrate that a species is synanthropic means to find that it forms stabilized and ecologically successful population within man's environment; the conclusion

DOI: 10.21248/contrib.entomol.32.2.195-282

that the species is synanthropic cannot be challenged by the mere fact that it is also ecologically successful outside man's environment". The large group of species characterized as above (and called "synanthropic s. lat.") can be considered according to GREGOR & POVOLNÝ (1958) in three main groups.

a) Eusynanthropic species. They are associated with human settlements in their entire life-history and their populations are almost exclusively confined to man's environment. No Sphaeroceridae belong here.

b) Hemisynanthropic species. They have wild populations besides those living in human settlements. A number of species of Sphaeroceridae can be classified as hemisynanthropic. There are three different habitats created by man and inhabited by some species of the subfamily Limosininae — refuse heaps, cellars and houses.

The refuse heaps have synanthropic populations of *Halidayina spinipennis*, *Spelobia luteilabris*, *S. pseudosetaria*, *Pullimosina heteroneura*, *Telomerina flavipes*, *Opalimosina liliputana* and *Kimosina empirica*. Such populations are sometimes very abundant and several species may then penetrate into houses, i.e. *Kimosina empirica* or *Spelobia pseudosetaria*. RICHARDS (1930) calls these species "domestic". The origin of synanthropic populations of *Herniosina bequaerti*, *Terrilimosina racovitzai* and *Apteromyia claviventris* in cellars is somewhat different. The two first mentioned species are true macrocavernicolous species (see above) and their cellar populations are usually ecologically more successful than wild ones. Possibly these species were already associated with man in the late pleistocene or early holocene when humans lived in caves.

c) Symbovilous species. Secondarily synanthropic species associated with dung of large domestic mammals. GREGOR & POVOLNÝ (1958) divided this group into two subgroups: stable species (living in stables and on manure) and pasture species (developing in excrement on pastures). The first subgroup is closely bound to human settlements — some populations of *Spelobia bifrons* may belong here. The second subgroup contains numerous species (e.g. *Opalimosina* spp., *Chaetopodella scutellaris*, *Spelobia clunipes*, *Telomerina pseudoleucoptera*, *Halidayina spinipennis*) whose connection with man's activities is very loose.

9. Importance

The species of the previous genus *Limosina* are not economically important and their significance in hygiene is negligable though some hemisynanthropic species also inhabit houses (see above).

However, their importance must be evaluated from the ecological point of view. It is necessary to realize that the species of Limosininae are an inseparable part of the complex of organisms which in various habitat-niches participate in the destruction and mineralization of dead bodies and waste products of animals. Not only are the mass-occurring species, utilizing for example excrement or carrion, of importance but also some less abundant species which live in confined and small ecosystems, such as caves or burrows of small mammals, decomposing various kinds of decaying organic matter.

Some species are thus advantageous to man, for example some hemisynanthropic species reducing refuse heaps, dustbins etc. These species (e.g. *Halidayina spinipennis*, *Spelobia luteilabris*, *Pullimosina heteroneura*, *Telomerina flavipes*, *Opalimosina liliputana*) are well adapted by their very fast preimaginal development and high fertility.

The only species which may be a pest is the fungivorous *Spelobia parapusio* occurring on mushroom cultures.

Zoogeography

Although Sphaeroceridae are among the most common and omnipresent flies, their zonal distribution is very insufficiently known. Their minute size, inconspicuous colouration, difficult identification and unstabile taxonomy have severely retarded knowledge of the distribution of particular species — this is particularly true for the species under study.

DOI: 10.21248/contrib.entomol.32.2.195-282

Therefore the zoogeographical characteristics given under the particular species in the systematic part is somewhat deductive, based on generalized, discontinuous and often very scattered distributional records.

According to WALTER (1954) species with the same type of distribution (with similar areal) are to be considered a particular geographical faunal element — a geoelement. The other kinds of elements presented by WALTER (1954) (genoelement, chronoelement, migroelement etc.) cannot be treated here as they are applicable only to taxa known in detail. For this reason, the handbook of DE LATTIN (1967) dealing with the causal zoogeography (thus with genoelements) is of less value for the present work. On the contrary the zoogeographical classification of regions (geoelements) by UDVARDY (1975) is thought to be too detailed and in many cases not applicable to Sphaeroceridae at all. Therefore the clear and synoptical system of geoelements used by botanists (WALTER, 1954; FREITAG, 1962) is adopted with some alterations here.

The European fauna of the previous genus *Limosina* can be classified according to following typology of geoelements (see Fig. 60).

1) Cosmopolitan geoelement — species distributed throughout the whole World or tending to reach such a distribution (i.e. known from most continents of New and Old World). In the group under study, there are some species of cosmopolitan distribution (see below) but all of them originally had a much more restricted distribution, most belonging to Holarctic or Palaearctic geoelements. The present cosmopolitan distribution of these species is secondary, caused by their synanthropy.

Examples: *Spelobia clunipes*, *S. luteilabris*, *S. bifrons*, *Pullimosina heteroneura*, *Kimosina empirica*, *Telomerina flavipes*, *Opalimosina mirabilis*.

2) Old World geoelement — species distributed throughout Europe, Asia and Africa. More or less secondary distribution (as in abovegeoelement) of some originally Palaearctic species.

Examples: *Chaetopodella scutellaris*, *Spinilimosina brevicostata*.

3) Holarctic geoelement — species distributed in the Holarctic Region, i.e. in North America, Europe, North Africa and Asia (except for the SE part).

Examples: *Limosina silvatica*, *Terrilimosina schmitzi*, *Spelobia ochripes*, *Halidayina spinipennis*.

4) Palaearctic geoelement — species widespread throughout the Palaearctic (sub)Region, i.e. in Europe, N.Africa and Asia (except for the SE part).

Examples: *Minilimosina vitripennis*, *M. albinervis*, *Spelobia pseudosetaria*, *Kimosina longisetosa*. Numerous species known only from the West Palaearctic or from Europe probably also belong to this geoelement but their occurrence in eastern areas of the Palaearctic was not documented. Examples: *Apteromyia claviventris*, *Terrilimosina racovitzai*, *Minilimosina fungicola*, *M. parvula*, *Spelobia nana*, *S. parapusio*, *Pullimosina pullula*, *Paralimosina fucata*, *Opalimosina liliputana* etc.

5) Eurosiberian geoelement — species with areal covering the large part of Palaearctic Region except for the northernmost part (Arctic Region) and southern parts (Mediterranean, Central Asian and Sino-Japanese Regions).

Examples: *Spelobia rufilabris*; some of the above European species may also belong here (*Spelobia nana*, *Pullimosina pullula*).

6a) Arctic geoelement — species distributed in the northernmost part of the whole Holarctic or only the Palaearctic Region in the tundra zone (Fig. 60, arc).

Examples: Hitherto unknown among European species of the group under study but *Spelobia ulla* spec. nov. might belong here.

6b) Arcto-alpine geoelement — a special case of the above type of distribution to which belong species with disjunctive areal which, besides the main Arctic areal, occur also in more southern high-mountaine exclaves above the upper timberline. For the explanation of the historical origin of this distribution see DE LATTIN (1967).

Examples: Hitherto unknown among group under study.

7a) Boreal geoelement — species distributed in the North Palaearctic in the taiga zone, i.e. south of the Arctic Region (Fig. 60, bor).

Examples: *Minilimosina hackmani* (probably).

DOI: 10.21248/contrib.entomol.32.2.195-282

7b) Boreo-alpine geoelement — species with disjunctive areal composed of the main boreal part and mountaine, more southern exclaves. Species belonging to this geoelement live, besides the Boreal areal, in the pine-forest zone of mountains and often on peat-bogs. The historic origin of this type of distribution was explained by DE LATTIN (1967).

Examples: *Minilimosina v-atrum*, *M. trogeri* spec. nov., *Pullimosina dahli*, *Spelobia cambrica*.

8) Central European geoelement — species distributed in Central Europe, in zone of deciduous forest (including the Atlantic coast, British Is. and submediterranean part of South Europe).

Examples: *Herniosina bequaerti*, *Minilimosina splendens*, *Spelobia pseudonivalis*, *Pullimosina meijerei*, *Telomerina pseudoleucoptera*, *Opalimosina czernyi*.

8a) Central European geoelement in narrower sense — species with rather restricted distribution in Central and West Europe, without Atlantic coast and British Is. and submediterranean part of South Europe (see Fig. 60, ces).

Examples: *Paralimosina trichopyga*, *Rudolfia rozkosnyi*.

8b) Atlantic geoelement — species with areal round the Atlantic coast from Portugal to South Norway including British Is., in zone of heaths with extreme oceanic climate (Fig. 60, atl).

Examples: *Xenolimosina setaria*.

8c) Submediterranean geoelement — in contrast to the following geoelement it includes species distributed in South Europe but with areal extended much more in the north, to Central Europe (Fig. 60, sme).

Examples: *Spelobia villosa*.

9) Mediterranean geoelement — species distributed on coast of the Mediterranean, in zone of non-deciduous sclerophylous forest (Fig. 60, me). The Balkan area may be considered to contain a particular (Balkan) geoelement, see WALTER (1954).

Examples: *Paralimosina beckeri*, *Spelobia baezi*, *S. quaesita* spec. nov., *Kimosina ciliata*.

10a) Pontic geoelement — species distributed in South East Europe (and West Asia) in zone of steppes with continental climate (Fig. 60, pon).

Examples: Hitherto unknown among the group under study.

10b) Ponto-(sub) mediterranean geoelement — species with areal as above geoelement but extended far to Mediterranean or Submediterranean Region.

Examples: *Spelobia simplicipes*.

10c) Panonian geoelement — its areal is often considered a Middle European exclave of Pontic Region, containing rather characteristic fauna with number of Pontic and Submediterranean elements (Fig. 60, pa).

Examples: Unknown among the group investigated.

11) Turanic geoelement — species distributed in Aralo-Caspian Region, in zone of semideserts with extreme arid climate (Fig. 60, tur). Some species may penetrate to South-East Europe.

Examples: Hitherto unknown among group under study.

12) Iranian geoelement — species with areal covering the northern part of the Near and Middle East and Asia minor (Fig. 60, ir). Some species may penetrate to South-East Europe, especially to Balkan area.

Examples: *Paralimosina macedonica*.

Phylogeny

This chapter is titled "Phylogeny" in spite of the fact that no direct evidence about the phylogenetic evolution of the groups under study (or the whole family Sphaeroceridae) is available. Only fossil material (hitherto unknown in Sphaeroceridae) can bring direct and conclusive evidence of evolution. However, it is possible to deduce some phylogenetic

DOI: 10.21248/contrib.entomol.32.2.195-282

trends by the method of cladistic classification. Thus, to be precise, the title should be "cladistic classification" but it is not because of convention.

The cladistic classification is strongly affected by the subjective approach of each author, primarily regarding the weighting given particular characters. Consequently the cladistic classification of the genera and subgenera recognized in the previous genus *Limosina* (see below) cannot be considered as definitive, although it was made as complete as possible. Further investigations, especially on preimaginal stages, cytotaxonomy, serotaxonomy etc. will certainly alter present opinions on the relationships and cladogen of the groups studied here. Despite this, it is hoped that the main aim of this chapter — to establish grounds for future "phylogenetic" studies in Limosininae — has been achieved.

The previous genus *Limosina* (sensu HACKMAN, 1969a) was clearly a polyphyletic taxon. As shown below, 7 groups of genera are recognized within it of which only 3 or 4 (*Limosina* genera-group, *Minilimosina* genera-group, *Spelobia* genera-group, and perhaps the genus *Kimosina*) might be derived from the same ancestral stock (but these suggestions are not confirmed by any synapomorphic characters!); the remaining 3 (genera *Opalimosina* and *Telomerina*, genus *Rudolfia*, genus *Halidayina*) do not appear to be related to the above groups of previous *Limosina* at all. Each of these 7 recognized groups is discussed separately, with an associated cladogram.

1. The *Limosina* genera-group (Figs. 61, 62)

The group is composed of 4 genera, *Limosina* MACQUART, 1835, *Gigalimosina* gen. nov., *Apteromyia* VIMMER, 1929 and *Herniosina* gen. nov. These genera differ essentially in that each is characterized by a complex mosaic of apomorphic and plesiomorphic features, and consequently it is very difficult to discover the most important shared synapomorphic features which would define their phylogenetic relationships. On the other hand, many aberrant and mostly autapomorphic characters of each of these groups, as well as the small number of species belonging to each of them, indicate that their relationship is not very close and support the theory that the present genera are relics of a much larger and diverse group, rich in species.

The *Limosina* genera-group and *Minilimosina* genera-group seem to have evolved from a common ancestor, although it cannot be demonstrated that they are really sister-groups because their shared features are either plesiomorphic or of uncertain interpretation. However, there is indirect evidence supporting the above supposition — the primitive formation of the female postabdomen in *Herniosina* which is narrow and telescopically retractile, a plesiomorphic feature common in the *Minilimosina* genera-group. Nevertheless, other characters of *Herniosina* confirm its placement in the *Limosina* genera-group which is characterized by the features given in the cladograms (Figs. 61, 62), the most characteristic of which are thought to be the reduced female *S9*, *C* not extended beyond R_{4+5} and the comparatively long phallophore. The latter character is possibly plesiomorphic (a long phallophore is a common feature in Copromyzinae) but is preserved only in the above group and might be considered as an ancestral feature.

For the above reasons, the interrelationship of the particular genera under discussion is meantime rather obscure. Two possible cladograms (Figs. 61, 62) were selected to show the most probable cladistic classification of them. The relationship of *Limosina* and *Gigalimosina* is beyond doubt (generally similar formation of the aedeagal complex and t_2 chaetotaxy), but the position of the remaining two genera and especially *Apteromyia* is unclear and has not been completely elucidated.

Because of its telescopic female postabdomen, *Herniosina* seems to be the most primitive member of the group, although its male abdomen is of unique construction. The genus *Apteromyia* is very aberrant and may be placed as the sister group of *Herniosina* (features in common: t_2 chaetotaxy, male cercus projecting ventrally, and a posterior projection of distiphallus which may be homologous with the posteroventral projection of phallophore of *Herniosina* supposing that it has evolved by secondary separation from the phallophore and subsequent fusion with distiphallus) — see cladogramm in Fig. 61, or of *Gigalimosina-Limosina* complex (shared apomorphic features: long and long haired postgonite, short female postabdomen) — see Fig. 62.

DOI: 10.21248/contrib.entomol.32.2.195-282

Moreover, the situation with the genus *Apteromyia* proved to be more complicated, especially when the features of puparium were taken in consideration. *Limosina* and *Herniosina* have shortly palmate anterior spiracular processes (see GODDARD, 1938) similar to those of *Minilimosina* or Copromyzinae and therefore they may be taken for a plesiomorphic feature, while *Apteromyia* has these processes distinctly although shortly spine-like (Fig. 20), a type occurring in more advanced groups (e.g. *Spelobia* genera-group). It must be noted that the taxonomic value of this character is impaired by the fact that the development of the anterior spiracular processes is probably directly influenced by the nature of the feeding substrate of the larva (larvae feeding in more liquid matter have longer, spine-like anterior spiracular processes), while some of the most advanced genera of Limosininae (e.g. *Leptocera* — see OKELY, 1974) have puparia with the "plesiomorphic", shortly palmate anterior spiracular processes.

2. The *Minilimosina* genera-group (Fig. 63)

A further apparently monophyletic group of genera in the previous genus *Limosina* comprises *Terrilimosina* gen. nov., *Minilimosina* gen. nov. and *Xenolimosina* gen. nov. This complex is considered to represent the most primitive group of the previous genus *Limosina* being probably closest to the hypothetical ancestor of it and of some other groups (*Limosina* genera-group, *Spelobia* genera-group) under study. It is characterized by a number of important plesiomorphic features, especially the formation of the female postabdomen which is narrow, long and telescopically retractile, with long, slender and long sinuate haired cerci, similar to that of the much more primitive subfamilies Ceropterinae and Copromyzinae. However, there are only a few apomorphic features shared by the above genera which delimit the *Minilimosina* genera-group, e.g. small size, comparatively short phallophore and often a narrow female *T9*.

The genera *Terrilimosina* and *Xenolimosina* are somewhat aberrant but *Minilimosina* and especially its subgenus *Svarciella* and *Minilimosina* s. str. indicate, at least by some features, the probable origin of some other genera-groups. The possible evolution of the *Limosina* genera-group and *Minilimosina* genera-group from a common ancestor has been discussed earlier (p. 221); also the shortened anterior spiracular process of the puparium (known in *Minilimosina* and some genera of the *Limosina* genera-group) might be considered further evidence for the relationship of these genera-groups but it is necessary to find it also in other included genera. The *Spelobia* genera-group presumably also branched off from this common ancestral stock. The latter supposition is based on the fact that some *Minilimosina* (s. str.) species have an internal postabdominal structure (see Figs. 285, 286) which is thought to be a primitive form of the spectacles-shaped sclerite characteristic of the *Spelobia* genera-group. The relationships of the genera-groups (outside of the *Minilimosina* genera-group) is very obscure and cannot be completely elucidated on the basis of known features.

On the contrary, the probable interrelationships within the *Minilimosina* genera-group was clarified (Fig. 63). The genus *Terrilimosina* is thought to have branched off from the common line earliest as it bears a number of apomorphic characters (strongly reduced phallophore, periandrium with dorsolateral hair, enlarged alula) combined with apparently plesiomorphic ones (large female *S8*, distinctly developed male cerci, t_2 with *av* below middle). *Terrilimosina racovitzai* (BEZZI), the most aberrant species of the genus (*av* below middle of t_2 absent, very reduced phallophore, short male and female cerci, deeply incised telomere) indicates a somewhat stronger affinity to *Minilimosina* (t_2 chaetotaxy).

The genus *Xenolimosina* seems to be better placed as a sister-group of the genus *Minilimosina* than of *Terrilimosina* because of its non-reduced phallophore, more reduced male cerci, t_2 without *av* below middle, small alula, similarly formed periandrium and telomere resembling that of *Minilimosina* s. str. Its autapomorphic characters (for example pre-epiphallus, distiphallus of complex form, peculiarly incised female *S9* and tendence to abbreviation of female postabdomen) are fairly progressive and delimit it as a somewhat aberrant genus of the discussed group.

The genus *Minilimosina* includes 3 subgenera. The most primitive, sg. *Svarciella* seems to be relatively close to the presumed ancestor of the whole genus and is characterized by a number of plesiomorphic features (2 *dc*, non-reduced female *S8*, long hypandrium).

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Its sister-group (see Fig. 63) is composed of the two remaining subgenera — *Minilimosina* s.str. and the most advanced sg. *Allolimosina*, characterized by more autapomorphies (1 *dc*, flattened telomere, reduced female *S8*, shorter hypandrium). *Minilimosina* s.str. and *Allolimosina* subgen. nov. are apparently closely related; the latter subgenus appears to be the more advanced having a number of progressive autapomorphic characters, especially shortened discal cell, female *S8* usually completely absent and very reduced hypandrium.

3. The *Spelobia* genera-group (Fig. 64)

This group of genera is formed by *Paralimosina* PAPP, 1973, *Spelobia* SPULER, 1924, *Pullimosina* gen. nov., *Spinilimosina* gen. nov. and *Chaetopodella* DUDA, 1920[4] being grouped on the basis of the structure of the female postabdomen (principally the presence of the spectacles-shaped sclerite). In addition the rich chaetotaxy of t_2, well sclerotized and rather complicated distiphallus are characteristic.

The *Spelobia* genera-group probably evolved from a common ancestral stock of the *Minilimosina* genera-group and *Limosina* genera-group. Although there is no direct evidence for such a theory, some features of more primitive members of the above genera-groups indicate this possibility, e.g. the presence of an internal sclerite in the female postabdomen of some *Minilimosina* (this structure may be considered as a primitive stage from which evolved the true spectacles-shaped sclerite), the sinuate R_{4+5} in *Paralimosina* (also persisting as a plesiomorphic feature in some *Spelobia*), shorter but sinuate haired female cerci in all taxa of *Spelobia* genera-group etc.

The supposed interrelationship between genera of the *Spelobia* genera-group is shown in the cladogram (Fig. 64). *Paralimosina* is thought to be a primitive and rather aberrant genus of this group, separated from the remaining genera by the characteristic short and bilobed telomere, reduced phallophore, comparatively long female *S8* and sinuate R_{4+5}. Its subgenus *Canarisina* subgen. nov. with only one species *P.(C.) beckeri* (DUDA) is placed in *Paralimosina* althought it is somewhat intermediate between *Paralimosina* s.str. and the genus *Spelobia* (especially in the structure of hypandrium, phallophore, female *S9*). In spite of all this, *Canarisina* is clearly closer to *Paralimosina* s.str. than any other known group, even though it might also be allied to some African species of the previous genus *Limosina* — it may be classified as a separate genus if necessary.

The genera *Spinilimosina* and *Chaetopodella* are provisionally considered as sister groups branching off quite early from other genera of the discussed group (synapomorphies: very complicated distiphallus, somewhat ventrally projecting phallophore, bilobed telomere) but their real relationships will probably be more complex (supposing that they are more close to insufficiently known non-Palaearctic taxa) because they differ considerably each from other.

The remaining 2 genera of the *Spelobia* genera-group, *Spelobia* and *Pullimosina*, are apparently more closely related (generally similar formation of the male genitalia and female postabdomen, existence of somewhat intermediate taxa — sg. *Bifronsina*, sg. *Dahlimosina*) and are probably correctly associated as sister-groups (see Fig. 64).

The genus *Spelobia* is divided into 3 subgenera, viz. *Eulimosina* subgen. nov., *Spelobia* s. str. and *Bifronsina* subgen. nov. While *Spelobia* s. str. is a large and homogeneous group (internal genitalia, telomere), the remaining subgenera contain only one European species each and are rather aberrant; they might even be considered as separate genera. However, their affinity to *Spelobia* s. str. is much more obvious than to any other group (*Pullimosina*, *Paralimosina*). Their supposed cladistic classification is presented in Fig. 64. Subgenus *Bifronsina* is placed as the sister-group of *Spelobia* s. str. on the basis of the armature of telomere, t_2 chaetotaxy and the form of the spectacles-shaped sclerite. Subgenus *Eulimosina* differs by some peculiar autapomorphic features (e.g. unique spectacles-shaped sclerite, absence of *av* below middle of t_2, very robust distiphallus).

The genus *Pullimosina* is composed of 2 subgenera. The subgenus *Dahlimosina* subgen. nov. has some similarity to *Spelobia* (*Bifronsina*), for example in the less curved R_{4+5},

[4] The tropical genus *Poecilosomella* DUDA, 1925 is not included in this work (one introduced species known from Canary Is.) but may also belong to the *Spelobia* genera-group judging from the structure of the telomere and male *S5* (DEEMING, 1969) but it is necessary to confirm this by study of the aedeagal complex and female postabdomen.

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slightly (although distinctly) overpassed by *C* or in the presence of additional sclerites posterior to female *S8*, but its close relationship with *Pullimosina* s. str. is beyond doubt (see Fig. 64). It seems to be more primitive than *Pullimosina* s. str.

Features of the puparium also indicate the relationships of some genera of the *Spelobia* genera-group; especially the long, spine-like anterior spiracular processes with short papillae are characteristic — known in *Spelobia* (s. str.), *S.* (*Bifronsina*), *Pullimosina* (s. str.), *Chaetopodella* (in larva — see Fig. 12, puparium is unknown). However, this feature cannot be considered as too important because some non-related genera (*Elachisoma* RONDANI, *Halidayina* DUDA) also have similar long anterior spiracular processes on the puparium (OKELY, 1974).

4. The genus *Kimosina* gen. nov. (Fig. 65)

Kimosina gen. nov. is a group of clear monophyletic origin — confirmed by a number of autapomorphies (3—5 *dc*, t_2 chaetotaxy, complex bipartite telomere, intraperiandrial sclerite connected by long arch-shaped arms with posterior part of telomeres and often with medial mesolobus, membraneous distiphallus, female *S8* extremely reduced but postabdomen short) — but its relationship to other genera-groups of the previous genus *Limosina* is rather obscure. The genus might have evolve from a stock parallel to that from which had arisen the *Spelobia* genera-group (indicated by shortened female postabdomen with short cerci, t_2 and head chaetotaxy), that is from some of the ancestors of the *Minilimosina* genera-group.

On the contrary, the numerous *dc*, often long and sparsely haired Cs_1 and sexual wing dimorphism in subgenus *Alimosina* and South American *Kimosina dolichoptera* (RICHARDS) and *K. phycophila* (RICHARDS) show some affinity between *Kimosina* and the genus *Thoracochaeta* DUDA, 1918 but the genitalia of the latter genus seem to be significantly different (HACKMAN, 1969a states that aedeagus is not distinctly divided in phallophore and distiphallus and that the telomere is simple). Further study of the male genitalia and female postabdomen of *Thoracochaeta* species is necessary to elucidate this question.

The genus *Kimosina* is divided into 3 subgenera which are classified according to the cladogram in Fig. 65. Subgenus *Collimosina* subgen. nov. is a rather aberrant group with some autapomorphic features but lacking some important progressive features of the remaining two subgenera (mesolobus, haired distiphallus) and is therefore considered more primitive than these subgenera (*Alimosina* subgen. nov. and *Kimosina* s. str.) which are more closely related each other and are placed as sister-groups in the cladogram (Fig. 65). The subgenus *Alimosina* might be somewhat related to a species-group formed by *K. dolichoptera* (RICHARDS) and *K. phycophila* (RICHARDS) from S. America (see discussion under sg. *Alimosina*, part II).

5. The genera *Telomerina* gen. nov. and *Opalimosina* gen. nov. (Figs. 66, 67)

Both *Telomerina* gen. nov. and *Opalimosina* gen. nov. are genera containing generally small species of very similar external appearance (short head with small eyes, a long row of *ads*, *pvt* always present, similar thoracic chaetotaxy, heavily dusted thorax). However, both these genera differ significantly in the configuration of the male and female terminalia, so that it is impossible to demonstrate their direct relationship; nevertheless, it is obvious that they are more closely allied than to all other genera of Limosininae. Indeed, the affinity of *Telomerina* and *Opalimosina* to other genera-groups of the previous genus *Limosina* is very doubtful.

The mutual relationship of *Telomerina* and *Opalimosina* can be infered not only from the general outer appearance which might be convergent evolution, but principally from some phylogenetically important features found in particular species of both genera. For example, the most primitive species of *Telomerina*, *T. antonini* spec. nov. has wing venation, simple spermathecae and little reduced female *T6* as some species of *Opalimosina*. Similarly, the more advanced *Telomerina* species (e.g. *T. pseudoleucoptera*, *T. flavipes*) have female cerci with short spines as in the subgenera *Pappiella* and *Hackmanina* of *Opalimosina*. On the other hand, *Opalimosina* (*H.*) *czernyi* (DUDA) has a narrow female *T6* and a complex female *S9* as in *Telomerina* species. Moreover, as noted in the discussion of the genus *Telomerina* (see part II), it is not impossible to imagine the evolution of certain

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structures of the aedeagal complex (epiphallus, postgonites) of *Opalimosina* (*Pappiella*) from a more primitive state similar to that of *Telomerina*.

The genus *Telomerina* is rather homogeneous while *Opalimosina* is a complex of somewhat diverse groups, considered as subgenera. The interrelationships of these subgenera, viz. *Pappiella* subgen. nov., *Hackmanina* subgen. nov., *Dentilimosina* subgen. nov. and *Opalimosina* s. str. is discussed below (see cladograms in Figs. 66, 67). I had great difficulty when constructing the cladograms of the above subgenera because they are distinctly delimited from each other by a number of apomorphic features but have only a few characters in common to make it possible to find the particular sister-groups. Eventually I was obliged to select 2 most probable possibilities, see Figs. 66, 67. Both suppose the close relationship of *Opalimosina* s. str. and sg. *Dentilimosina* but differ in the classification of sg. *Pappiella* and sg. *Hackmanina*. The latter subgenus can be placed as sister-group either of *Dentilimosina-Opalimosina* complex (Fig. 66 — on the basis of the form of the aedeagal complex, mainly the epiphallus) or of sg. *Pappiella* (Fig. 67 — synapomorphies: additional seta between *occi* and *occe*, double female *S9*). Thus, the problem of the cladistic classification of these subgenera has not been completely elucidated.

Despite the great diversity of the subgenera of *Opalimosina*, they obviously evolved from a common ancestor and the genus *Opalimosina* is therefore thougt to be of monophyletic origin (most significant autapomorphic features: large epiphallus, small female *T9*, small female *S8*, female cerci with reduced setosity — see also cladograms in Figs. 66, 67).

6. The genus *Rudolfia* gen. nov.

The genus *Rudolfia* gen. nov., containing only one species *R. rozkosnyi* (Roháček), is a very distinctive taxon whose relationship to other genera of Palaearctic Limosininae is very obscure. I have not found any similar related group among hitherto described taxa of Sphaeroceridae. Although the venation of its wing, pruinose body and presence of *pvt* indicate some resemblance to *Opalimosina* or *Telomerina*, the other characters are quite different. The long costal bristle on the basis of Cs_1, 1 *dc* combined with 1 very long prescutellar *ac*, large external male genitalia (peculiarly haired periandrium, distinctive cerci and telomere), small aedeagal complex, strongly modified female postabdomen (*T9* fused with cerci, *S7* enlarged, *S8* and *S9* reduced, additional minute sclerites below gonopore) and unusual cerci are considered to be unique features which do not allow association of this genus with any other group of Palaearctic Sphaeroceridae.

7. The genus *Halidayina* Duda, 1918

This genus does not seem to be related to any group of the previous genus *Limosina*; for a more thorough discussion see part II. Hackman (1969a, b) was incorrect in including the genus *Halidayina* under the genus *Limosina* because it is clearly more closely allied to the genus *Elachisoma* Rondani, 1880 than to any group of *Limosina* in his sense. Papp (1973c) correctly considered it as a separate genus and also recognized its affinity to *Elachisoma*. Further suggestions of the *Elachisoma-Halidayina* relationship are discussed under the genus *Halidayina* (see part II). However, only detailed study of the terminalia of *Elachisoma* species can solve the problem.

Table 1.
Comparison of terms of the male genitalia used by recent authors

Kim & Cook (1966)	Richards (1973)	Griffiths (1972)	present work
T8 + *T9*	*T9*	*S8* + periandrium	periandrium
hypandrium (*S9*)	forked plate	hypandrium	hypandrium
valvula lateralis	genital forceps	telomere	telomere
valvula medialis	cercus	cercus	cercus
—	—	—	subanal plate
—	—	—	intraperiandrial sclerite
—	—	—	mesolobus
phallus	aedeagus	aedeagus	aedeagus
distiphallus	—	distiphallus	distiphallus
basiphallus	—	phallophore	phallophore
epiphallus	—	epiphallus	epiphallus
—	—	—	pre-epiphallus
gonite	posterior gonapophysis	postgonite	postgonite
phallapodeme	supporting plate	aedeagal apodeme	aedeagal apodeme
—	—	ejaculatory apodeme	ejaculatory apodeme

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Table 2.

Mites (*Acarina*) found attached on species of the previous genus *Limosina*
Abbreviations to,,Biological characteristics of host,,: (1) Feeding: c — coprophagous, f — fungivorous, p — phytosaprophagous, s — polysaprophagous; (2) Preferred habitat: B — burrows of small mammals, D — dump and compost heaps, E — excrement of mammals, F — decaying fungi, M — decaying vegetation in open places (meadows, fields), U — ubiquitous species without habitat preference, W — decaying vegetation in woods; (3) Synanthropy: o — symbovilous, x — hemisynanthropic

Host	Biological characteristic of host (1)	(2)	(3)	Mite
Limosina silvatica (MEIGEN)	p	W	—	*Crassicheles holsaticus* (WILLMANN, 1937)
Terrilimosina schmitzi (DUDA)	p	W	—	*Pediculaster incompletus* SAMŠIŇÁK, 1982
Minilimosina fungicola (HALIDAY)	s	U	—	*Pediculaster limosinae* SAMŠIŇÁK, 1982
Minilimosina parvula (STENHAMMAR)	f	F	—	*Dendrolaelaps* spec.
Spelobia ochripes (MEIGEN)	p	M	—	*Pediculaster moravicus* SAMŠIŇÁK, 1982
Spelobia clunipes (MEIGEN)	s	U	o, x	*Cornigamasus lunaris* (BERLESE, 1882)
Spelobia clunipes (MEIGEN)	s	U	o, x	*Gamasodes spiniger* (TRÄGÅRDH, 1910)
Spelobia clunipes (MEIGEN)	s	U	o, x	*Crassicheles holsaticus* (WILLMANN, 1937)
Spelobia clunipes (MEIGEN)	s	U	o, x	*Anoetus* spec. (?)
Spelobia clunipes (MEIGEN)	s	U	o, x	*Myianoetus virgatus* SCHEUCHER, 1957
Spelobia clunipes (MEIGEN)	s	U	o, x	*Pediculaster* spec.
Spelobia talparum (RICHARDS)	s	B	—	*Cornigamasus lunaris* (BERLESE, 1882)
Spelobia talparum (RICHARDS)	s	B	o, x	*Bonomoia sphaerocerae* VITZTHUM, 1922
Spelobia talparum (RICHARDS)	s	B	o, x	*Glyphanoetus phyllotrichus* (BERLESE, 1881
Spelobia pseudosetaria (DUDA)	p	D	x	*Dendrolaelaps* spec.
Spelobia rufilabris (STENHAMMAR)	p	W	—	*Myianoetus rohaceki* SAMŠIŇÁK, 1982
Spelobia luteilabris (RONDANI)	s	D	x	*Crassicheles holsaticus* (WILLMANN, 1937)
Spelobia parapusio (DAHL)	f	F	—	*Eviphis* ?
Spelobia cambrica (RICHARDS)	s	E, F	—	*Dendrolaelaps* spec.
Spelobia cambrica (RICHARDS)	s	E, F	—	*Myianoetus* spec.
Spelobia bifrons (STENHAMMAR)	c, p	E, M	o	*Bonomoia sphaerocerae* VITZTHUM, 1922
Pullimosina heteroneura (HALIDAY)	s	U	x	*Dendrolaelaps* spec.
Kimosina plumosula (RONDANI)	p	M, W	—	*Pediculaster pfefferianus* SAMŠIŇÁK, 1982
Kimosina plumosula (RONDANI)	p	M, W	—	*Pediculaster hispanicus* SAMŠIŇÁK, 1982
Opalimosina mirabilis (COLLIN)	c	E	o	*Eviphis* ?
Halidayina spinipennis (HALIDAY)	c, p	E, D	o, x	*Dendrolaelaps* spec.

* as *Parasitus*, ** as *Alliphis halleri*, *** as *Pediculoides mesembrinae*

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Systematic classification	Stage	Presumed nature of host-symbiont relation	Infestation (%)	Author
Mesostigmata Eviphidae	deutonymph	? predation	14.3	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female phoretomorph	phoresy parasitism	20.0	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female phoretomorph	phoresy parasitism	—	SAMŠIŇÁK 1982
Mesostigmata Rhodocaridae	deutonymph	? predation	10.0	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female phoretomorph	phoresy parasitism	—	SAMŠIŇÁK 1982
Mesostigmata Gamasidae	deutonymph	? predation	—	RICHARDS 1930*
Mesostigmata Gamasidae	deutonymph	? predation	5.5	SAMŠIŇÁK 1982
Mesostigmata Eviphidae	deutonymph	? predation	—	RICHARDS 1930** EVANS 1980
Sarcoptiformes Anoetidae	? hypopus	phoresy	—	RICHARDS 1930
Sarcoptiformes Anoetidae	hypopus	phoresy	2.8—20	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female	phoresy parasitism	—	RICHARDS 1930***
Mesostigmata Gamasidae	deutonymph	? predation	—	SAMŠIŇÁK 1982
Sarcoptiformes Anoetidae	hypopus	phoresy	—	SAMŠIŇÁK 1982
Sarcoptiformes Anoetidae	hypopus	phoresy	—	SAMŠIŇÁK 1982
Mesostigmata Rhodocaridae	deutonymph	? predation	—	SAMŠIŇÁK 1982
Sarcoptiformes Anoetidae	hypopus	phoresy	—	SAMŠIŇÁK 1982
Mesostigmata Eviphidae	deutonymph	? predation	25.0	SAMŠIŇÁK 1982
Mesostigmata Eviphidae	deutonymph	? predation	—	SAMŠIŇÁK 1982
Mesostigmata Rhodocaridae	deutonymph	? predation	—	SAMŠIŇÁK 1982
Sarcoptiformes Anoetidae	hypopus	phoresy	—	SAMŠIŇÁK 1982
Sarcoptiformes Anoetidae	hypopus	phoresy	8.3	SAMŠIŇÁK 1982
Mesostigmata Rhodocaridae	deutonymph	? predation	—	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female phoretomorph	phoresy parasitism	—	SAMŠIŇÁK 1982
Trombidiformes Pyemotidae	female phoretomorph	phoresy parasitism	—	SAMŠIŇÁK 1982
Mesostigmata Eviphidae	deutonymph	? predation	14.3	SAMŠIŇÁK 1982
Mesostigmata Rhodocaridae	deutonymph	? predation	20.0	SAMŠIŇÁK 1982

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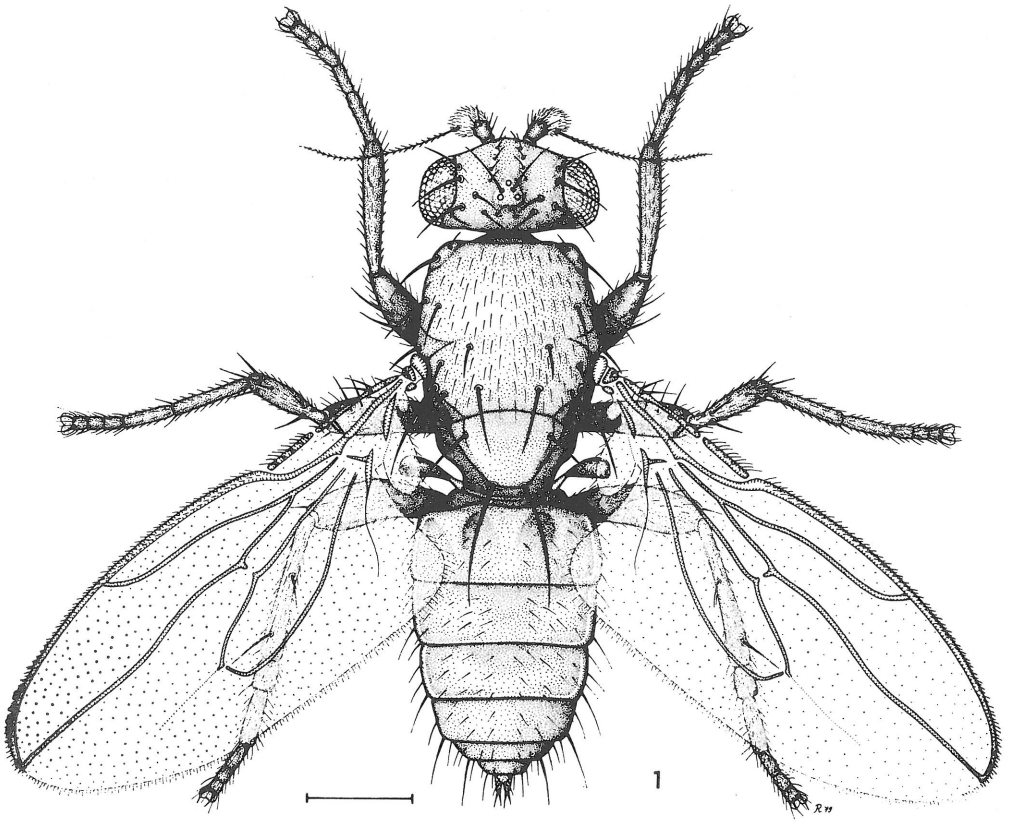

Fig. 1. *Limosina silvatica* (MEIGEN), female (Czechoslovakia). Scale = 0.5 mm.

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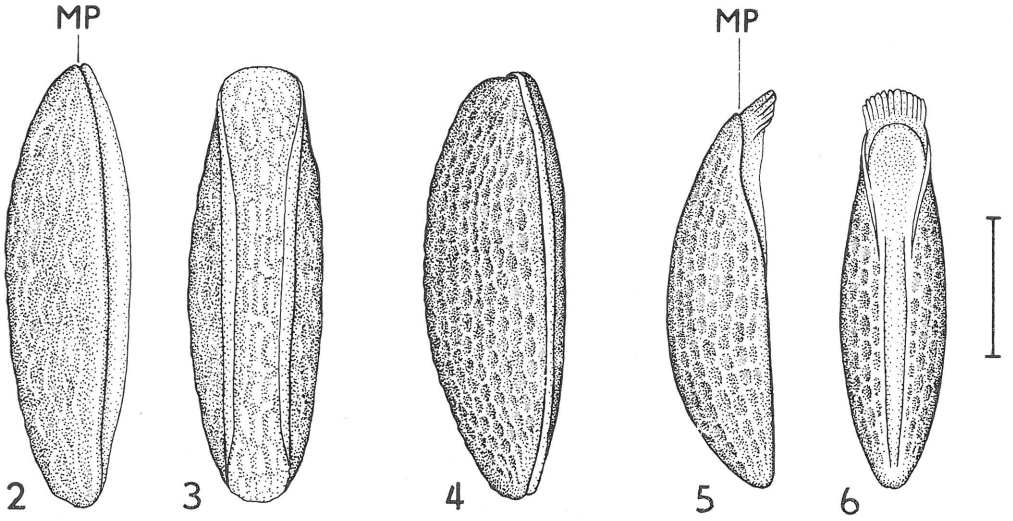

Figs. 2–6. Eggs. 2 – *Spelobia luteilabris* (RONDANI), egg laterally; 3 – dtto dorsally; 4 – *Spelobia parapusio* (DAHL), egg laterally; 5 – *Opalimosina simplex* (RICHARDS), egg laterally; 6 – dtto dorsally. All figures based on specimens from Czechoslovakia. Scale = 0.2 mm. Abbreviations: see p. 198.

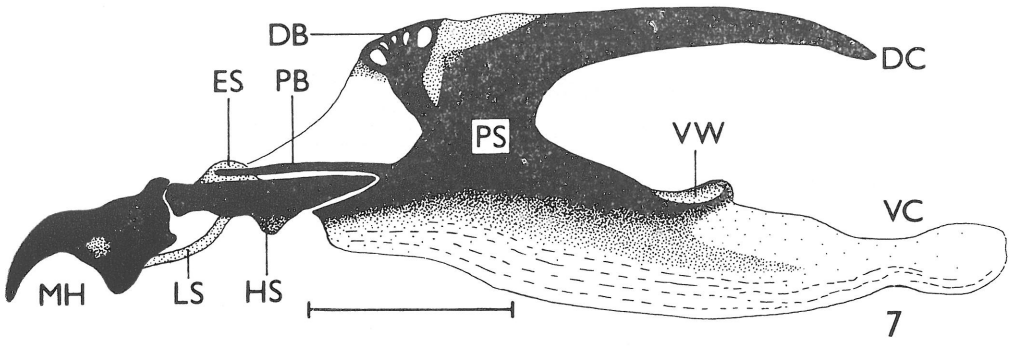

Fig. 7. Cephalopharyngeal skeleton of *Spelobia palmata* (RICHARDS), 3rd instar larva, laterally (Czechoslovakia). Scale = 0.1 mm. Abbreviations: see p. 198.

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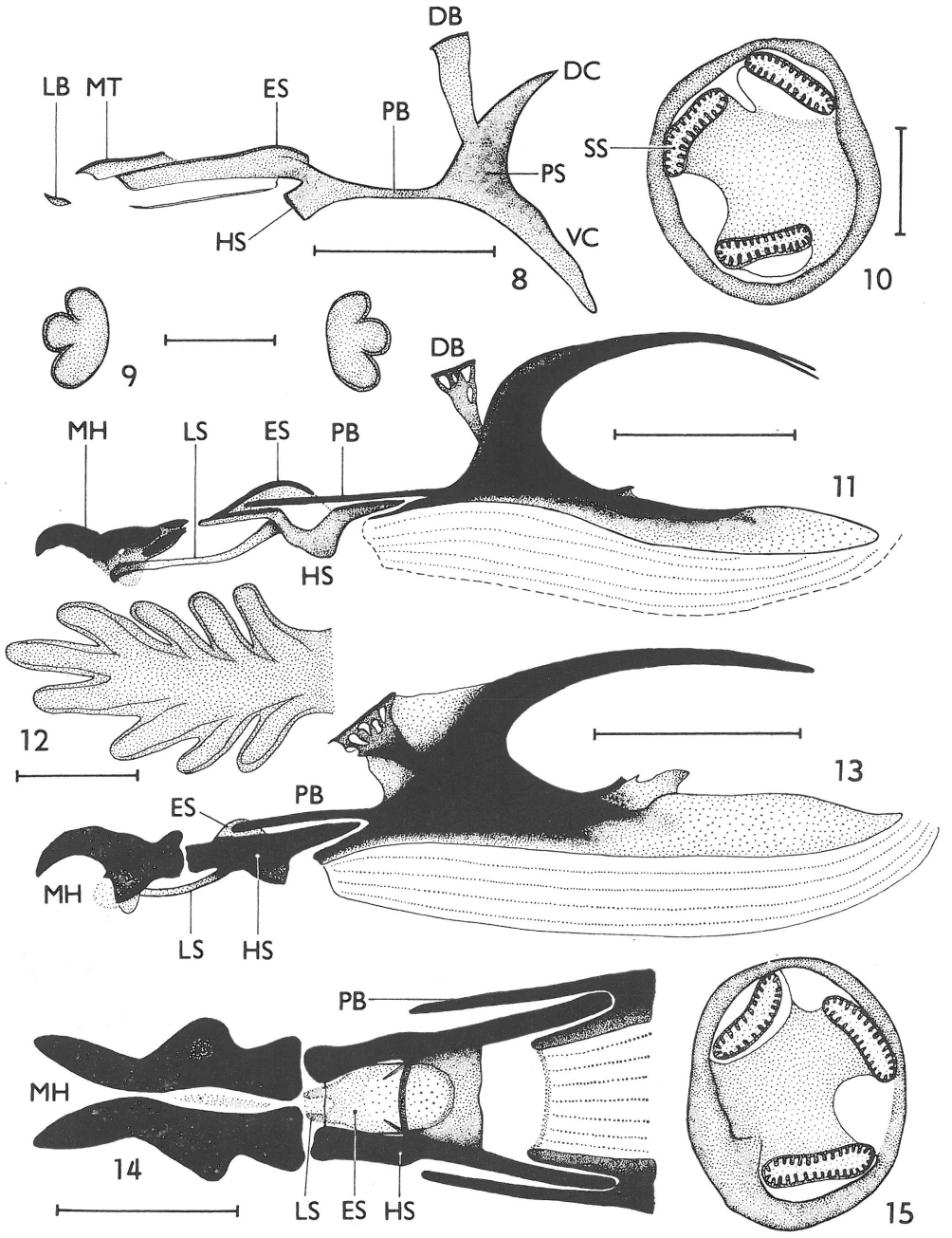

Figs. 8—15. Larval morphology of *Chaetopodella scutellaris* (HAL.). 8 — cephalopharyngeal skeleton of 1st instar laterally; 9 — posterior spiracles of 2nd instar; 10 — left posterior spiracle of 3rd instar; 11 — cephalopharyngeal skeleton of 2nd instar laterally; 12 — anterior spiracular projection of 3rd instar; 13— cephalopharyngeal skeleton of 3rd instar laterally; 14 — dtto, anterior part dorsally; 15 — right posterior spiracle of 3rd instar. Scales: Figs. 8, 11, 14 = 0.05 mm, Figs. 9, 10 = 0.03 mm, Fig. 12 = 0.02 mm, Fig. 13 = 0.1 mm. All figures by courtesy of Dr. H. SCHUMANN. Abbreviations: see p. 198.

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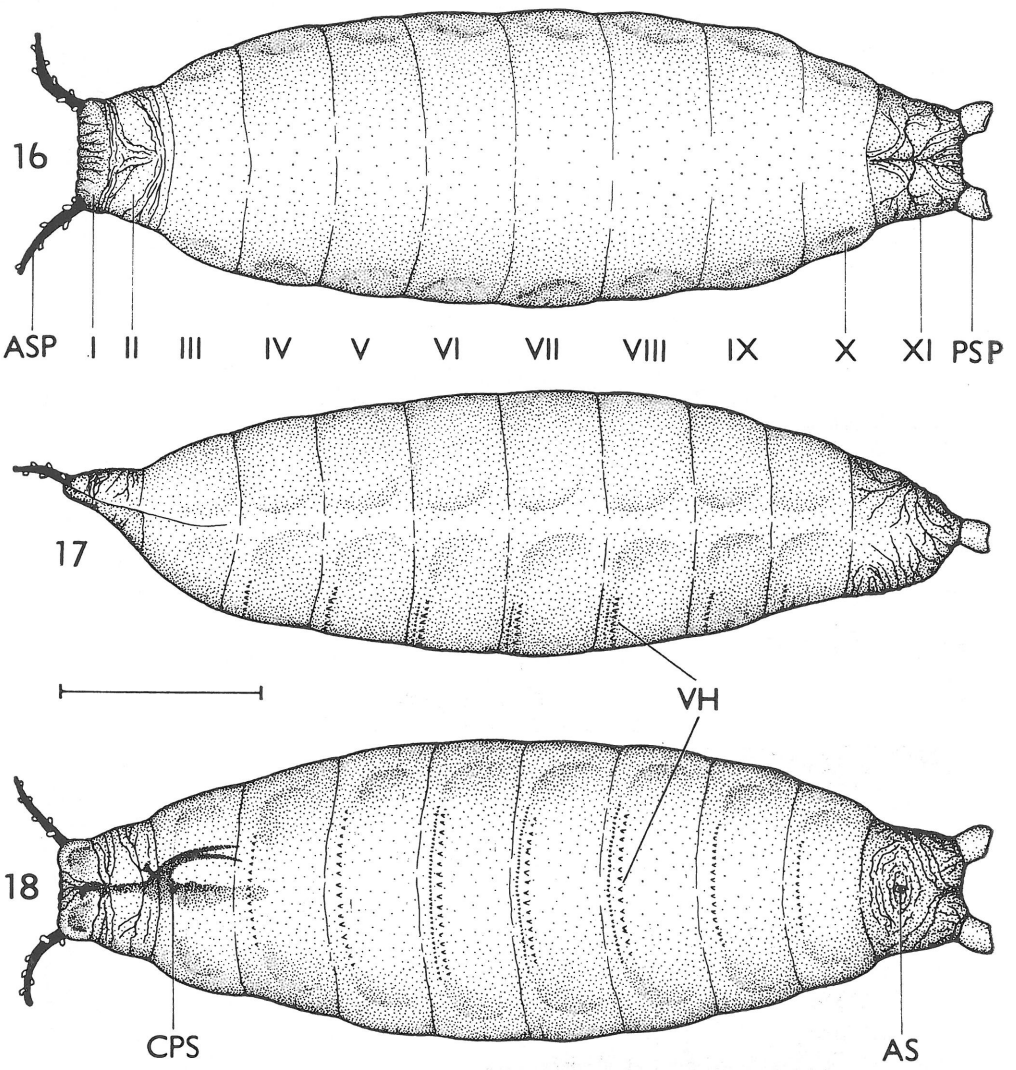

Figs. 16–18. Puparium of *Spelobia parapusio* (DAHL) (Czechoslovakia). 16 – dorsally; 17 – laterally; 18 – ventrally. Scale = 0.5 mm. Abbreviations: see p. 198.

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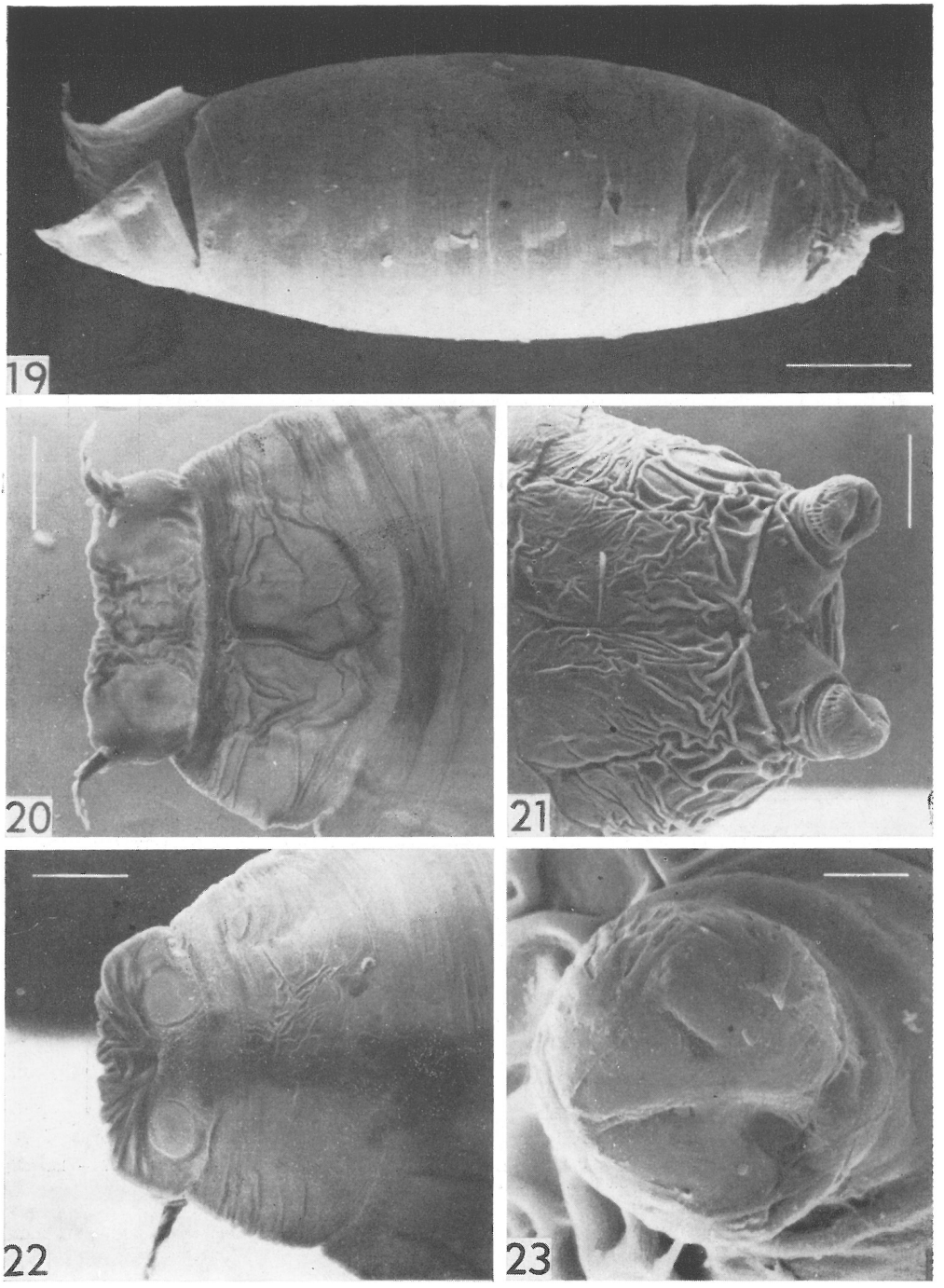

Figs. 19–23. Morphology of puparium of *Apteromyia claviventris* (STROBL) (Czechoslovakia). 19 – vacant puparium laterally; 20 – anterior part of puparium dorsally; 21 – posterior part of puparium dorsally; 22 – anterior part of puparium ventrally; 23 – posterior spiracular process caudally. Scales: Fig. 19 = 0.4mm, Figs. 20–22 = 0.1 mm, Fig. 23 = 0.02 mm. SEM micrographs by B. W. RASMUSSEN.

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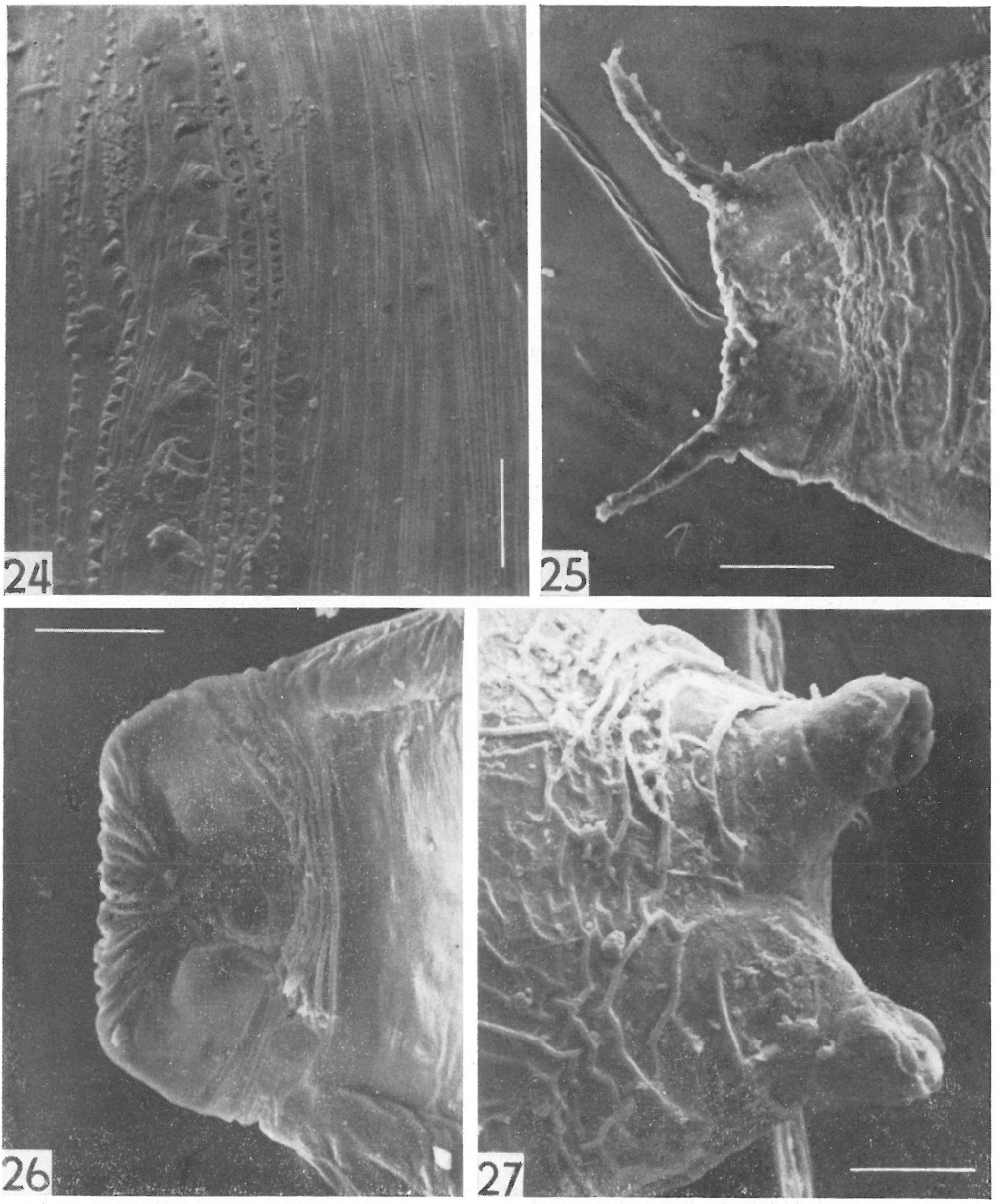

Figs. 24–27. Morphology of puparium. 24 – *Apteromyia claviventris* (STROBL), ventral hooklets and spines on segment VI; 25 – *Spelobia parapusio* (DAHL), anterior part of puparium dorsally; 26 – *Spelobia palmata* (RICHARDS), anterior part of puparium ventrally; 27 – same species, posterior part of puparium dorsally. All figures based on specimens from Czechoslovakia. Scales: Fig. 24 = 0.04 mm, Figs. 25–27 = 0.1 mm. SEM micrographs by B. W. RASMUSSEN.

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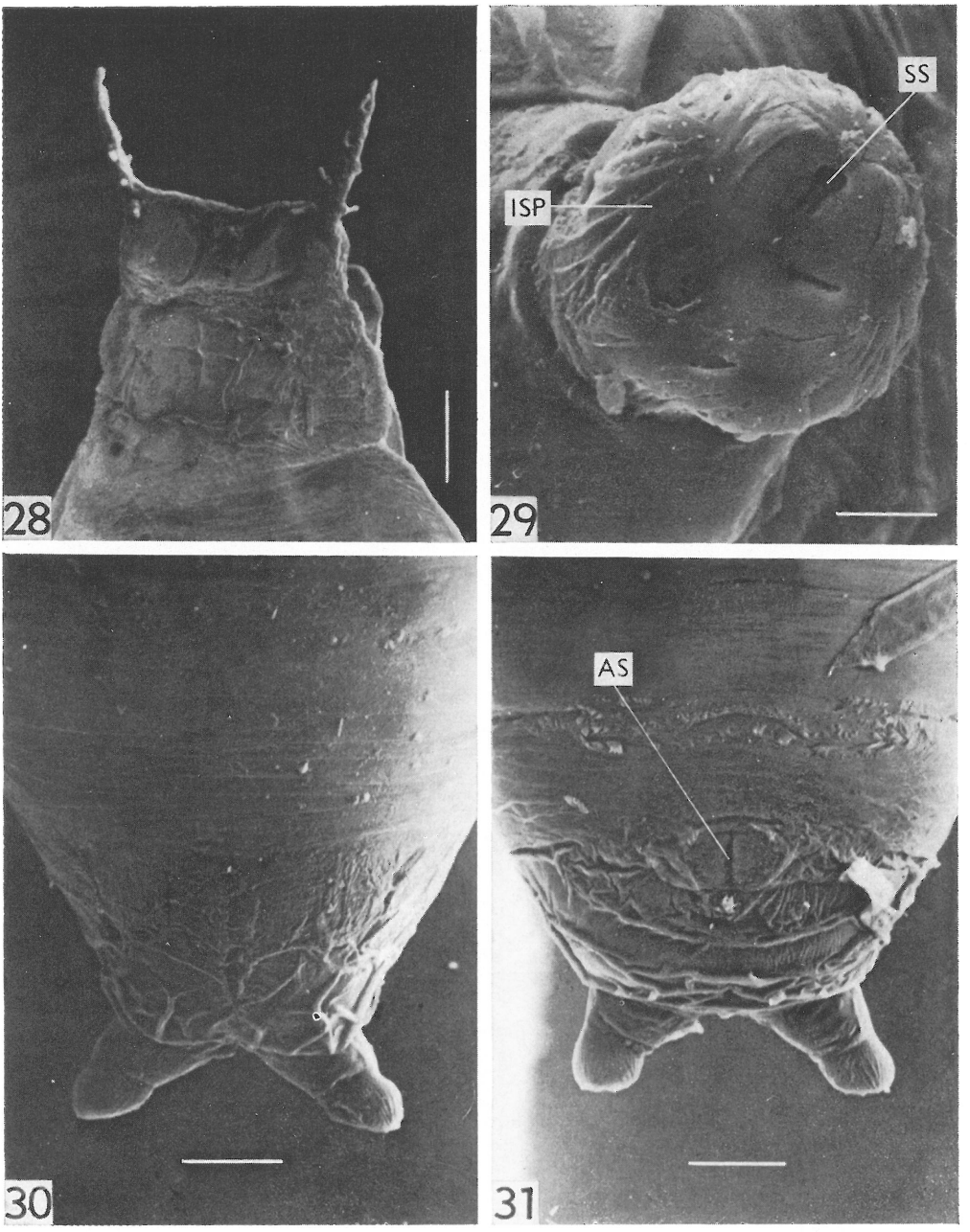

Figs. 28–31. Morphology of puparium of *Pullimosina pullula* (ZETT.) (Czechoslovakia). 28 – anterior part of puparium dorsally; 29 – posterior spiracular process caudally; 30 – posterior part of puparium dorsally; 31 – dtto ventrally. Scales: Figs. 28, 30, 31 = 0.1 mm, Fig. 29 = 0.02 mm. Abbreviations: see p. 198. SEM micrographs by B. W. RASMUSSEN.

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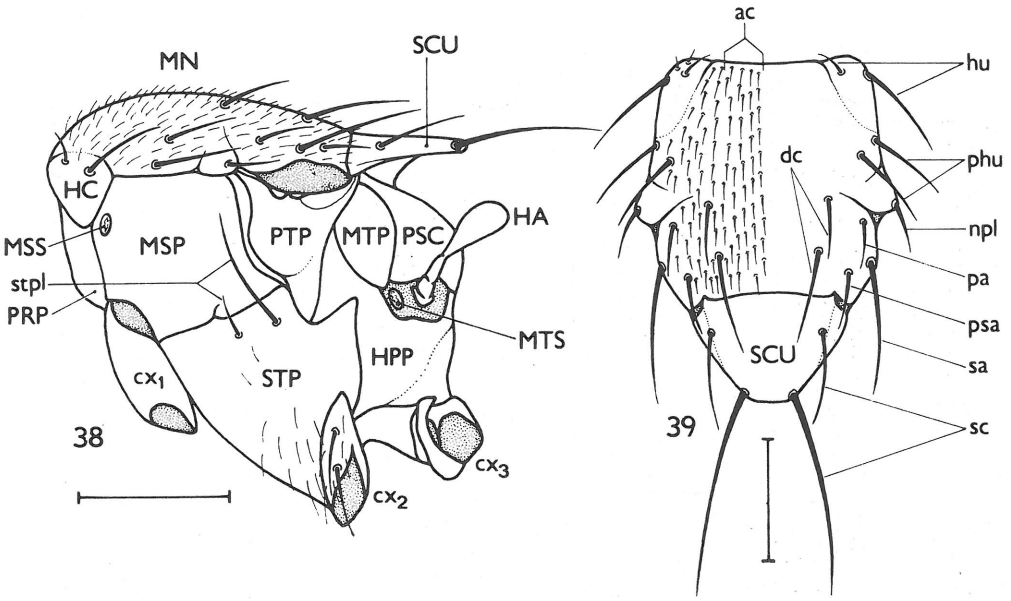

Figs. 38–39. *Limosina silvatica* (MEIGEN) (♀, Czechoslovakia), thorax. 38 – laterally; 39 – dorsally. Scale = 0.5 mm. Abbreviations: see p. 198.

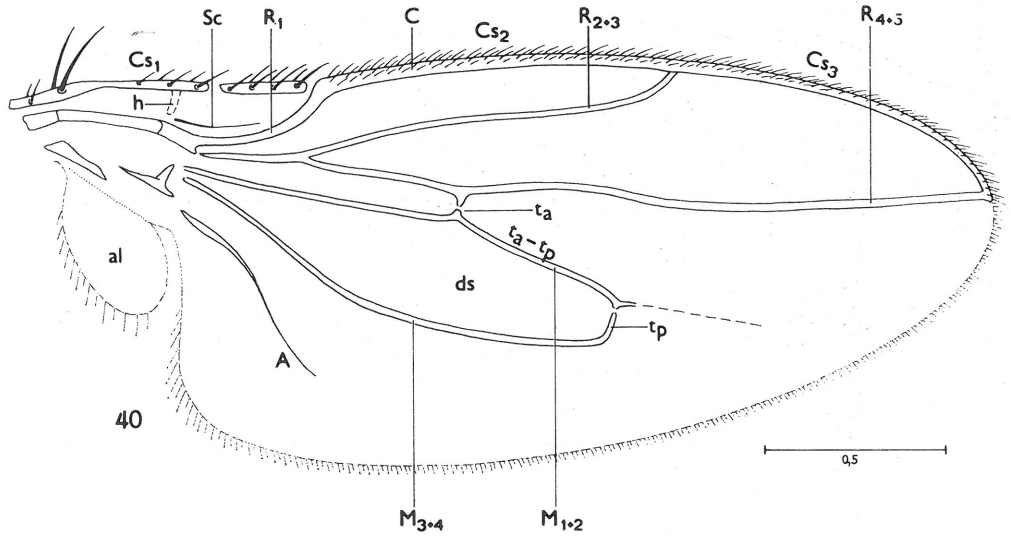

Fig. 40. *Limosina silvatica* (MEIGEN) (♂, Czechoslovakia), wing. Scale = 0.5 mm. Abbreviations: see p. 198.

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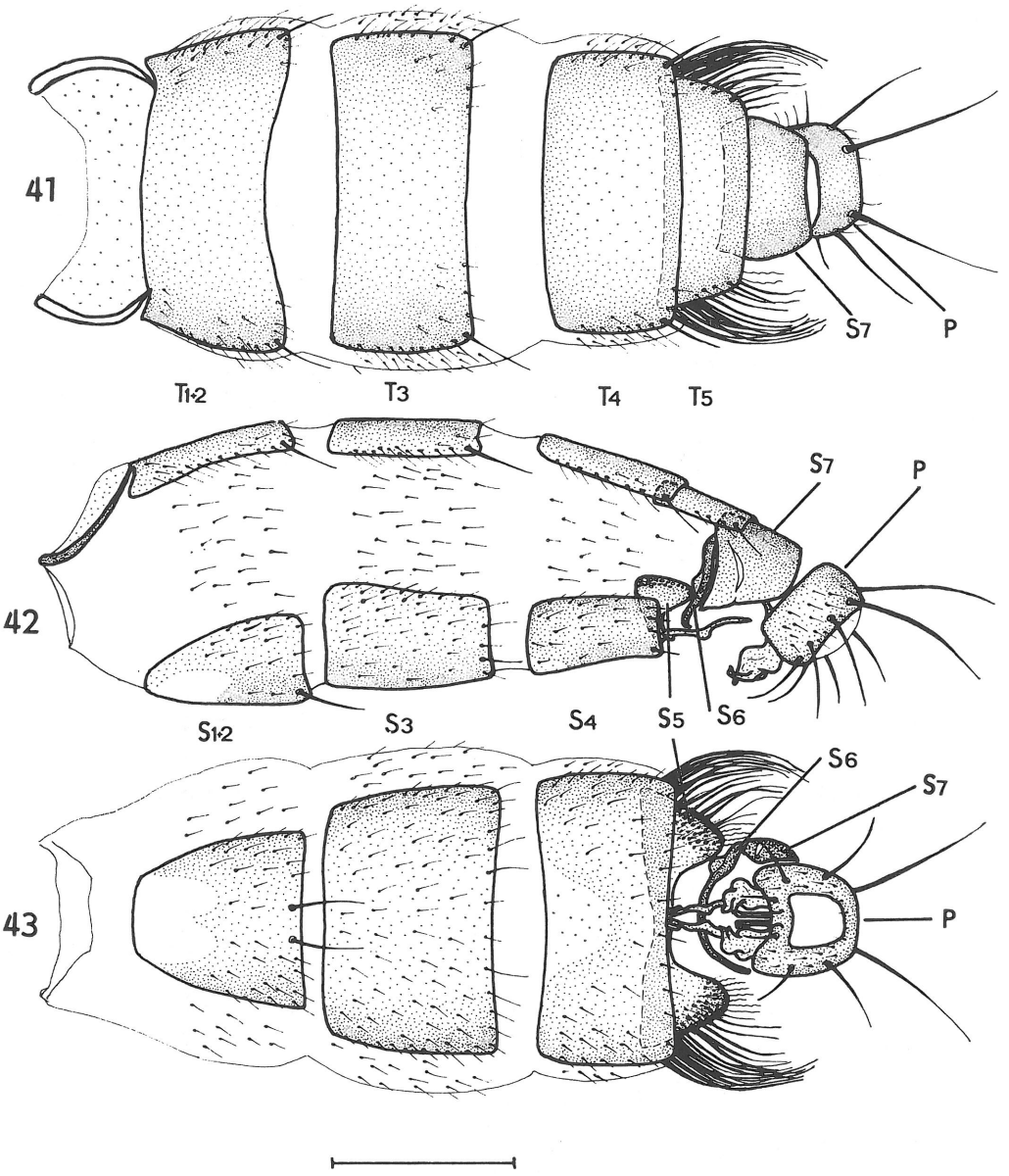

Figs. 41–43. *Limosina silvatica* (MEIGEN) (Czechoslovakia), male abdomen. 41 – dorsally; 42 – laterally; 43 – ventrally. Scale = 0.5 mm. Abbreviations: see p. 198.

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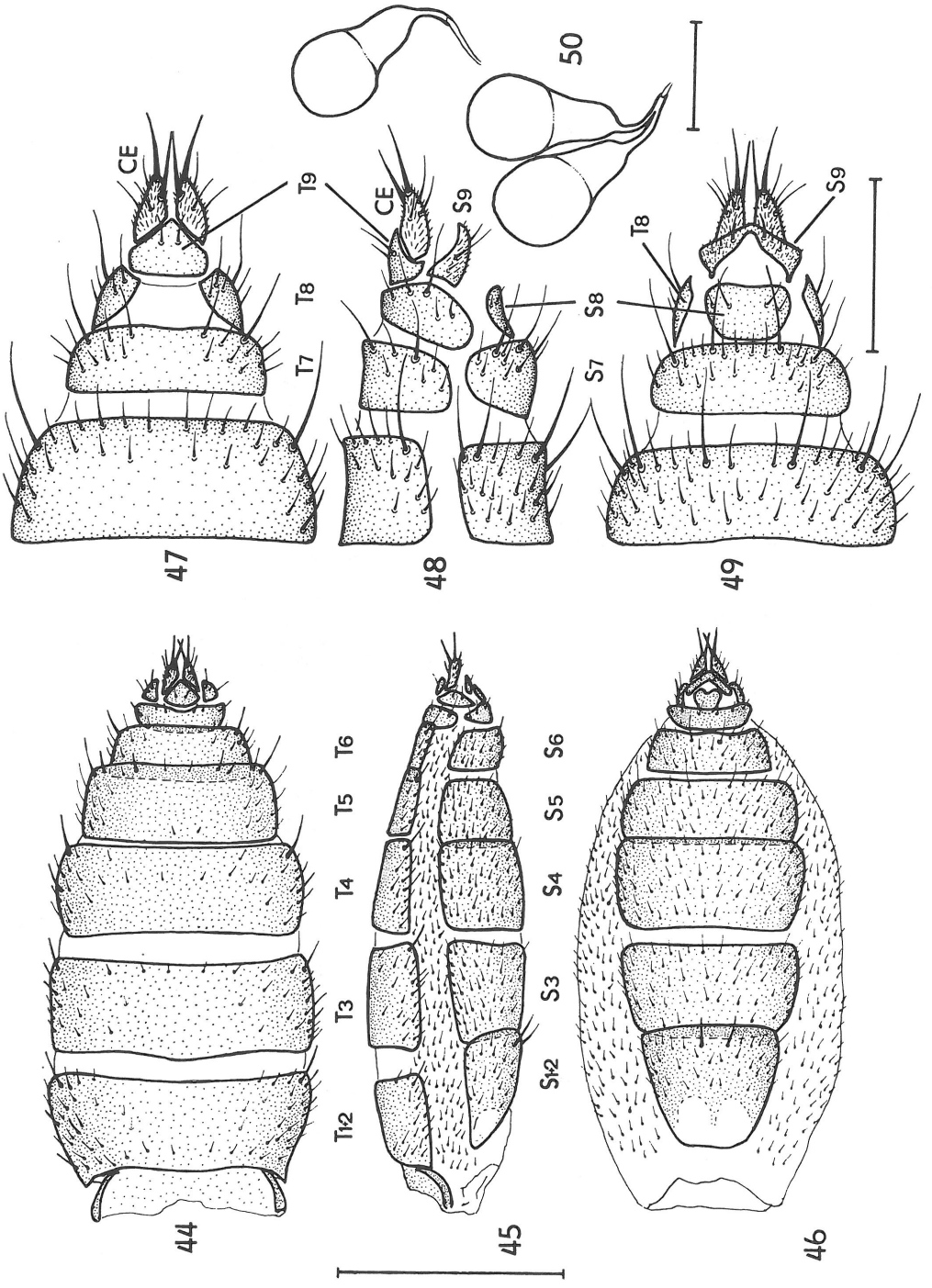

Figs. 44–50. *Limosina silvatica* (MEIGEN) (Czechoslovakia), female abdomen and postabdomen. 44 – abdomen dorsally; 45 – dtto laterally; 46 – dtto ventrally; 47 – postabdomen dorsally; 48 – dtto laterally; 49 – dtto ventrally; 50 – spermathecae. Scales: Figs. 44–46 = 1.0 mm Figs. 47–49 = 0.5 mm, Fig. 50 = 0.1 mm. Abbreviations: see p. 198.

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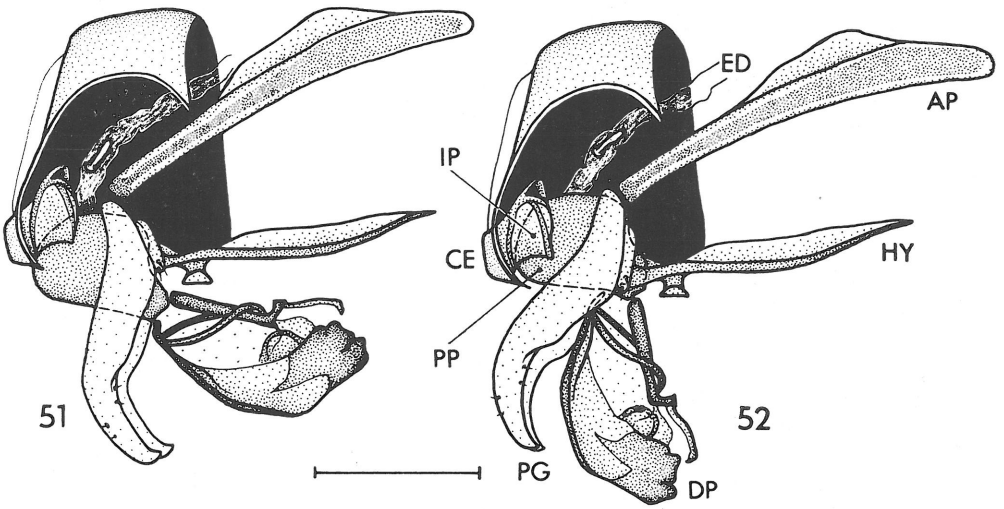

Figs. 51–52. *Spelobia clunipes* (MEIGEN) (Czechoslovakia), male genitalia laterally; telomeres and part of periandrium omitted. 51 – rest position of aedeagal complex; 52 – erected position of aedeagal complex. Scale = 0.1 mm. Abbreviations: see p. 198.

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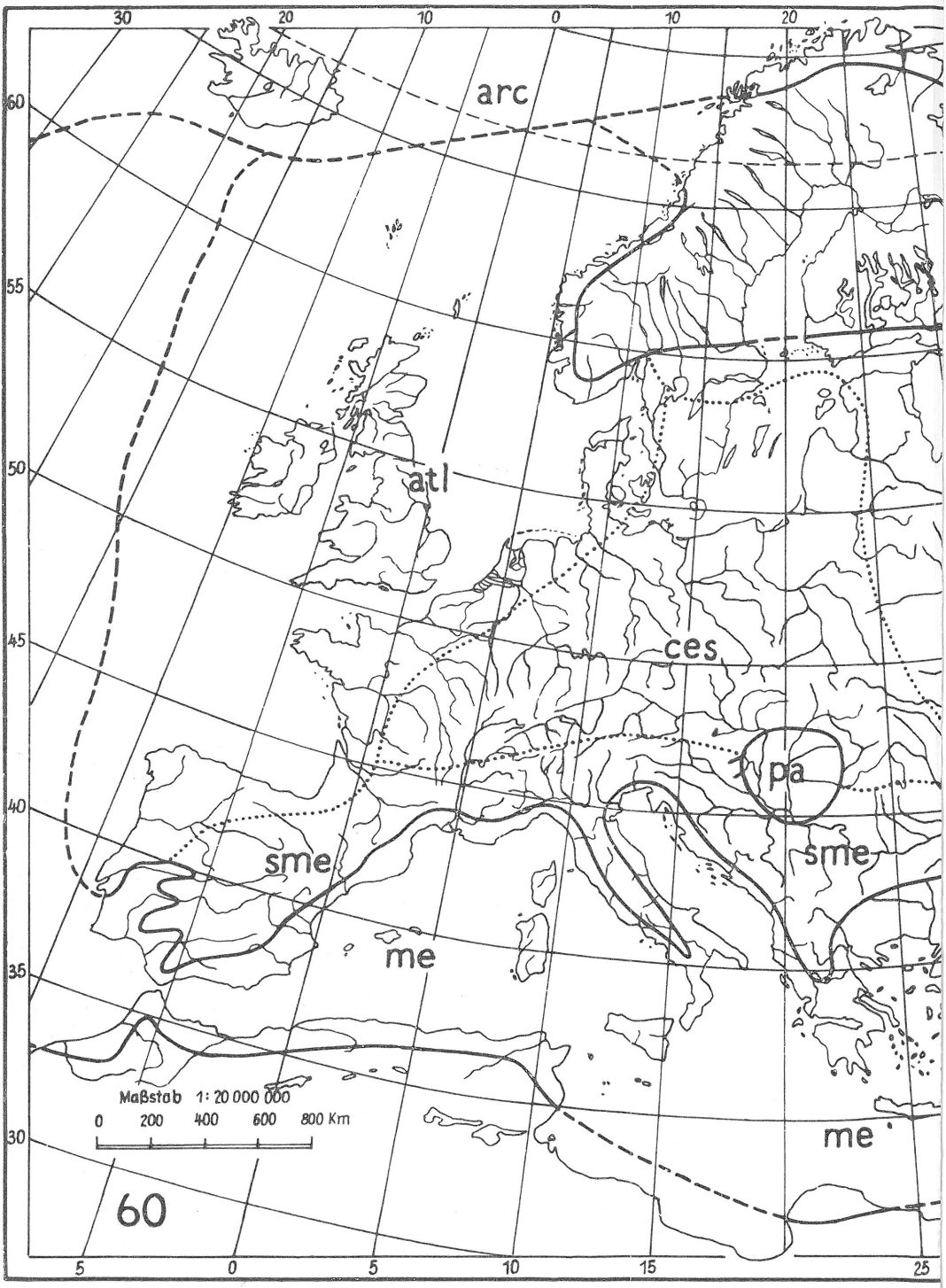

Fig. 60. Zoogeographical classification and geographical contribution of the species. arc — Arctic, atl — Atlantic, bor — Boreal, ces — Cen

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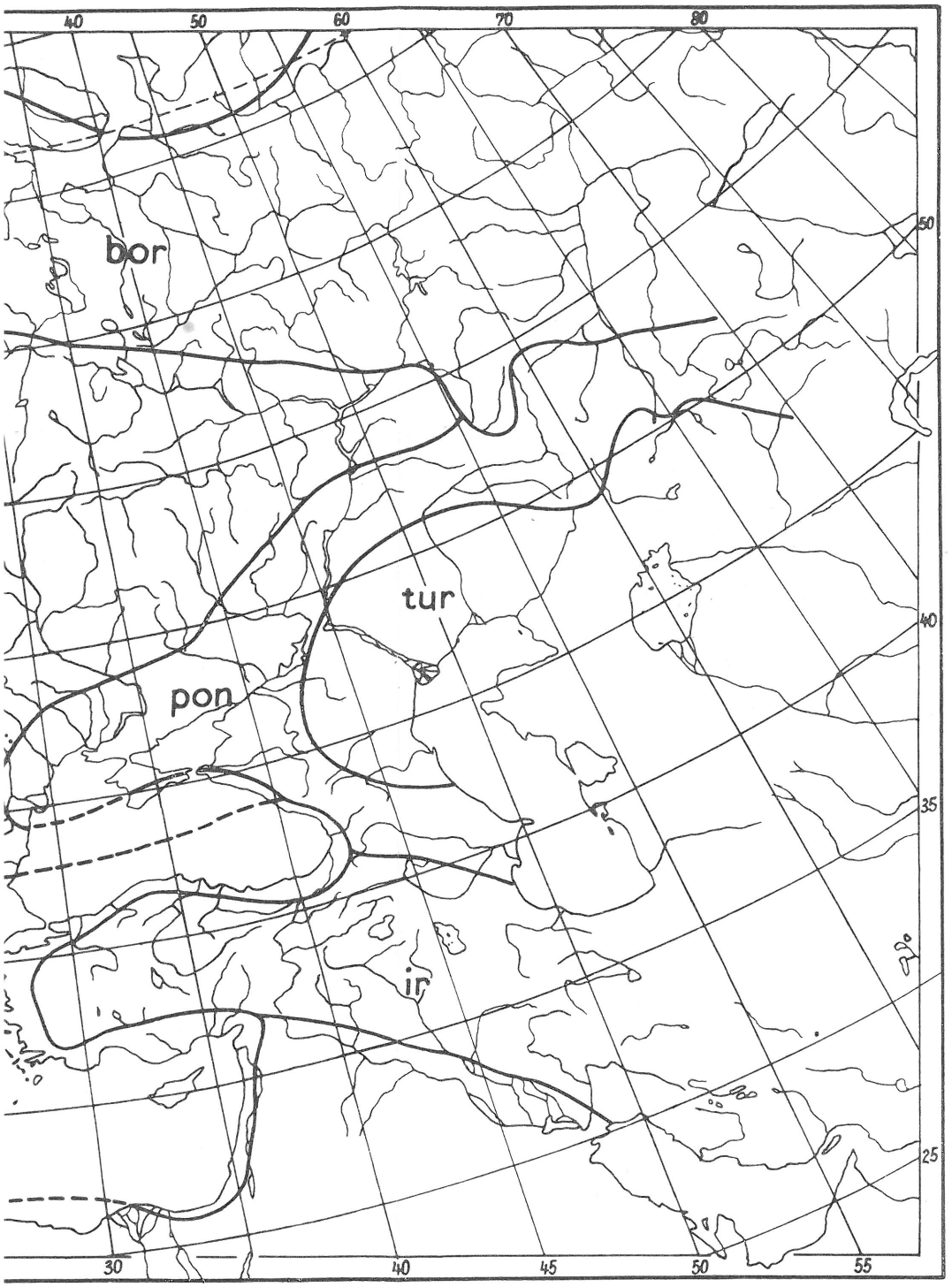

ral European (s. str.), ir — Iranian, me — Mediterranean, pa — Panonian, po — Pontic, sme — Submediterranean, tur — Turanic.

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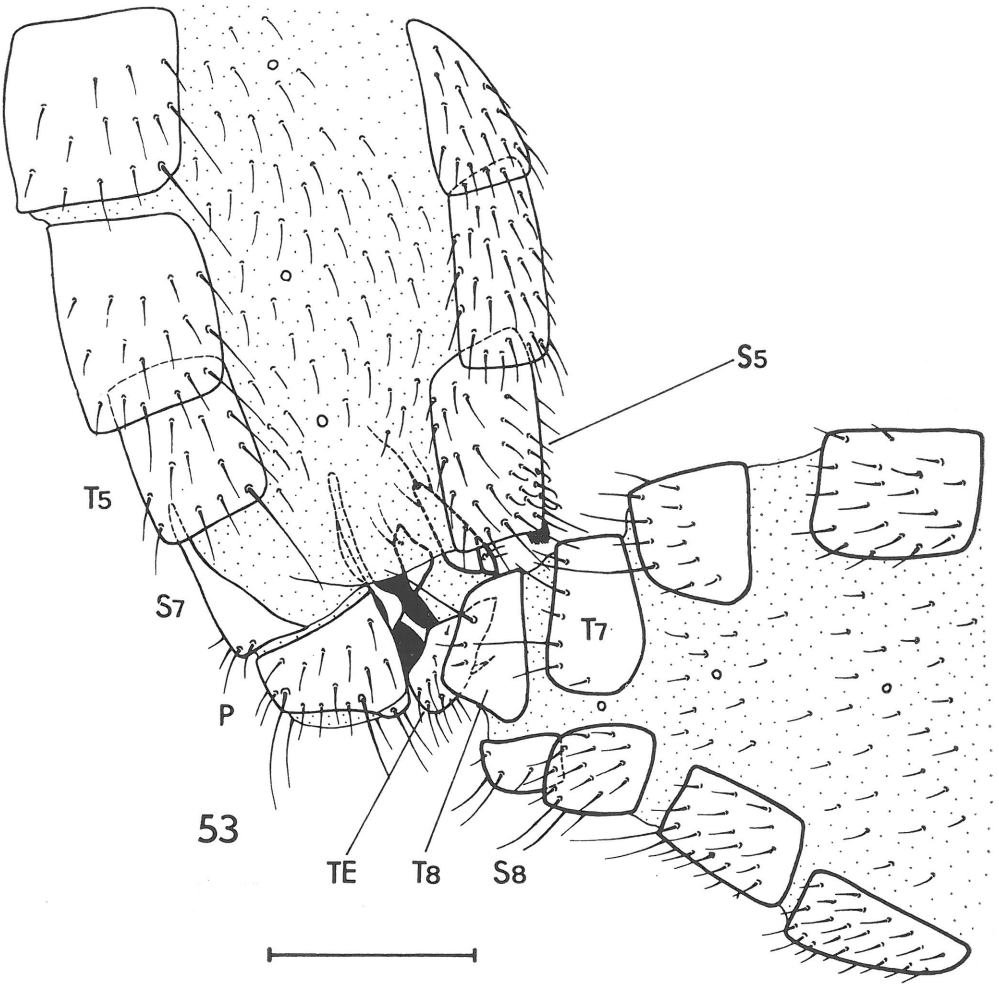

Fig. 53. *Spelobia clunipes* (MEIGEN) (Czechoslovakia) in copula—coupled postabdomina laterally. Scale = 0.2 mm. Abbreviations: see p. 198.

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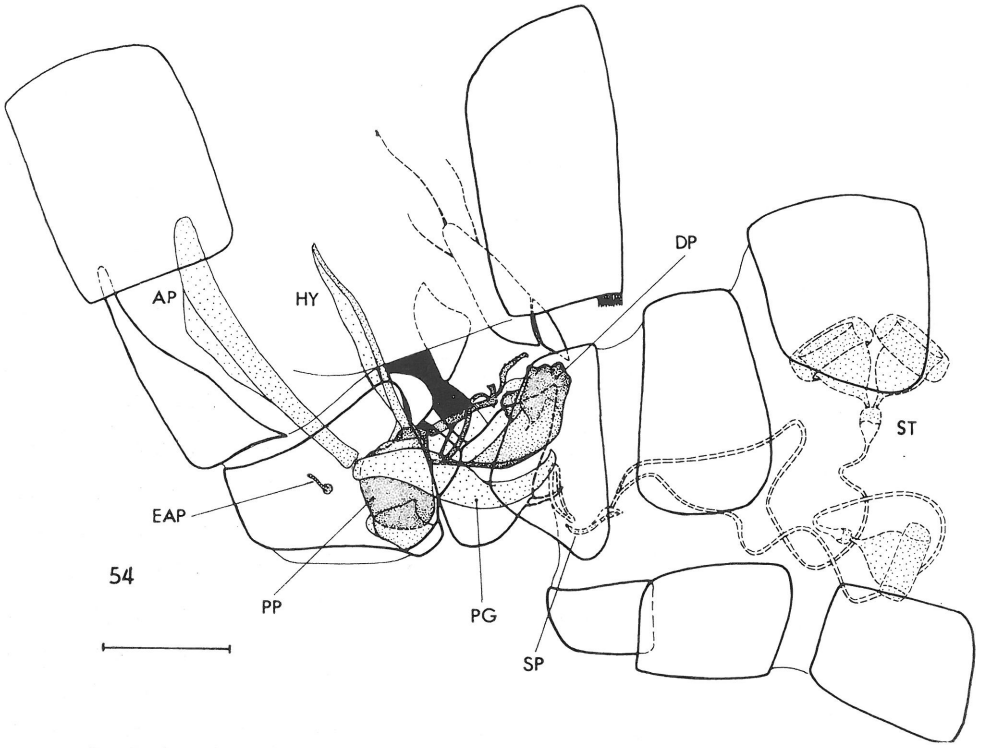

Fig. 54. *Spelobia clunipes* (MEIGEN) (Czechoslovakia) in copula — coupled postabdomina laterally. Setosity completely omitted; internal structures dotted. Scale = 0.1 mm. Abbreviations: see p. 198.

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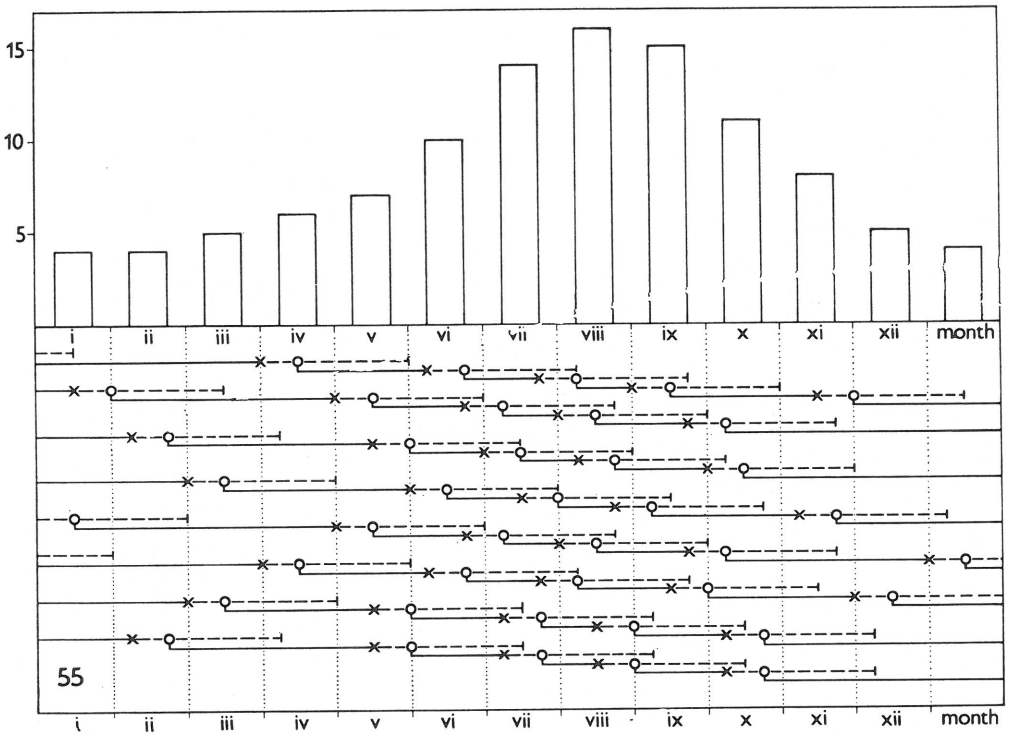

Fig. 55. A schematical diagram showing the dependence of seasonal variation (dynamics) of the occurrence of adults of *Spelobia clunipes* (MEIGEN) on the shortening of the preimaginal development during warm season. ———— preimaginal development; – – – – – survival of imago; ○ — oviposition; × — pupal emergence.

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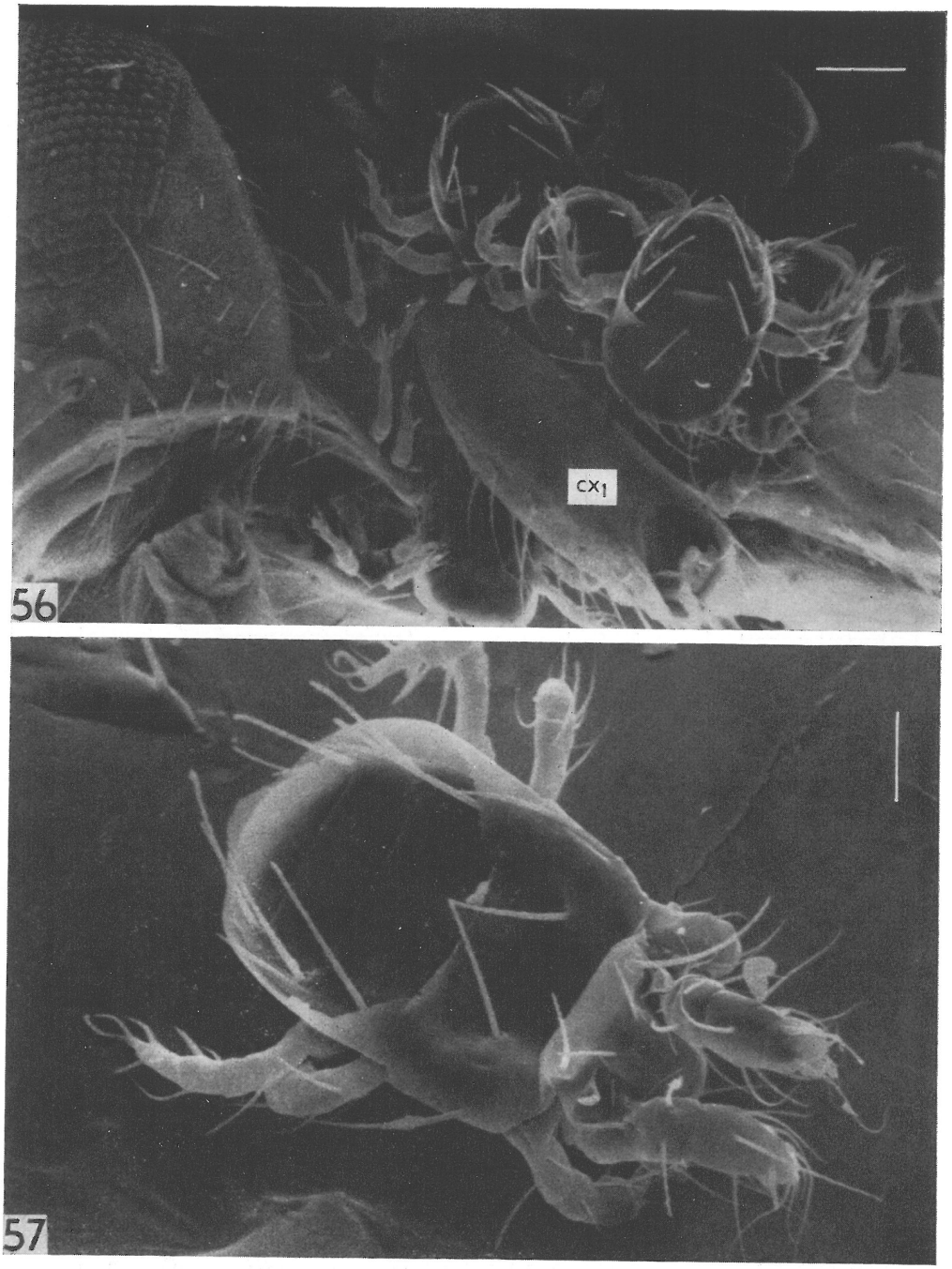

Figs. 56–57. 56 – *Pediculaster* spec., a cluster of mites attached on membrane above fore coxa of *Kimosina plumosula* (RONDANI) (♀, Spain); 57 – dtto, female phoretomorph in larger magnification. Scales: Fig. 56 = 0.1 mm, Fig. 57 = 0.04 mm. Abbreviations: see p. 198. SEM micrographs by B. W. RASMUSSEN.

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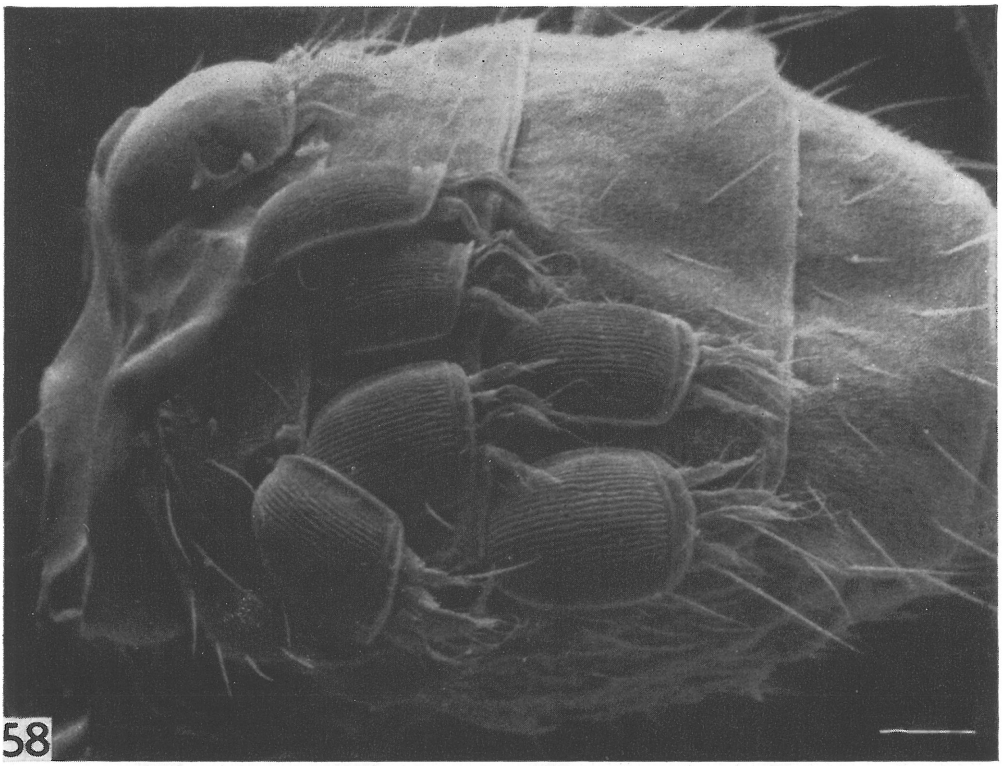

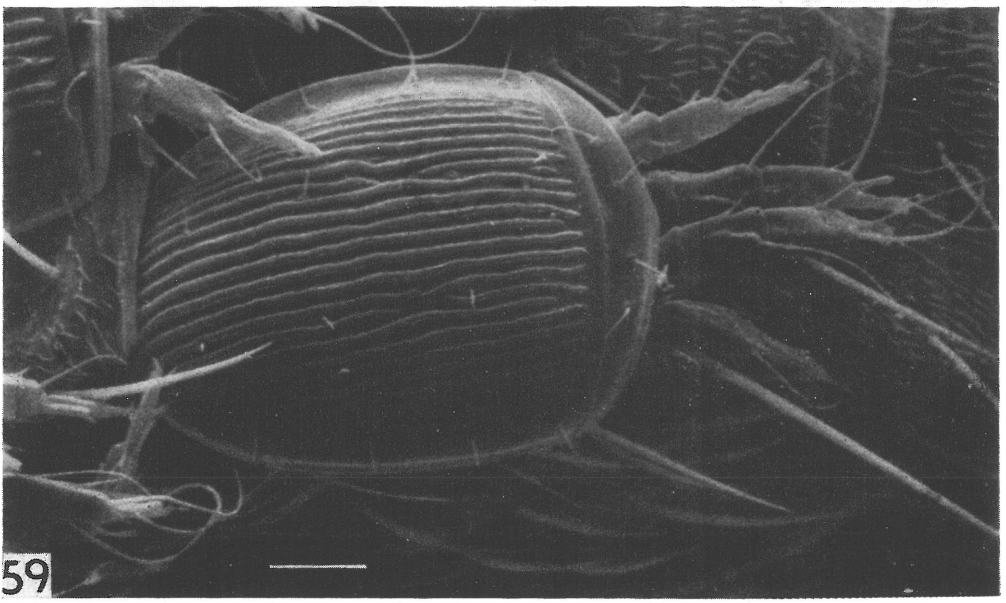

Figs. 58–59. 58 – hypopi of *Myianoetus virgatus* SCHEUCHER attached on female abdomen of *Spelobia clunipes* (MEIGEN) (Czechoslovakia); 59 – dtto, single hypopus in larger magnification. Scales: Fig. 58 = 0.1 mm, Fig. 59 = 0.04 mm. SEM micrographs by B. W. RASMUSSEN.
Fig. 60 see enclosed map.

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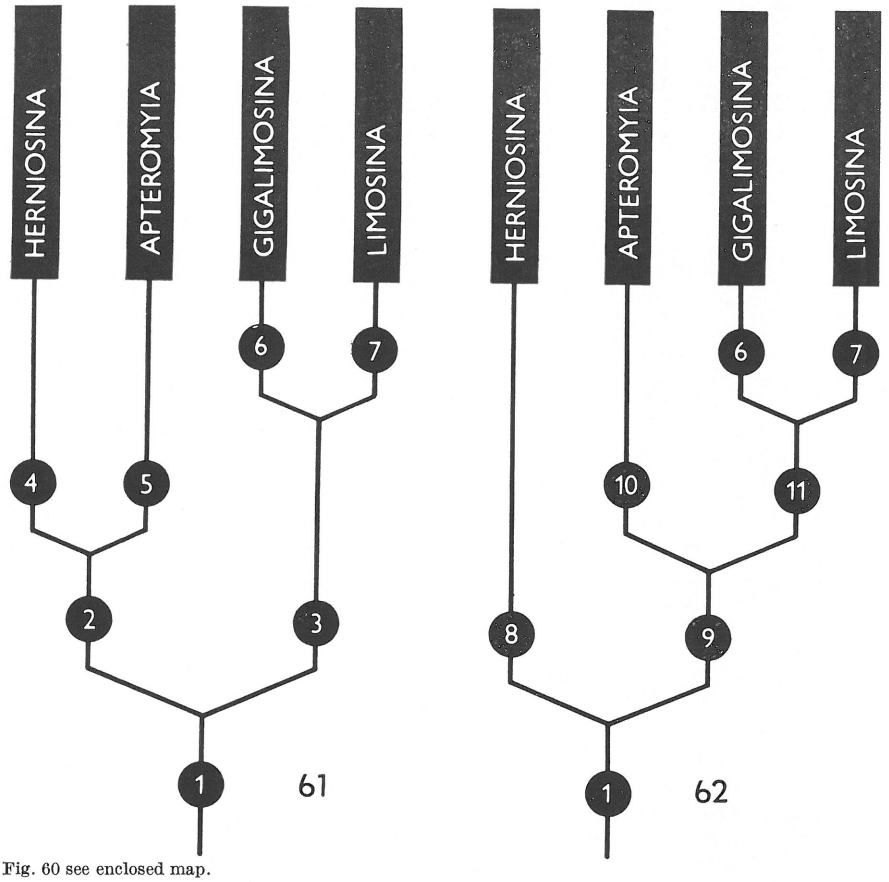

Fig. 60 see enclosed map.

Figs. 61–62. Cladograms showing the supposed interrelationship of the genera of the *Limosina* genera-group. The characters of the clades are as follows: 1 – female postabdomen short (except for *Herniosina*), female *S9* reduced (both apomorphic), *C* not extended beyond R_{4+5}, spermathecae pear-shaped (interpretation uncertain), large species, R_{4+5} sinuate, phallophore long (except for *Apteromyia*) (all plesiomorphic); 2 – phallophore projecting ventrally, male cerci projecting ventrally (apomorphic) + characters plesiomorphic to clade 3; 3 – t_2 with proximal *pd*, postgonite with long hairs (apomorphic) + characters largely plesiomorphic to clade 2; 4 – male *S1* + *2* with bulge, male *S5* reduced, postgonite short (apomorphic) + characters plesiomorphic to clade 5; 5 – male *S4* peculiarly modified, distiphallus with posterior projection, female postabdomen short (apomorphic) + characters largely plesiomorphic to clade 4; 6 – male *S3*–*S5* anteriorly incised, male *S6* and *S7* strongly developed, female *T6*–*T8* reduced, female *S7* tapered anteriorly (apomorphic) + characters plesiomorphic to clade 7; 7 – *C*-index much smaller than 1.8, t_3 with 3 bristles, male *S5* with tufts of long hairs, periandrium with very long bristles, female cerci shortly bristled (apomorphic) + characters plesiomorphic to clade 6; 8 – as in clade 4, phallophore projecting ventrally (apomorphic) + characters plesiomorphic to clade 9; 9 – postgonite long haired, female postabdomen short + characters plesiomorphic to clade 8; 10 – telomere bipartite, distiphallus enlarged, male *S4* peculiarly modified (apomorphic) + characters plesiomorphic to clade 11; 11 – t_2 with proximal *pd*, hypandrium long and slender, ejaculatory apodeme absent (apomorphic) + characters largely plesiomorphic to clade 10.

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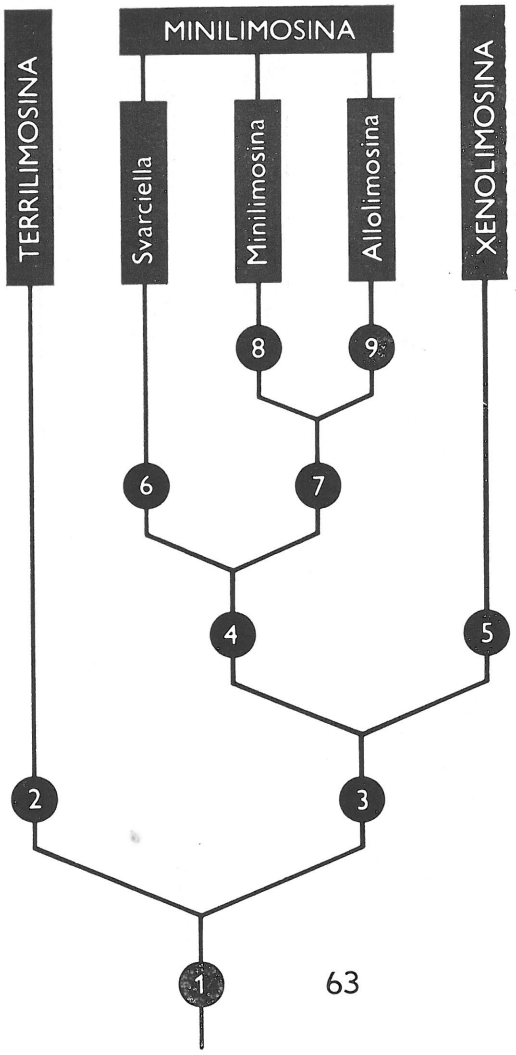

Fig. 63. A cladogram showing the supposed interrelationship of the genera and subgenera of the *Minilimosina* genera-group. The characters of the clades are as follows: 1 – phallophore relatively short, small species (all apomorphic), *C* extended beyond R_{4+5} (interpretation uncertain), t_2 with reduced chaetotaxy, female postabdomen long, narrow, telescopically retractile, female *S9* large and broad, female cerci long and long sinuate haired (all plesiomorphic); 2 – alula enlarged, periandrium with a long dorsolateral bristle, phallophore strongly reduced (apomorphic) + characters largely plesiomorphic to clade 3; 3 – *av* in the middle of t_2 absent, male cerci reduced, female *S8* more reduced (except for sg. *Svarciella*) (apomorphic) + characters largely plesiomorphic to clade 2; 4 – wing smaller, R_{4+5} curved or indistinctly sinuate, t_3 without *d* bristle, female *T9* narrow (apomorphic) + characters plesiomorphic to clade 5; 5 – only 1 *stpl*, phallophore with pre-epiphallus, distiphallus complicated (apomorphic) + characters largely plesiomorphic to clade 4; 6 – *pvt* absent, 4–6 rows of *ac* hairs, *T1* + *2* long (apomorphic) + characters largely plesiomorphic to clade 7; 7 – only 1 *dc*, telomere smaller and flat, hypandrium shorter, female *S8* strongly reduced (apomorphic) + characters plesiomorphic to clade 6; 8 – male f_2 with ventral row of short bristles, telomere with posterior robust spine (apomorphic) + characters largely plesiomorphic to clade 9; 9 – discal cell shortened, hypandrium strongly reduced, female *S8* strongly reduced or absent, female *S9* with anterior incision (apomorphic) + characters largely plesiomorphic to clade 8.

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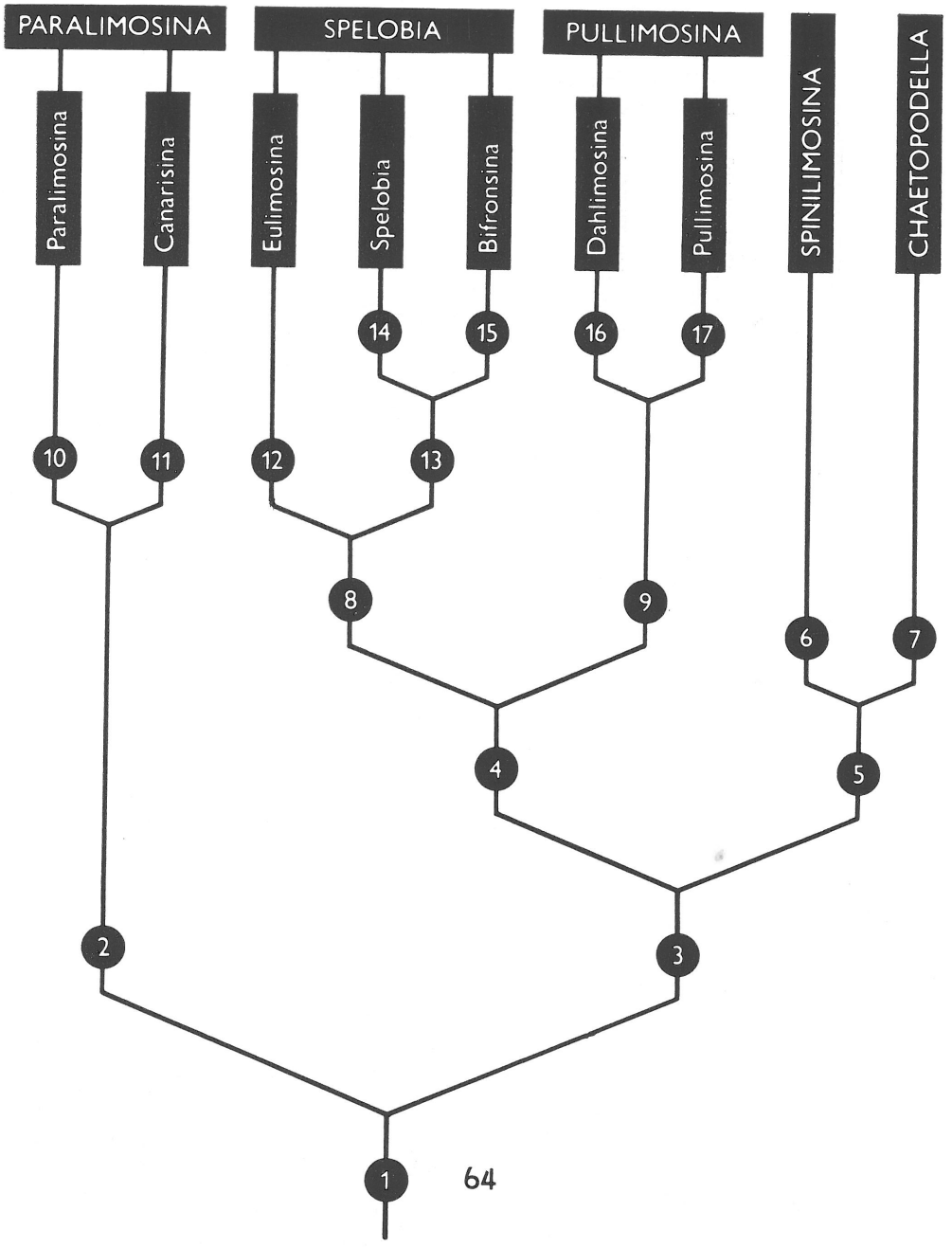

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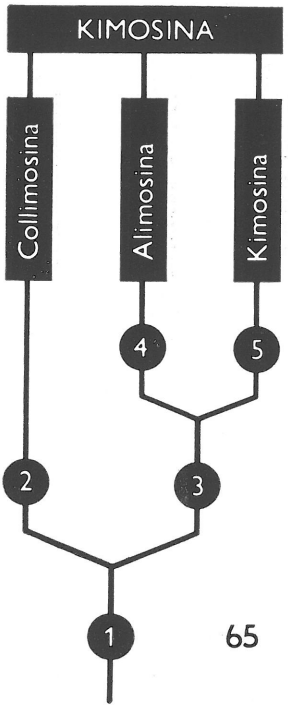

Fig. 65. A cladogram showing the supposed interrelationship of the subgenera of the genus *Kimosina* gen. nov. The characters of the clades are as follows: 1 — 3—5 *dc*, male cerci large, with robust intraperiandrial sclerite, telomere bipartite, distiphallus membraneous, with small dorsal sclerite connected with hypandrium, female *S8* reduced to 1—3 small sclerites (all apomorphic); 2 — wing short and broad, periandrium with a row of lateral bristles at ventral margin, female *S7* large, with oval posterior membraneous area, female *S9* tripartite (apomorphic) + characters largely plesiomorphic to clade 3; 3 — intraperiandrial sclerite with mesolobus, phallophore somewhat produced ventrally, distiphallus finely haired, postgonite angularly bent (apomorphic) + characters plesiomorphic to clade 2; 4 — wing sexually dimorphic, *S1* + *2* modified, *S3* very long, female *S9* long (apomorphic) + characters plesiomorphic to clade 5; 5 — Cs_1 long and sparsely haired, female cercus with a short, thick spine (apomorphic) + characters largely plesiomorphic to clade 4.

◀ Fig. 64. A cladogram showing the supposed interrelationship of the genera and subgenera of the *Spelobia* genera-group. The characters of the clades are as follows: 1 — t_2 dorsally with numerous bristles, female postabdomen short, spectacles-shaped sclerite distinctly developed (all apomorphic), female cerci short but sinuate haired, distiphallus well sclerotized (all plesiomorphic); 2 — telomere low and bilobed, phallophore reduced (apomorphic), scutellum short and wide (interpretation uncertain) + characters largely plesiomorphic to clade 3; 3 — R_{4+5} straight or regularly curved (except for some *Spelobia*), dorsolateral bristle on periandrium (except for sg. *Dahlimosina* and 1 species of *Spelobia*) (apomorphic), scutellum longer (interpretation uncertain) + characters largely plesiomorphic to clade 2; 4 — tendency to brachyptery, spermathecae usually tyre-shaped (apomorphic) + characters largely plesiomorphic to clade 5; 5 — telomere bilobed, phallophore more or less projecting ventrally, distiphallus very complicated (apomorphic) + characters largely plesiomorphic to clade 4; 6 — R_{4+5} strongly bent to *C*, discal cell short, male *S5* with a comb of spines, spermathecae dish-shaped (apomorphic), 1 *dc* (interpretation uncertain) + characters plesiomorphic to clade 7; 7 — scutellum velvety black, mt_2 with *av* bristle (apomorphic), 3—4 *dc* (interpretation uncertain) + characters plesiomorphic to clade 6; 8 — alula enlarged (except for sg. *Bifronsina*), male *S5* with posteromedial comb of dense spines (apomorphic) + characters largely plesiomorphic to clade 9; 9 — *pvt* reduced, additional sclerite(s) between female *S8* and *S9* present, R_{4+5} upcurved and overpassed by *C* (apomorphic) + characters plesiomorphic to clade 8; 10 — frons with velvety black M-shaped mark, hypandrium with ventral appendage, phallophore reduced, female *S9* long and anteriorly incised (apomorphic) + characters plesiomorphic to clade 11; 11 — telomere with ventral robust spines, distiphallus spinulate, *S5* modified (apomorphic) + characters largely plesiomorphic to clade 10; 12 — male cerci reduced, *av* below middle of t_2 absent, spectacles-shaped sclerite peculiarly modified (apomorphic), telomere simple (plesiomorphic); 13 — telomere with single robust ventral spine and micropubescence on outer side (apomorphic) + characters plesiomorphic to clade 12; 14 — alula large (apomorphic), telomere shorter (interpretation uncertain) + characters plesiomorphic to clade 15; 15 — 3 *dc*, hypandrium reduced, distiphallus complicated (apomorphic), telomere longer (interpretation uncertain), alula small (plesiomorphic); 16 — 1 *dc*, scutellum with additional small setulae, periandrium secondarily without any long bristle (apomorphic) + characters plesiomorphic to clade 17; 17 — R_{4+5} far overpassed by *C*, distiphallus more complicated, female *S8* small and additional sclerite well developed (apomorphic) + characters plesiomorphic to clade 16.

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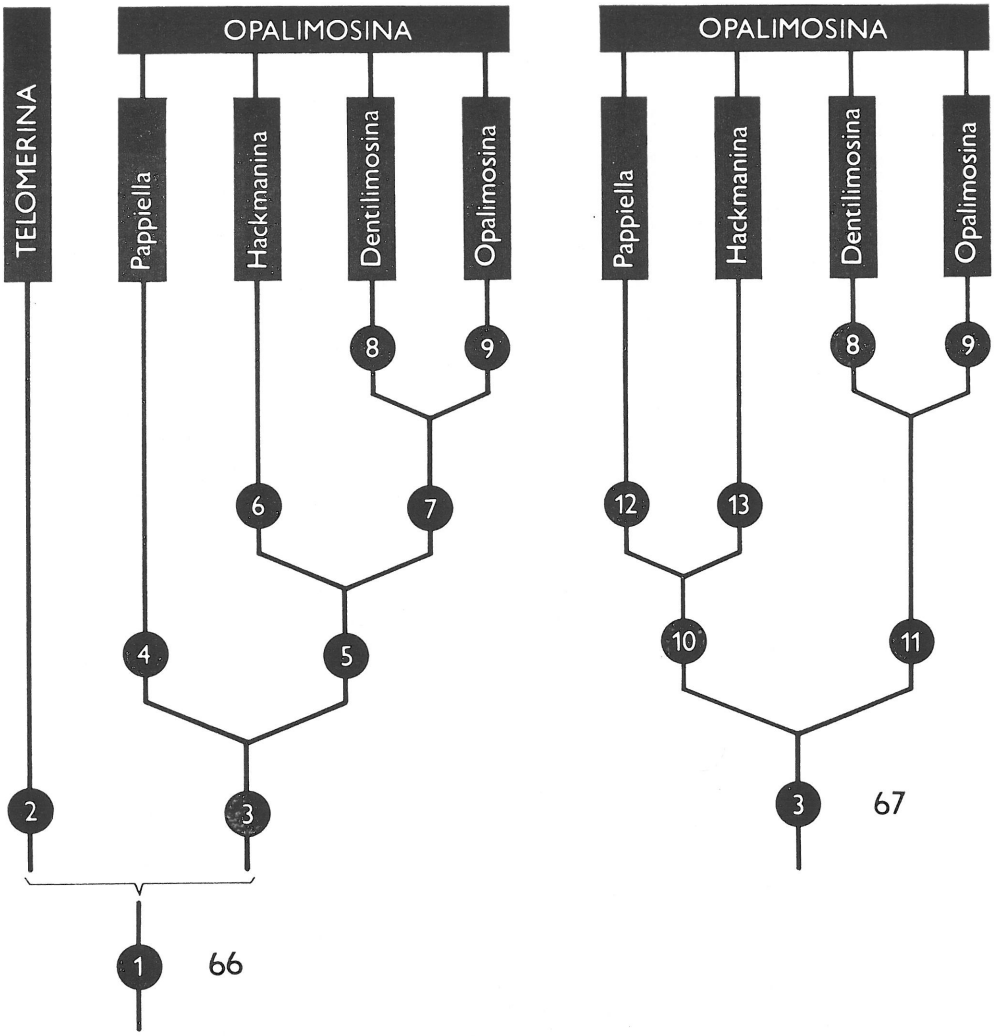

Figs. 66–67. Cladograms showing the supposed interrelationship of the subgenera of the genus *Telomerna* gen. nov. and *Opalimosina* gen. nov. The characters of the clades are as follows: 1 – a long row of *ads*, eye small and flat, thorax dusted and dull, tendency to reduction of setosity of female cerci (apomorphicr), *pvt* well developed (plesiomorphic); 2 – subanal plate and intraperiandrial sclerite absent, telomere long (high) and slender, postgonite pubescent, female *S9* of complex form, spermathecae usually with slender terminal projection (apomorphic); 3 – large epiphallus, female *T9* small, often fused with cerci, female *S8* small, female cerci short, with reduced setae (apomorphic), ejaculatory apodeme present, telomere small and simple (plesiomorphic); 4 – distiphallus with double and long posteroventral projection, postgonite slender and curved several times, female *T7* with flat lateral appendages, female *T8* divided, female *S6* very long (apomorphic), phallophore with bifurcate epiphallus (interpretation uncertain); 5 – epiphallus simple (interpretation uncertain) + characters largely plesiomorphic to clade 4; 6 – an additional seta between *occi* and *occe*, postgonite bare, female *T9* enlarged, female *S9* bipartite (apomorphic), female cercus with 2 thick, short spines (interpretation uncertain) + characters plesiomorphic to clade 7; 7 – female *S8* small (apomorphic), female cercus with small and short setulae (interpretation uncertain) + characters largely plesiomorphic to clade 6; 8 – scutellum with small additional seta in front of basal *sc*, epiphallus very long and slender, female *S7* large (apomorphic) + characters plesiomorphic to clade 9; 9 – male *S5* with peculiar cuticular structures on posterior margin, distiphallus of more complex form, female *T8* with posteroventral projections, female *S8* modified, t_3 with ventropreapical curved spine (apomorphic) + characters plesiomorphic to clade 8; 10 – an additional seta between *occi* and *occe*, female *S9* double (bipartite) (apomorphic), female cerci with short, spine-like bristles (interpretation uncertain) + characters plesiomorphic to clade 11; 11 – female *T9* fused with cerci (apomorphic), female cerci with small setulae (interpretation uncertain) + characters plesiomorphic to clade 10; 12 – as in clade 4, epiphallus bifurcate (interpretation uncertain) + characters plesiomorphic to clade 13; 13 – as in clade 6, epiphallus simple (interpretation uncertain) + characters plesiomorphic to clade 12.

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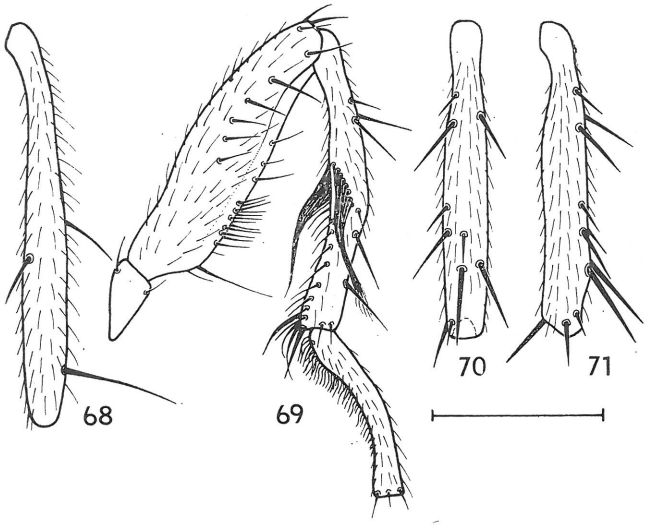
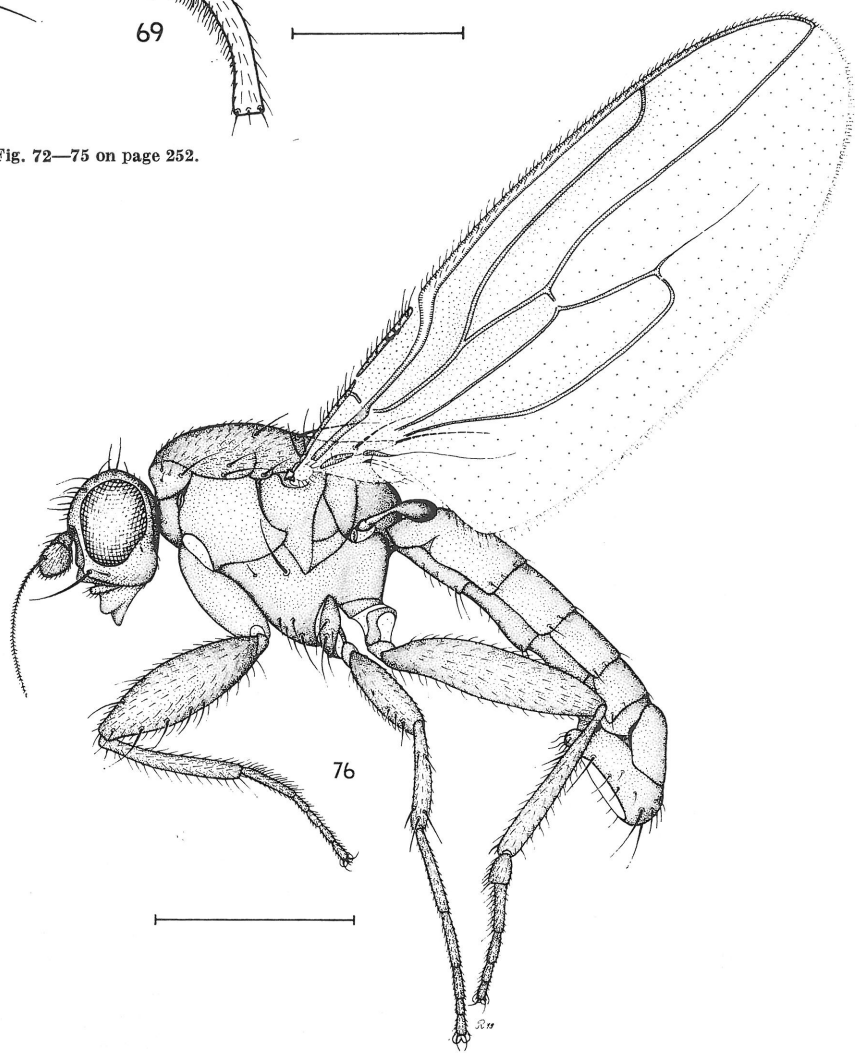


Fig. 72—75 on page 252.



Figs. 68—71. *Limosina silvatica* (MEIGEN) (Czechoslovakia). 68 — female t_3 anteriorly; 69 — male trochanter, f_2, t_2 and mt_2 anteriorly; 70 — female t_2 dorsally, 71 — dtto anteriorly. Scale = 0.5 mm.

Fig. 76. *Gigalimosina flaviceps* (ZETTERSTEDT), male (Czechoslovakia). Scale = 1.0 mm.

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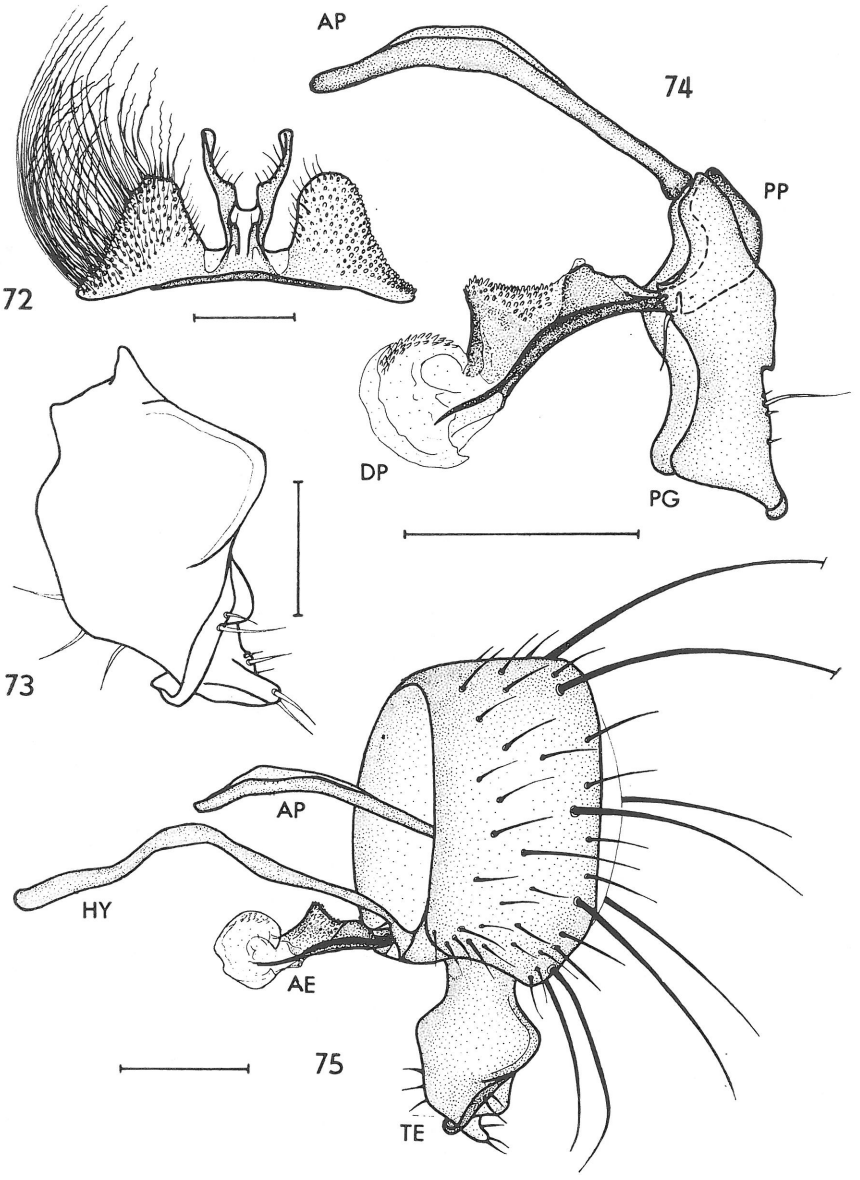
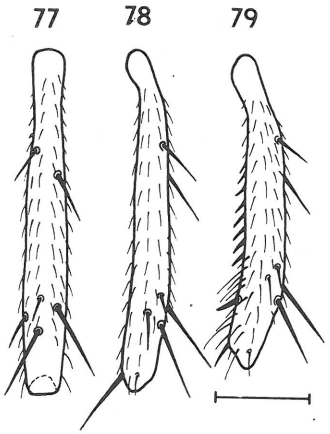
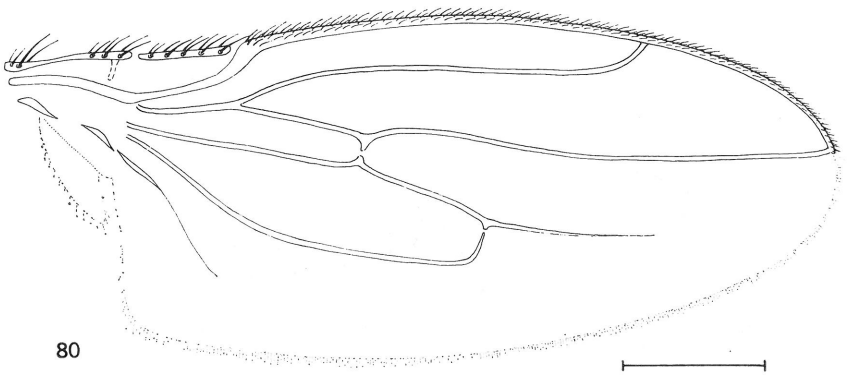


Figs. 72—75. *Limosina silvatica* (MEIGEN) (♂, Czechoslovakia). 72—*S5* (setosity partly omitted); 73 — telomere; 74 — aedeagal complex laterally; 75 — male genitalia laterally. Scales: Fig. 72 = 0.2 mm, Fig. 73 = 0.05 mm, Figs. 74—75 = 0.1 mm. Abbreviations: see p. 198.

DOI: 10.21248/contrib.entomol.32.2.195-282





Figs. 77—79. *Gigalimosina flaviceps* (ZETTERSTEDT) (Czechoslovakia). 77 — female t_2 dorsally; 78 — dtto anteriorly; 79 — male t_2 anteriorly. Scale = 0.2 mm.

Fig. 80. *Gigalimosina flaviceps* (ZETTERSTEDT) (♂, Czechoslovakia), wing. Scale = 0.5 mm.

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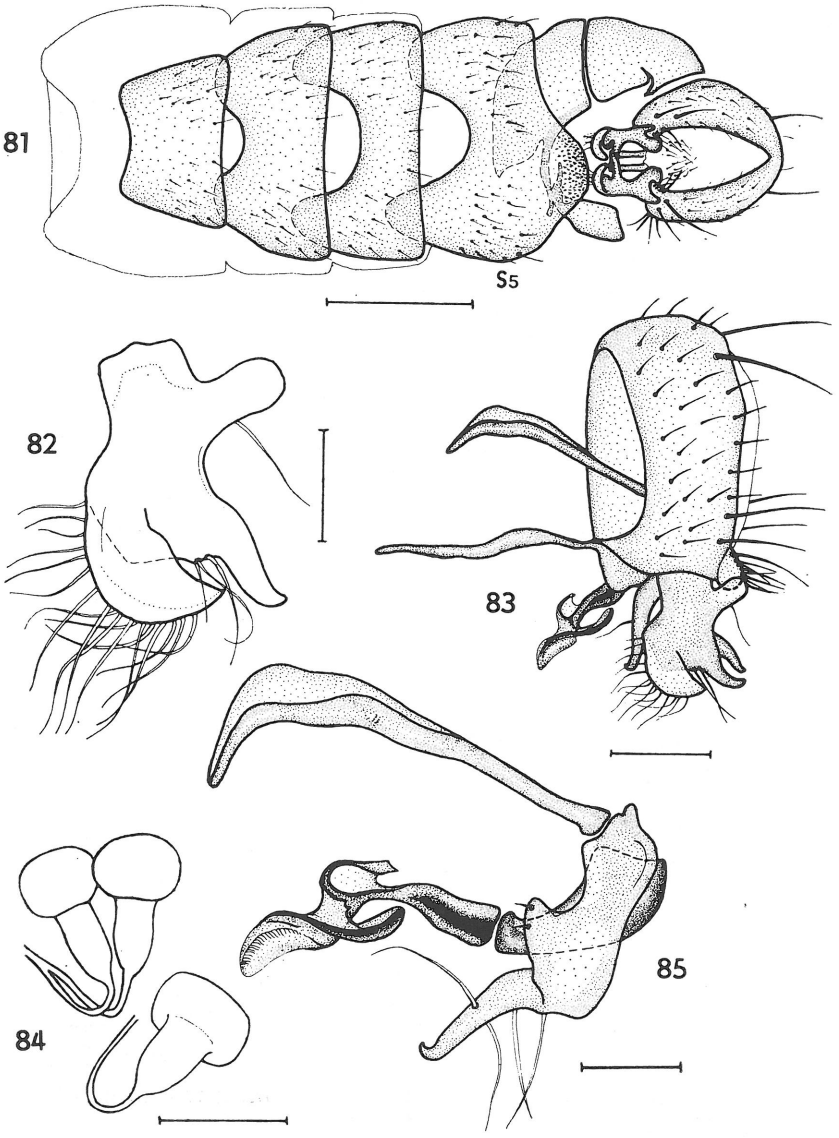
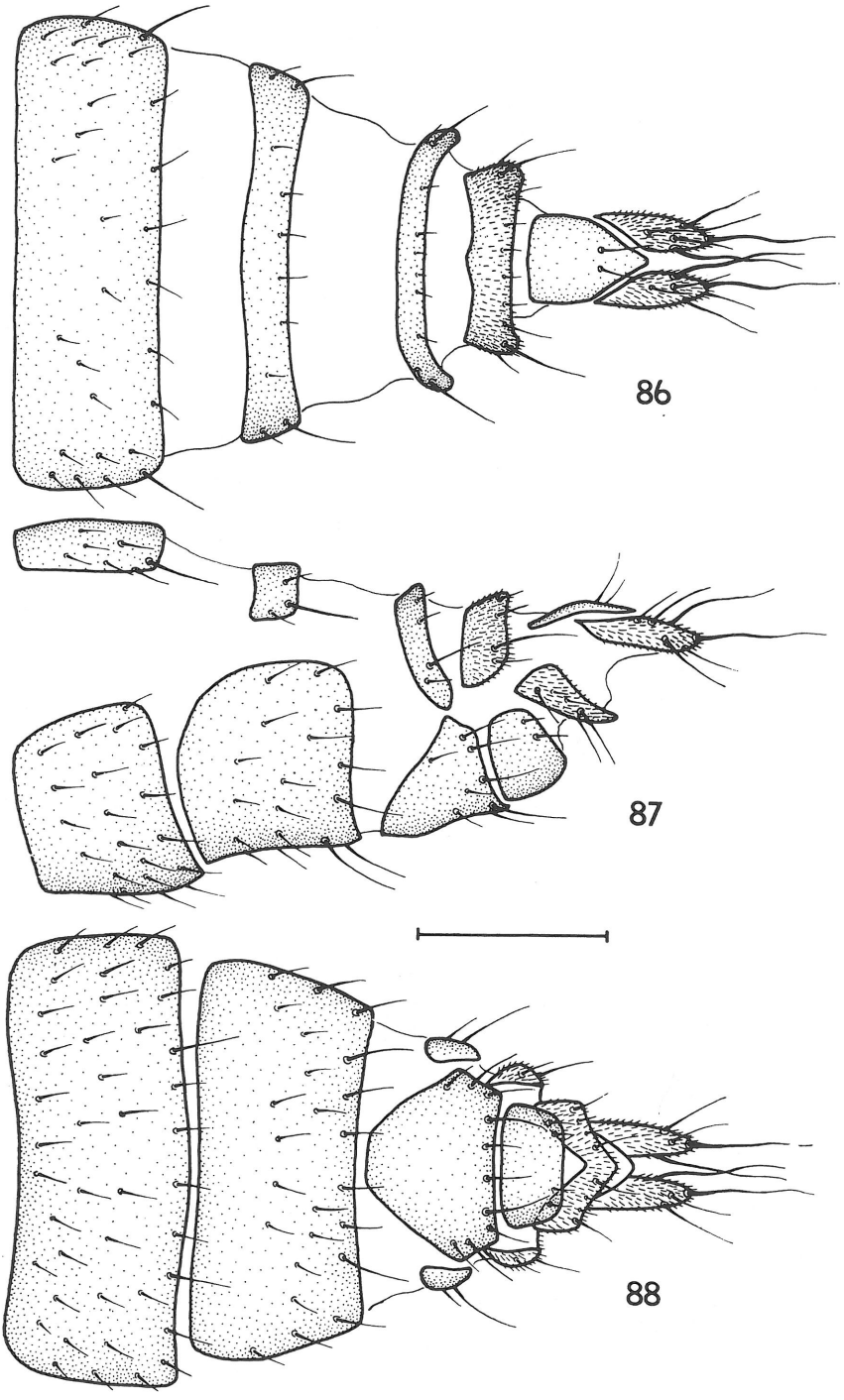


Figs. 81—85. *Gigalimosina flaviceps* (ZETTERSTEDT) (Czechoslovakia). 81 — male abdomen ventrally; 82 — telomere; 83 — male genitalia laterally; 84 — spermathecae; 85 — aedeagal complex laterally (only left postgonite figured). Scales: Fig. 81 = 0.5 mm, Figs. 82, 84, 85 = 0.1 mm, Fig. 83 = 0.2 mm. Abbreviations: see p. 198.

DOI: 10.21248/contrib.entomol.32.2.195-282



Figs. 86–88. *Gigalimosina flaviceps* (ZETTERSTEDT) (♀, Czechoslovakia). 86 – postabdomen (+5th segment) dorsally; 87 – dtto laterally; 88 – dtto ventrally. Scale = 0.5 mm

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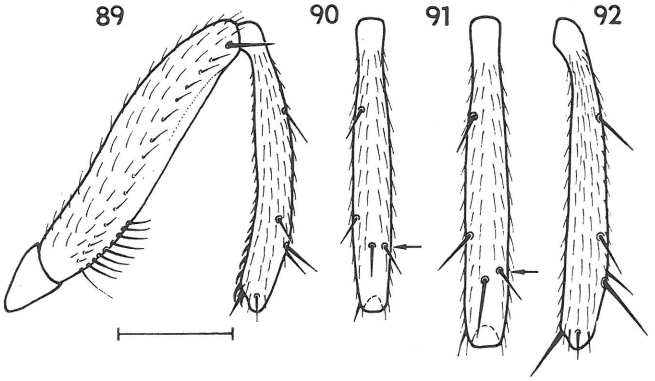

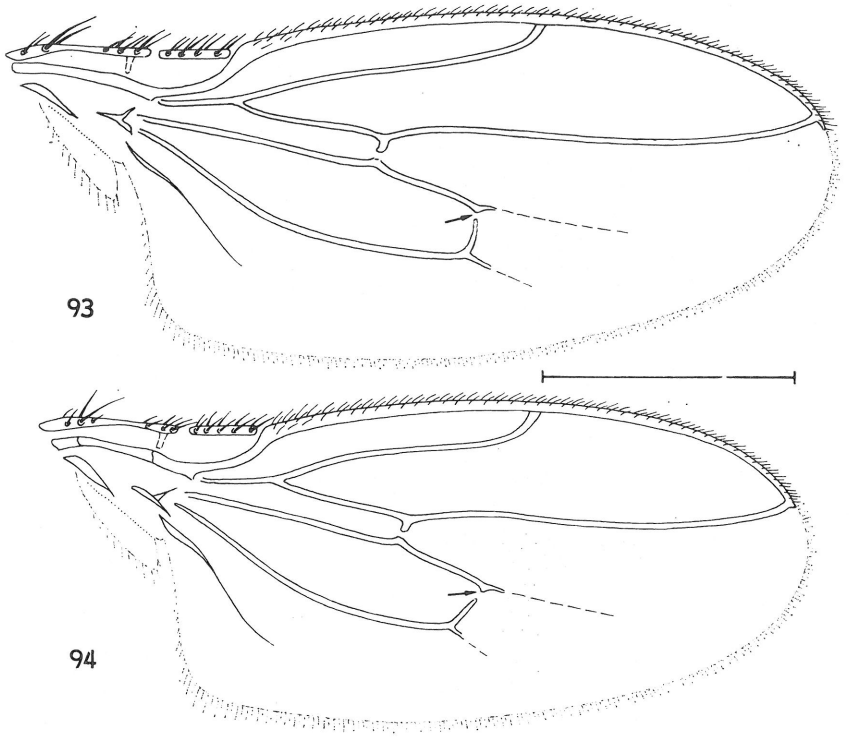

Figs. 89–92. *Apteromyia claviventris* (STROBL) (Czechoslovakia). 89 – male mid trochanter, f_2 and t_2 anteriorly; 90 – male t_2 dorsally; 91 – female t_2 dorsally; 92 – dtto anteriorly. Scale = 0.2 mm. Arrows indicate different position of *pd* in male and female.

Figs. 93–94. *Apteromyia claviventris* (STROBL) (♂, Czechoslovakia), wings. Scale = 0.5 mm. Arrows indicate the variability of discal cell.

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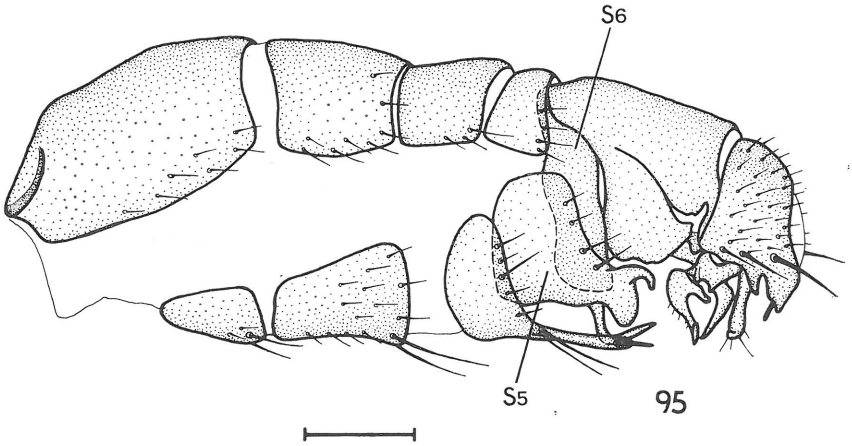

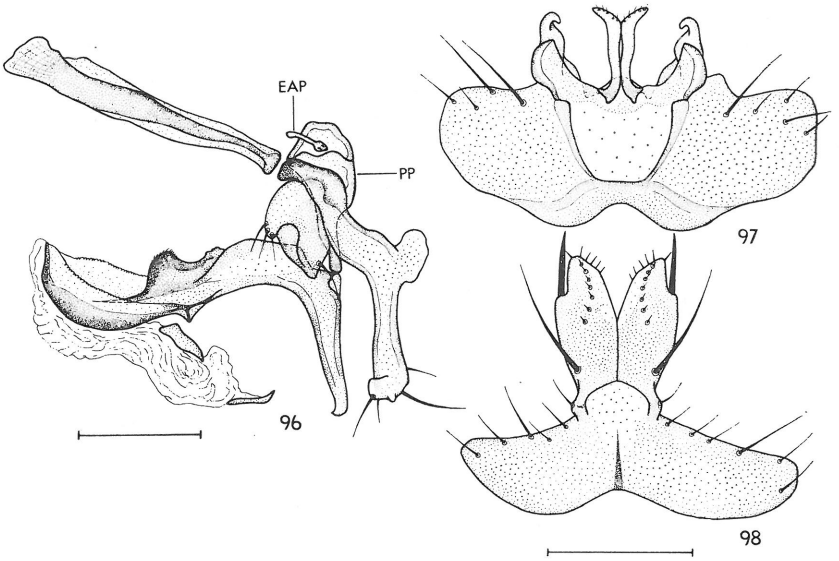

Fig. 95. *Apteromyia claviventris* (STROBL) (Czechoslovakia), male abdomen laterally. Scale = 0.2 mm. Abbreviations: see p. 198.

Figs. 96–98. *Apteromyia claviventris* (STROBL) (♂, Czechoslovakia). 96 – aedeagal complex laterally (only left postgonite figured); 97–*S5*; 98–*S4*. Scales: Fig. 96 = 0.1 mm, Figs. 97,98 = 0.2 mm. Abbreviations: see p. 198.

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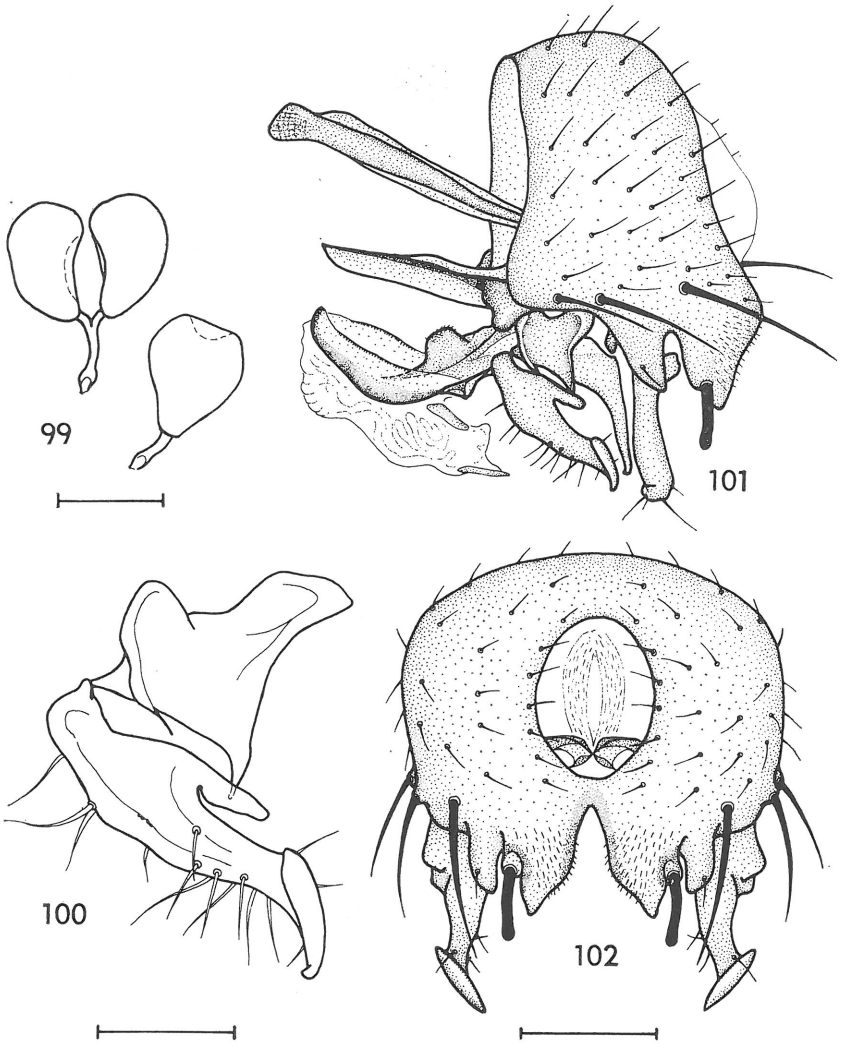

Figs. 99—102. *Apteromyia claviventris* (STROBL) (Czechoslovakia). 99 — spermathecae; 100 — telomere; 101 — male genitalia laterally; 102 — dtto caudally (aedeagal complex omitted). Scales: Figs. 99,100 = 0.05 mm, Figs. 101—102 = 0.1 mm.

Figs. 103—105. *Apteromyia claviventris* (STROBL) (♀, Czechoslovakia). 103 — postabdomen dorsally; 104 — dtto laterally; 105 — dtto ventrally. Scale = 0.2 mm. Abbreviations: see p. 198.

▶

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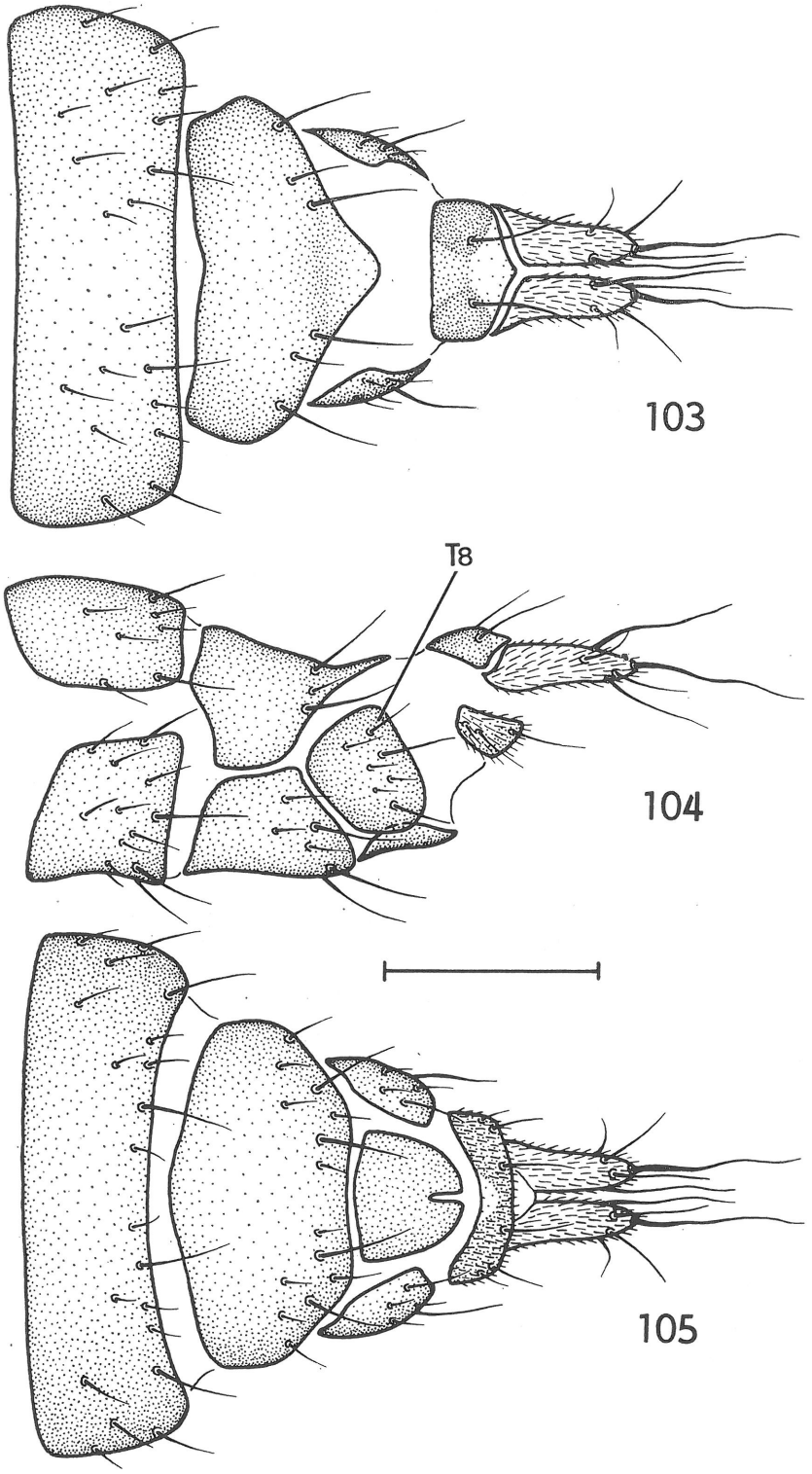

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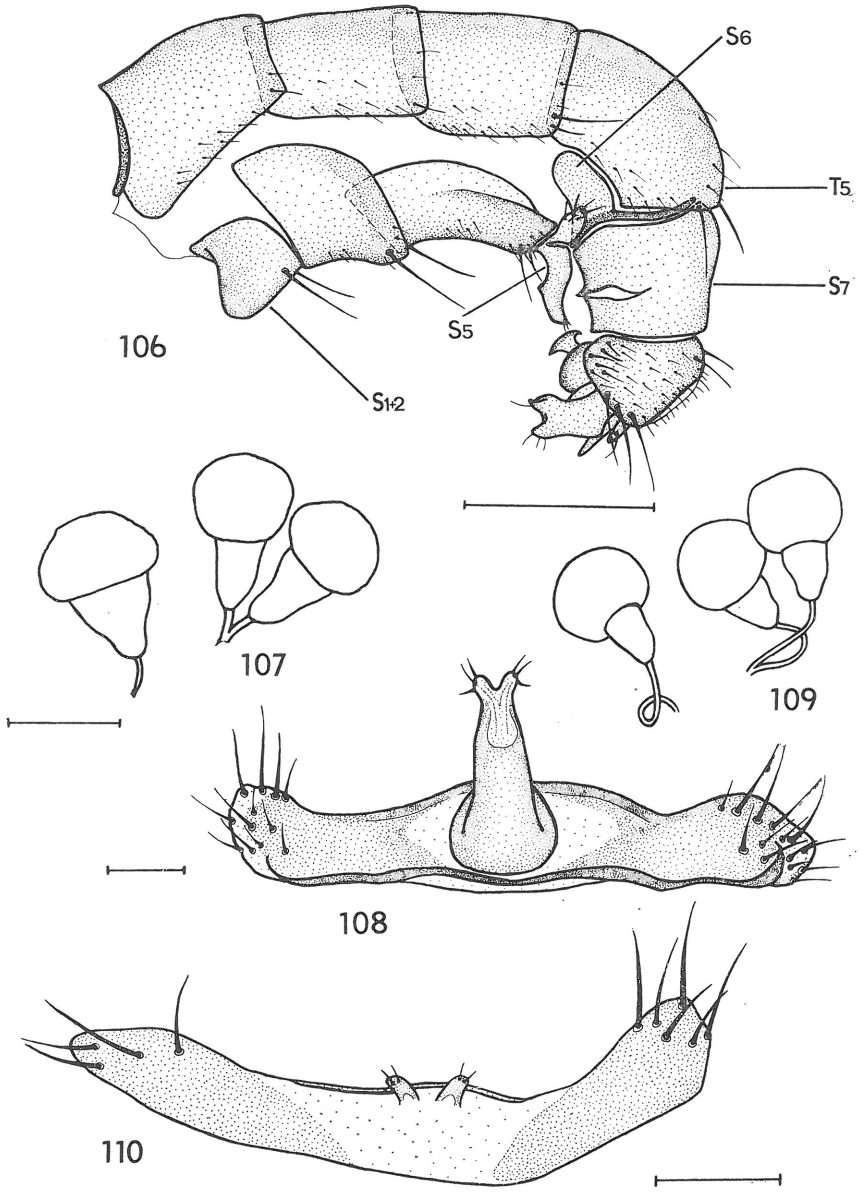

Figs. 106—110. Figs. 106—108. *Herniosina bequaerti* (VILLENEUVE) (Czechoslovakia). 106 — male abdomen laterally; 107 — spermathecae; 108 — male *S5*. Figs. 109—110. *Herniosina horrida* (ROHÁČEK) (paratypes). 109 — spermathecae; 110 — male *S5*. Scales: Fig. 106 = 0.5 mm, Figs. 107—110 = 0.1 mm. Abbreviations: see p. 198.

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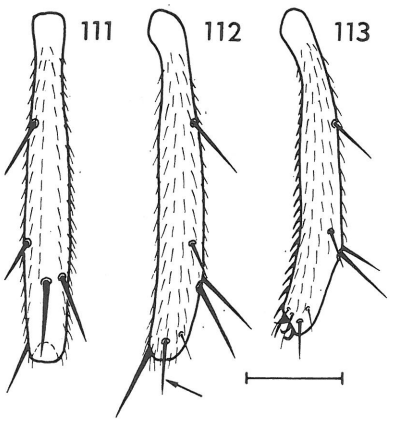

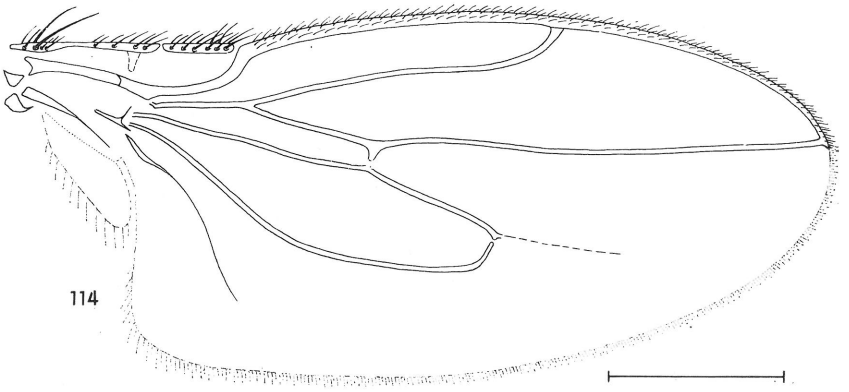

Figs. 111—113. *Herniosina bequaerti* (VILLENEUVE) (Czechoslovakia). 111 — female t_2 dorsally; 112 — ditto anteriorly; 113 — male t_2 anteriorly. Scale = 0.2 mm. Arrow indicates the enlarged anteroapical bristle in female.

Fig. 114. *Herniosina bequaerti* (VILLENEUVE) (♂, Czechoslovakia), wing. Scale = 0.5 mm.

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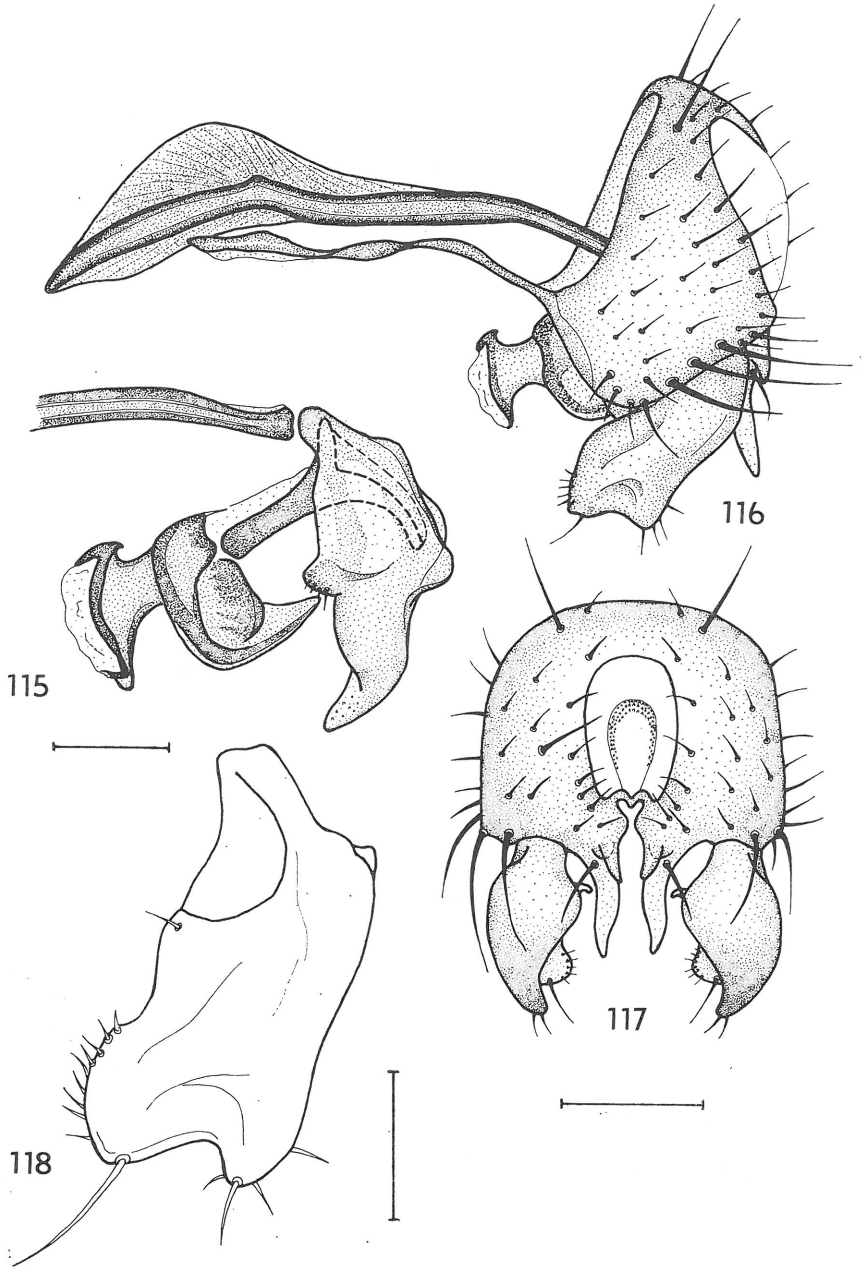

Figs. 115—118. *Herniosina bequaerti* (VILLENEUVE) (♂, Czechoslovakia). 115 — aedeagal complex laterally (right postgonite and apical part of aedeagal apodeme omitted); 116 — genitalia laterally; 117 — dtto caudally (aedeagal complex omitted); 118 — telomere. Scales: Figs. 115,118 = 0.1 mm, Figs. 116,117 = 0.2 mm.

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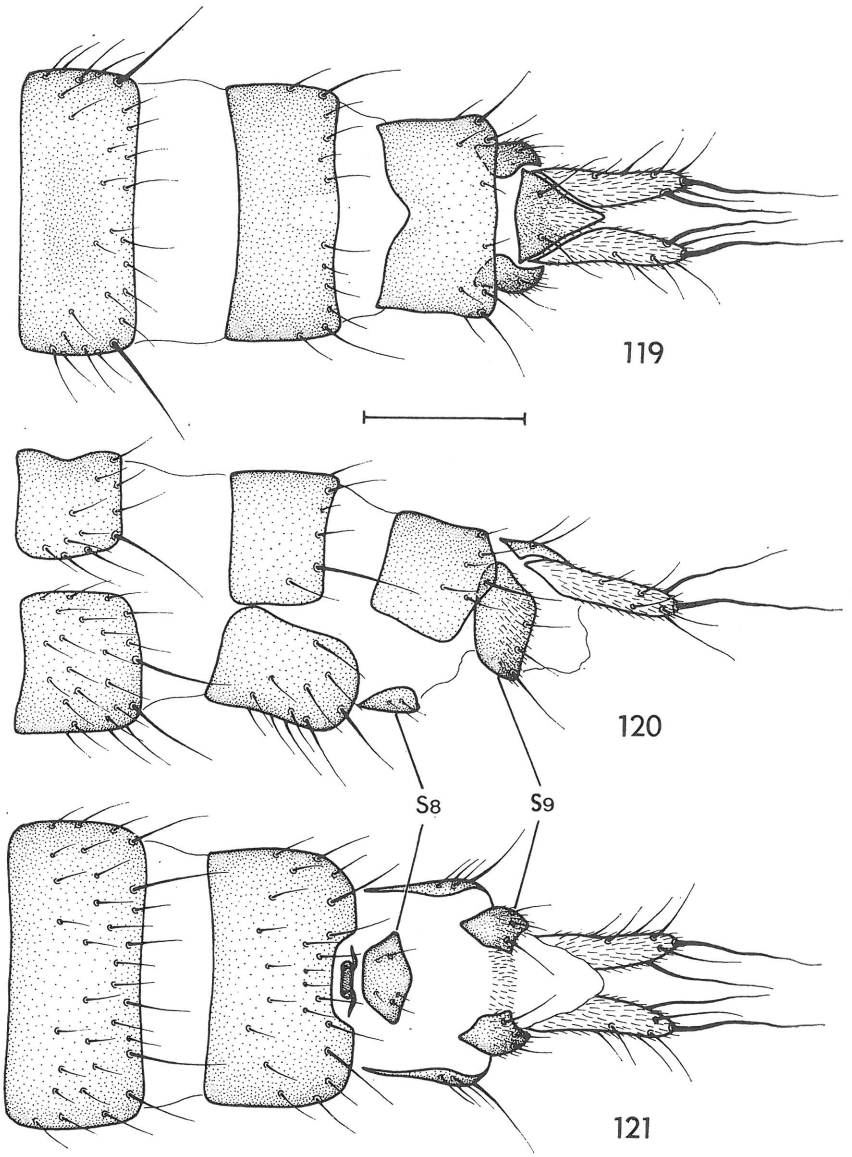

Figs. 119—121. *Herniosina bequaerti* (VILLENEUVE) (♀, Czechoslovakia). 119 — postabdomen dorsally; 120 — dtto laterally; 121 — dtto ventrally. Scale = 0.2 mm. Abbreviations: see p. 198.

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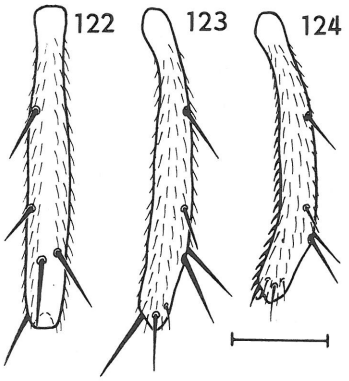

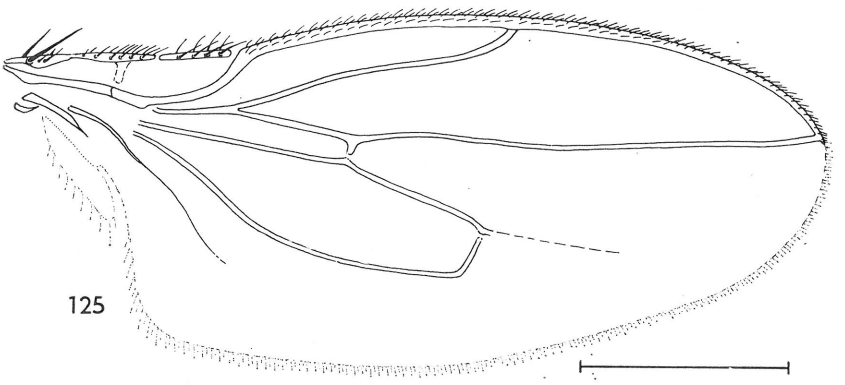

Figs. 122—124. *Herniosina horrida* (ROHÁČEK) (paratypes). 122 — emale t_2 dorsally; 123 — dtto anteriorly; 124 — male t_2 anteriorly. Scale = 0.2 mm

Fig. 125. *Herniosina horrida* (ROHÁČEK) (♂, paratype), wing. Scale = 0.5 mm.

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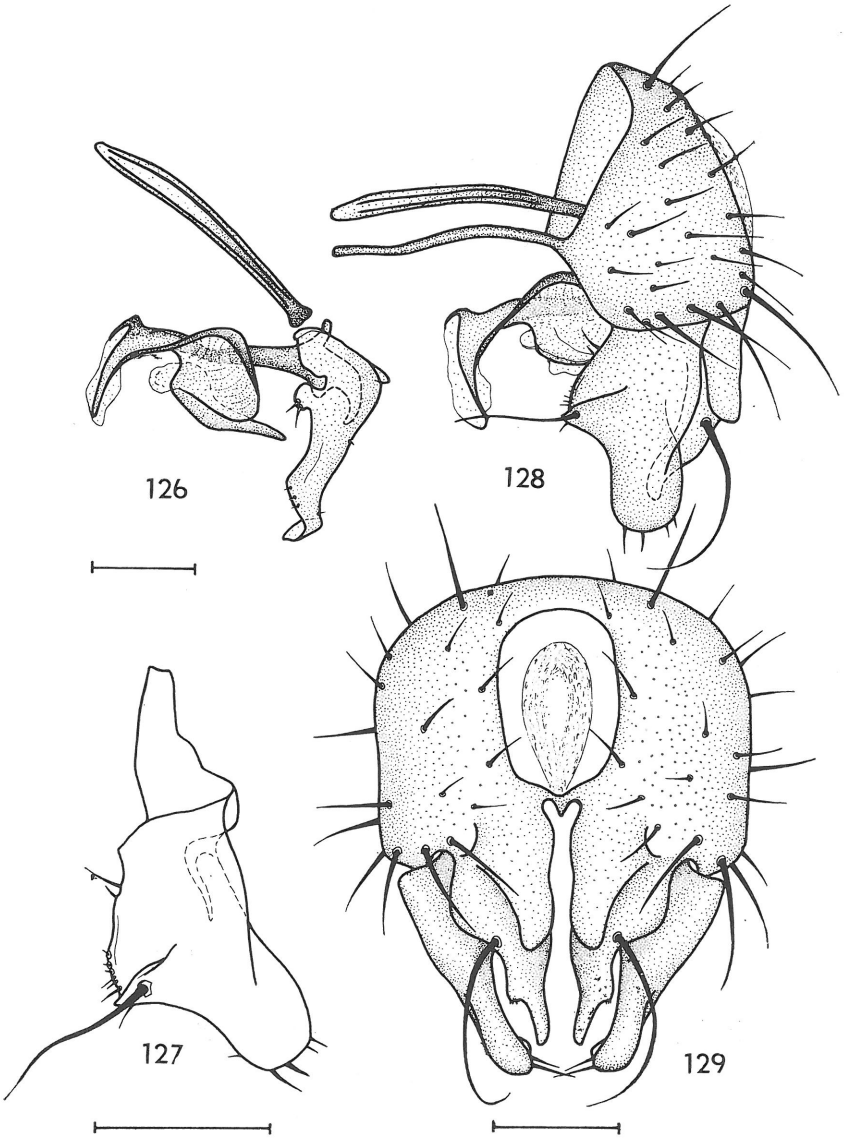

Figs. 126–129. *Herniosina horrida* (ROHÁČEK) (♂, paratype). 126 – aedeagal complex laterally (only le postgonite figured); 127 – telomere; 128 – genitalia laterally; 129 – dtto caudally (aedeagal complex omitted) Scales: 0.1 mm.

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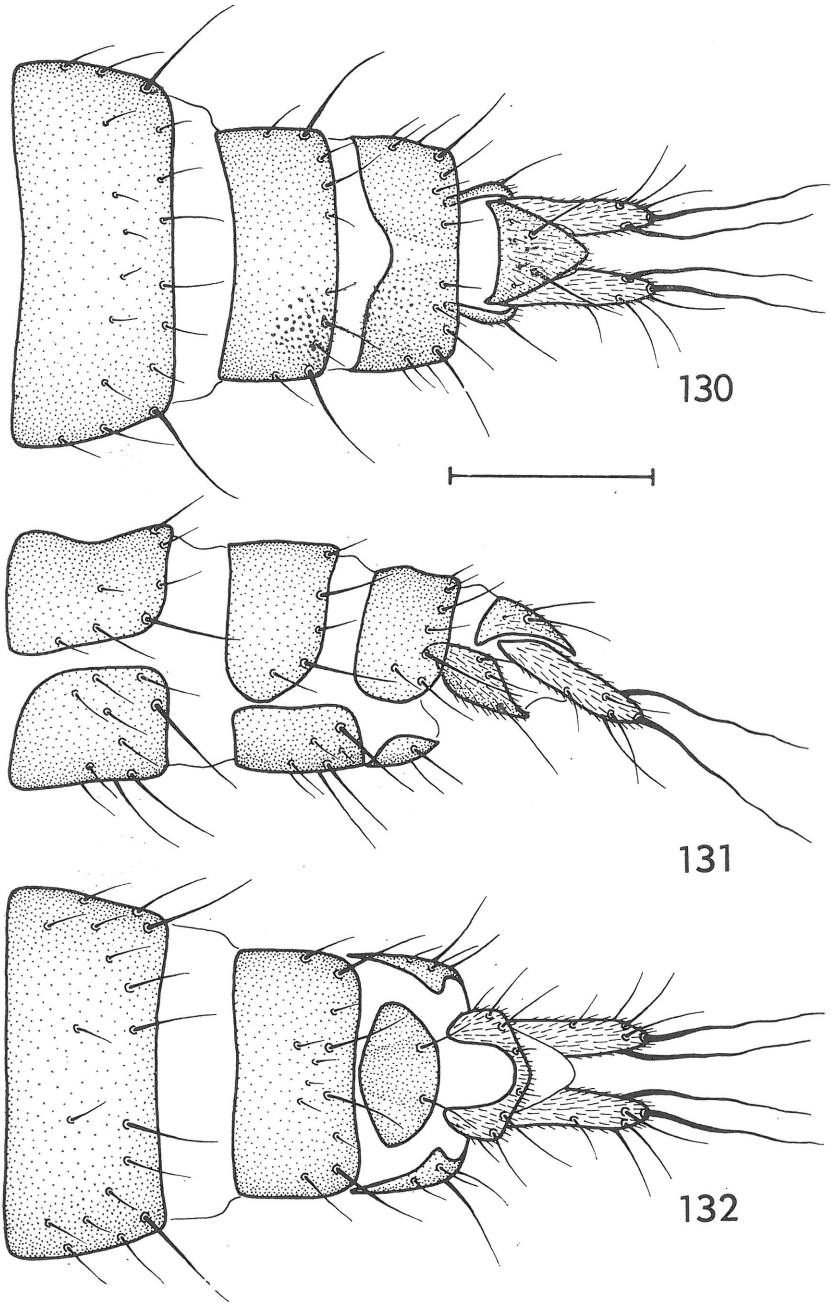

Figs. 130–132. *Herniosina horrida* (ROHÁČEK) (♀, paratype). 130 – postabdomen dorsally; 131 – dtto laterally; 132 – dtto ventrally. Scale = 0.2 mm.

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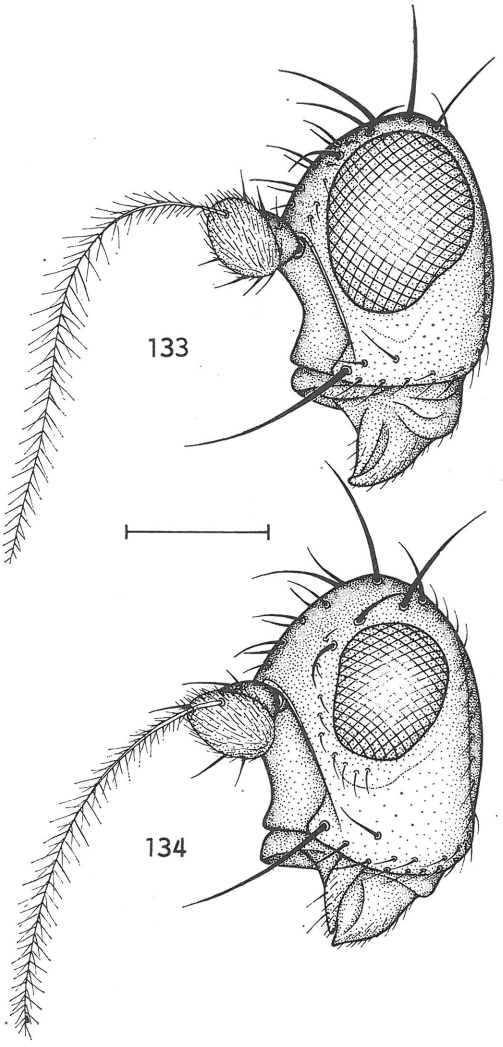
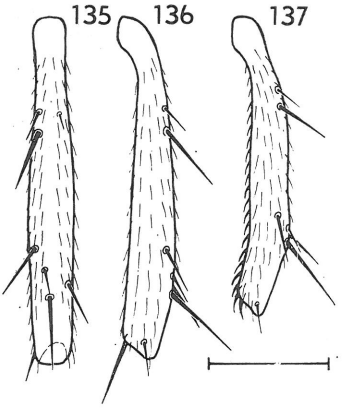
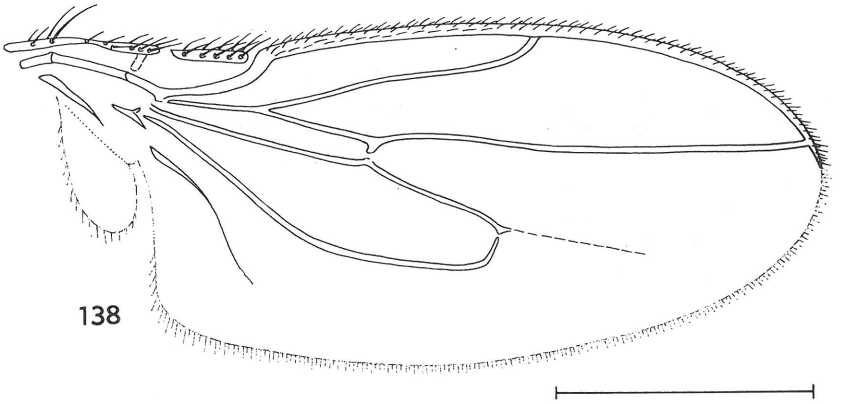




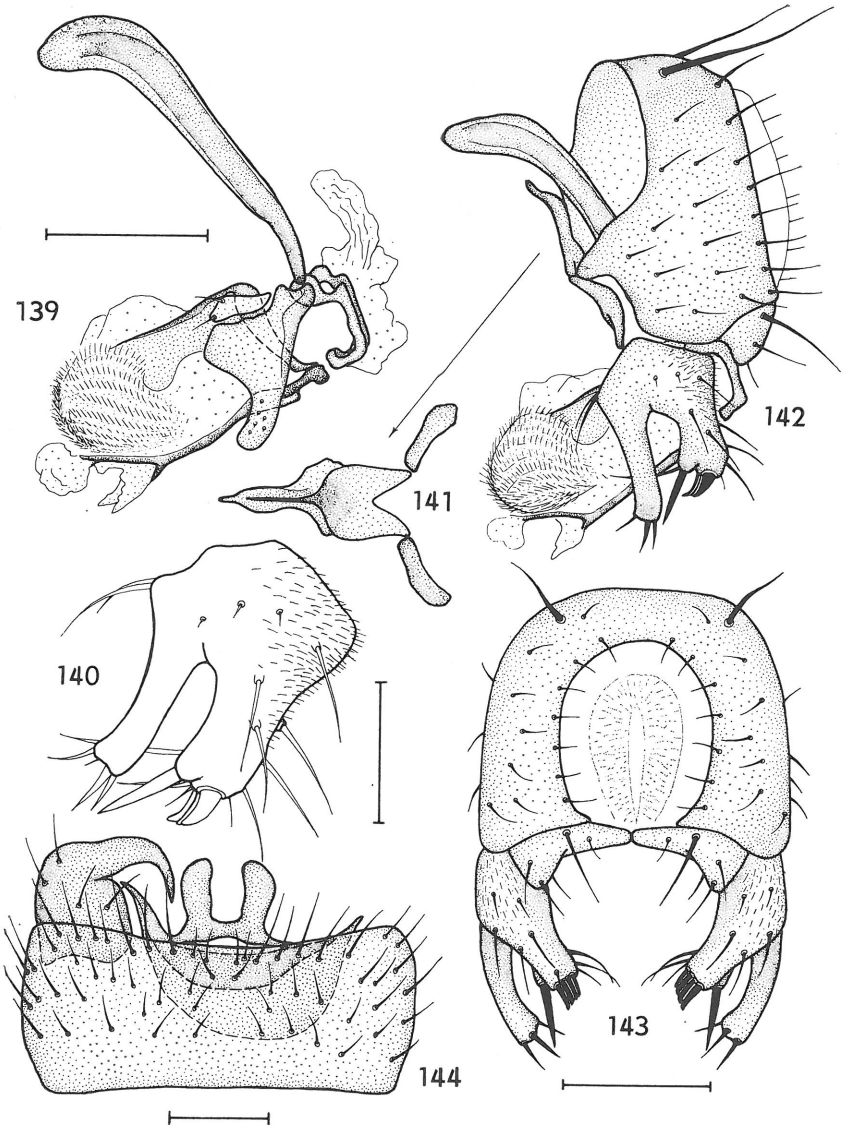


Figs. 133—134. Head of *Terrilimosina* species laterally. 133 — *T. schmitzi* (DUDA) (♂, Czechoslovakia); 134 — *T. racovitzai* (BEZZI) (♂, Czechoslovakia). Scale = 0.2 mm.

Figs. 135—137. *Terrilimosina racovitzai* (BEZZI) (Czechoslovakia). 135 — female t_2 dorsally; 136 — dtto anteriorly; 137 — male t_2 anteriorly. Scale = 0.2 mm.

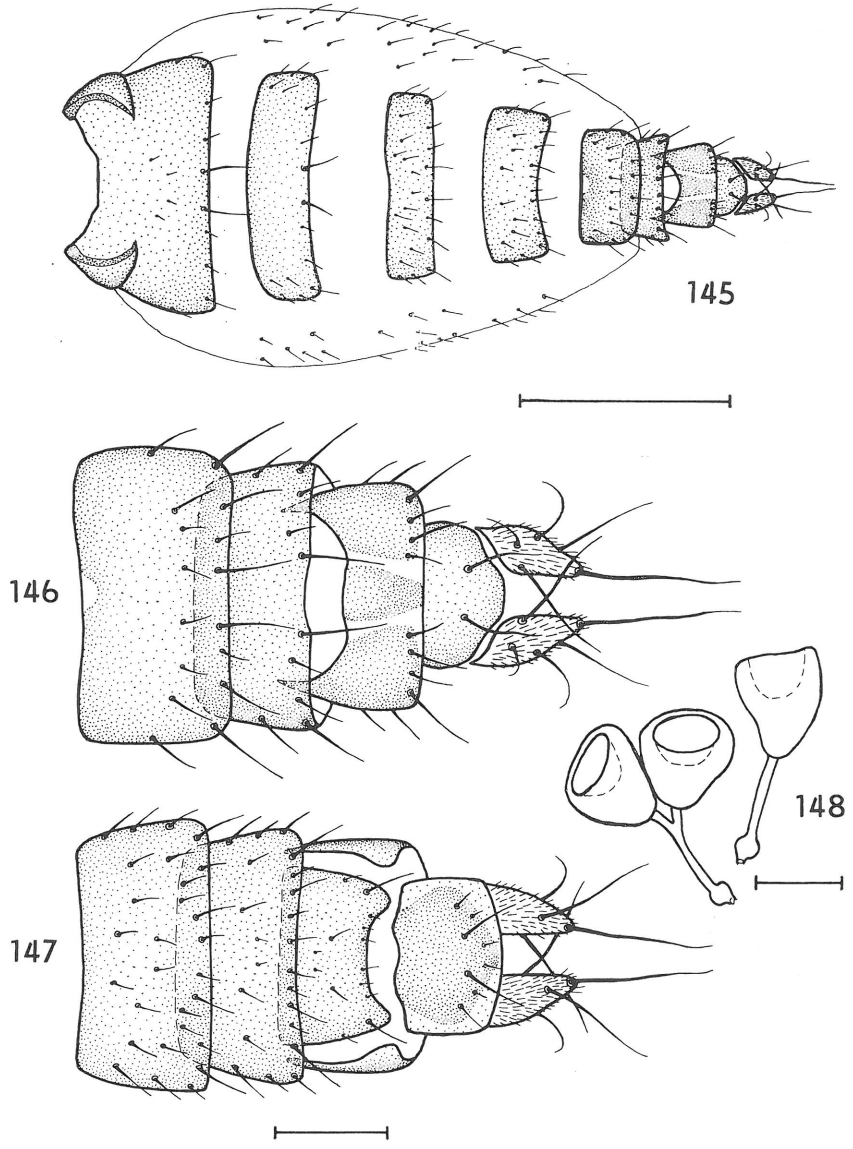
DOI: 10.21248/contrib.entomol.32.2.195-282

Fig. 138. *Terrilimosina racovitzai* (BEZZI) (♂, Czechoslovakia), wing. Scale = 0.5 mm.



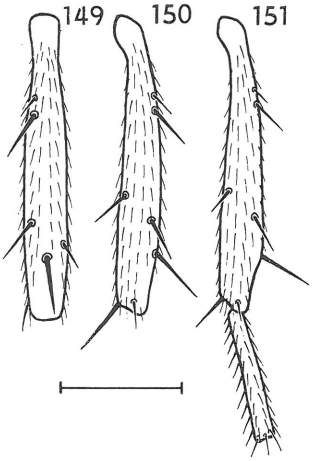
Figs. 139—144. *Terrilimosina racovitzai* (BEZZI) (♂, Czechoslovakia). 139 — aedeagal complex laterally (only left postgonite figured); 140 — telomere; 141 — hypandrium dorsally; 142 — genitalia laterally; 143 — dtto caudally (aedeagal complex omitted); 144 — *S5*, *S6*, *S7* ventrally. Scales: Figs. 139, 141—144 = 0.1 mm, Fig. 140 = 0.05 mm.

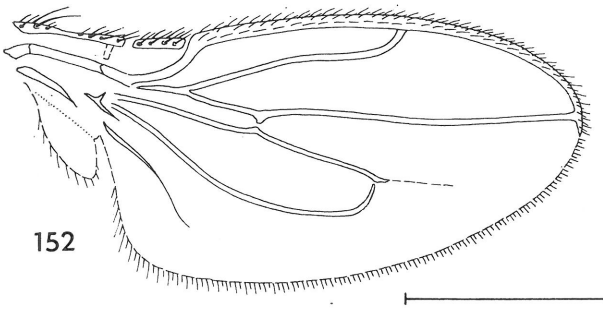
DOI: 10.21248/contrib.entomol.32.2.195-282

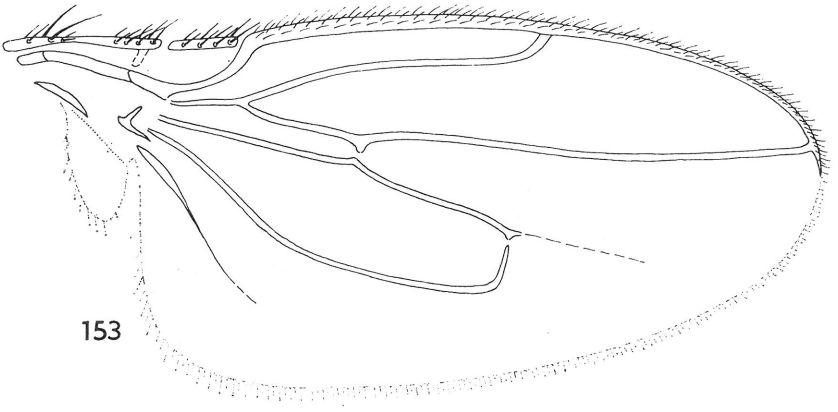


Figs. 145—148. *Terrilimosina racovitzai* (BEZZI) (♀, Czechoslovakia). 145 — abdomen dorsally; 146 — post-abdomen dorsally; 147 — dtto ventrally; 148 — spermathecae. Scales: Fig. 145 = 0.5 mm, Figs. 146,147 = 0.1 mm, Fig. 148 = 0.05 mm.

DOI: 10.21248/contrib.entomol.32.2.195-282



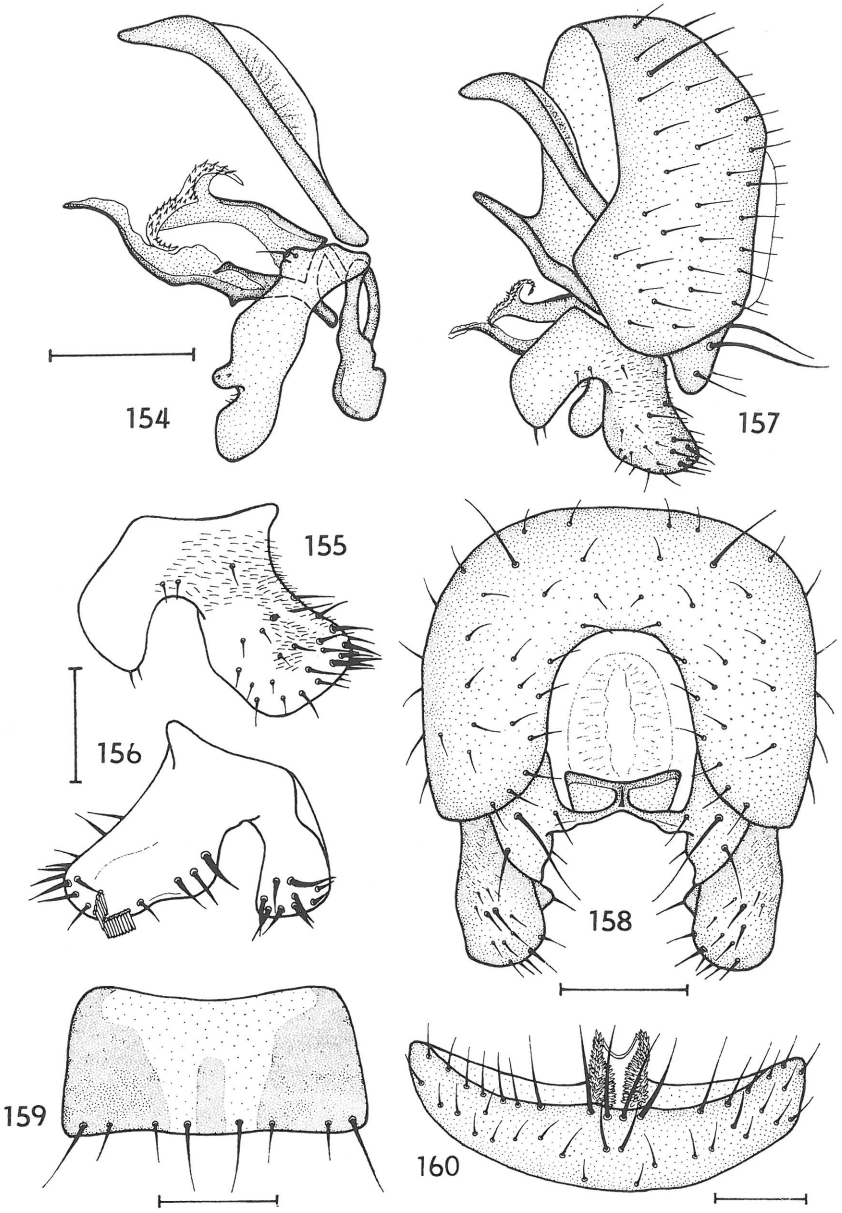




Figs. 149—151. *Terrilimosina sudetica* (ROHÁČEK) (Czechoslovakia). 149 — female t_2 dorsally; 150 — dtto anteriorly; 151 — male t_2 and mt_2 anteriorly. Scale = 0.2 mm.

Figs. 152—153. *Terrilimosina sudetica* (ROHÁČEK), wings. 152 — male (holotype); 153 — female (Bohemia, Czechoslovakia). Scale = 0.5 mm.

DOI: 10.21248/contrib.entomol.32.2.195-282



Figs. 154—160. *Terrilimosina sudetica* (ROHÁČEK) (♂, holotype). 154 — aedeagal complex laterally (only left postgonite figured); 155 — telomere; 156 — dtto internally; 157 — genitalia laterally; 158 — dtto caudally (aedeagal complex omitted); 159 — *T1 + 2* dorsally; 160 — *S5*. Scales: Figs. 154, 157, 158, 160 = 0.1 mm, Figs. 155, 156 = 0.05 mm, Fig. 159 = 0.2 mm.

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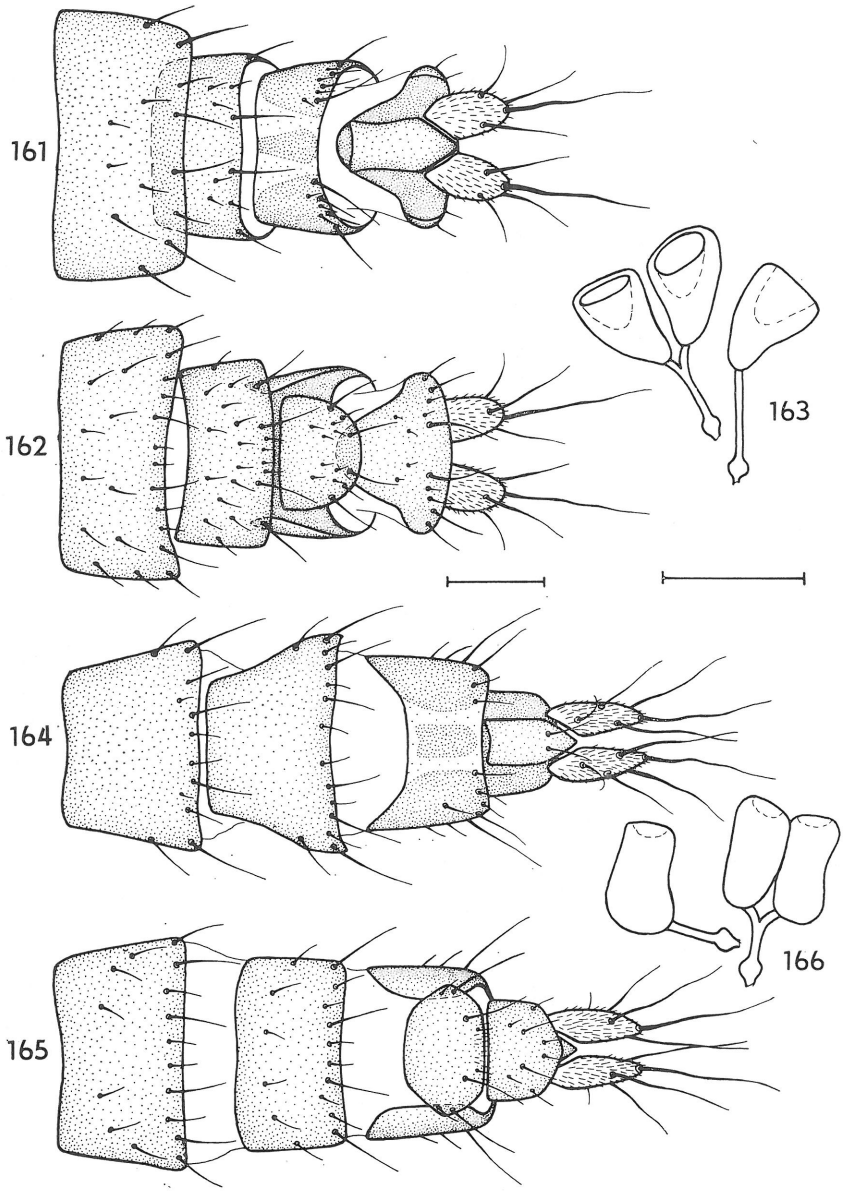

Figs. 161—166. Figs. 161—163. *Terrilimosina sudetica* (ROHÁČEK) (♀, Czechoslovakia). 161 — postabdomen dorsally; 162 — dtto ventrally; 163 — spermathecae. Figs. 164—166. *Terrilimosina schmitzi* (DUDA) (♀, Czechoslovakia). 164 — postabdomen dorsally; 165 — dtto ventrally; 166 — spermathecae. Scales = 0.1 mm.

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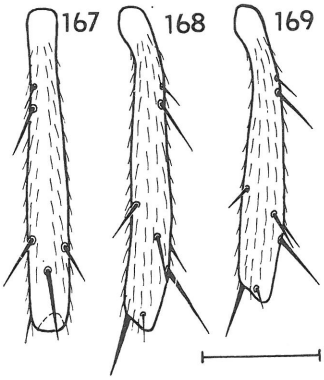

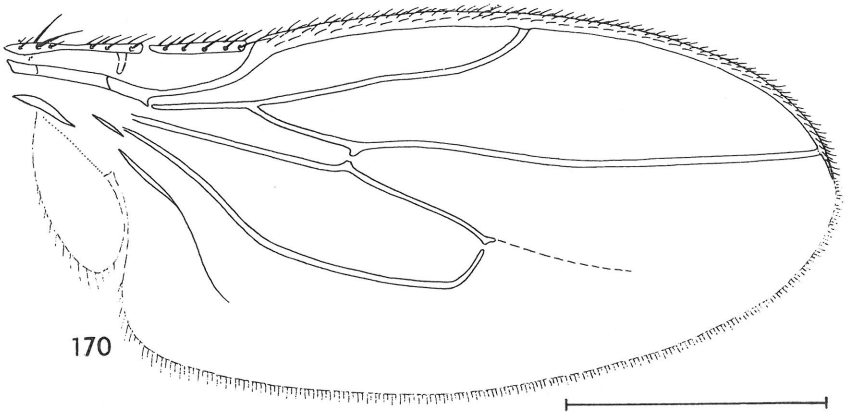

Figs. 167–169. *Terrilimosina schmitzi* (DUDA) (Czechoslovakia). 167 – female t_2 dorsally; 168 – dtto anteriorly; 169 – male t_2 anteriorly. Scale = 0.2 mm.

Fig. 170. *Terrilimosina schmitzi* (DUDA) (♂, Czechoslovakia), wing. Scale = 0.5 mm.

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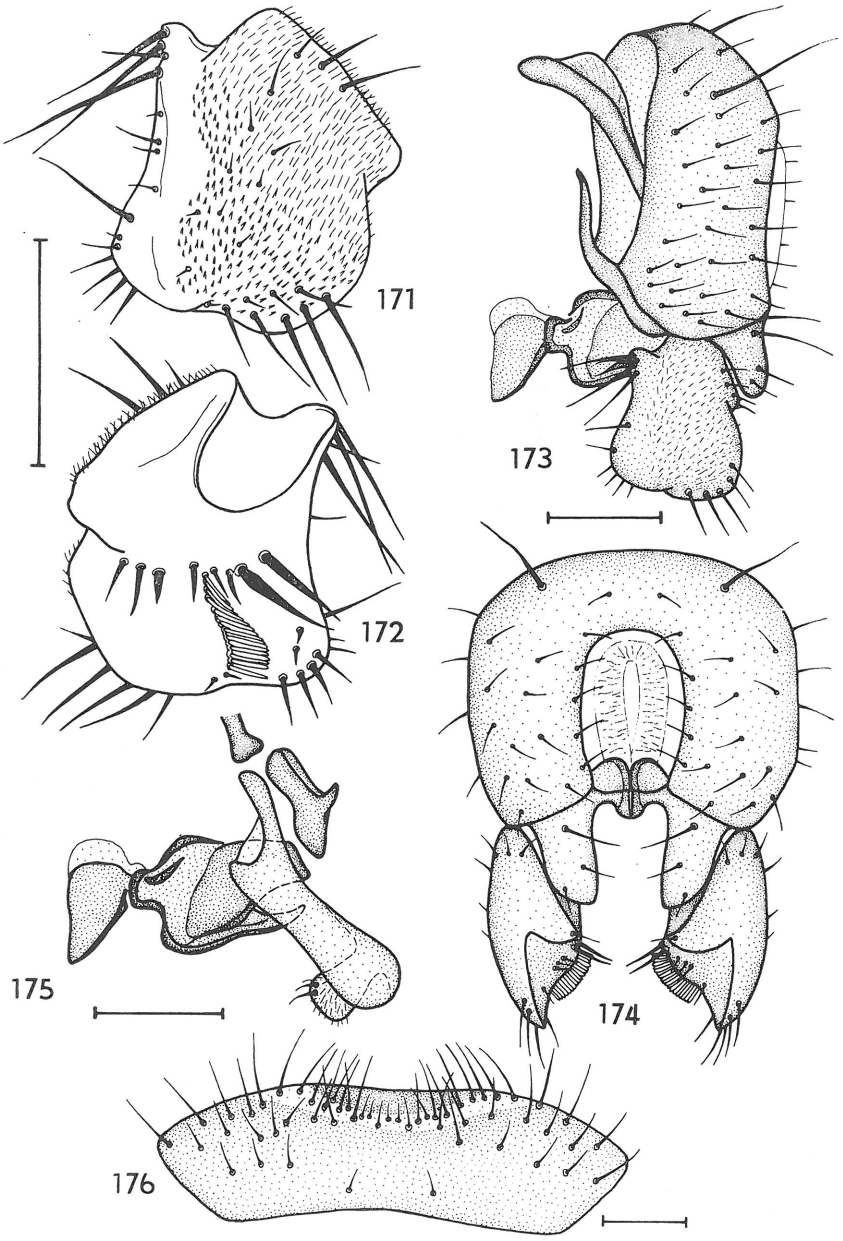

Figs. 171—176. *Terrilimosina schmitzi* (DUDA) (♂, Czechoslovakia). 171 — telomere; 172 — dtto internally; 173 — male genitalia laterally; 174 — dtto caudally (aedeagal complex omitted); 175 — aedeagal complex laterally (right postgonite and aedeagal apodeme omitted), 176—*S5*. Scales = 0.1 mm.

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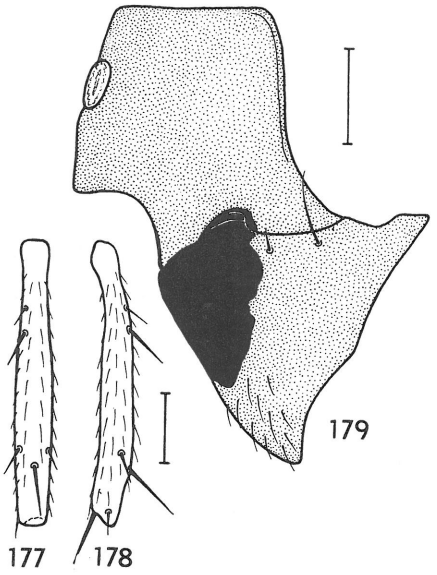

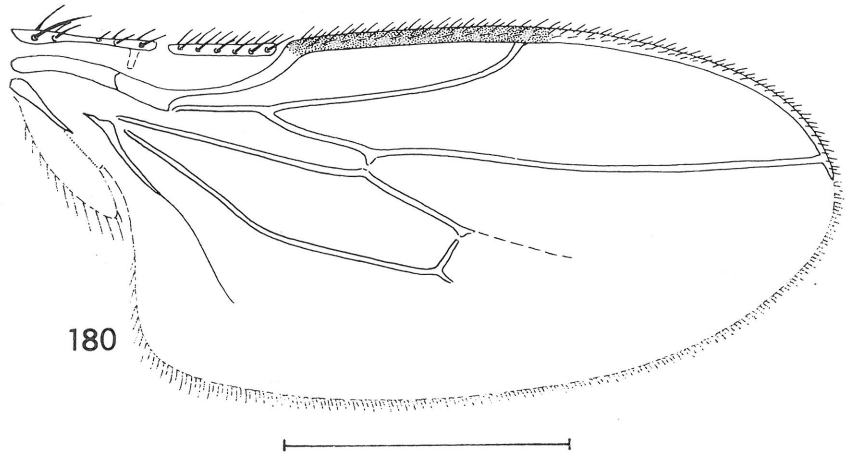

Figs. 177—179. *Minilimosina* (*S.*) *vitripennis* (ZETTERSTEDT) (♂, Denmark). 177 — t_2 dorsally; 178 — dtto anteriorly; 179 — mesopleuron and sternopleuron (pruinose area dotted). Scales = 0.1 mm.

Fig. 180. *Minilimosina* (*S.*) *vitripennis* (ZETTERSTEDT) (♀, Denmark), wing. Scale = 0.5 mm.

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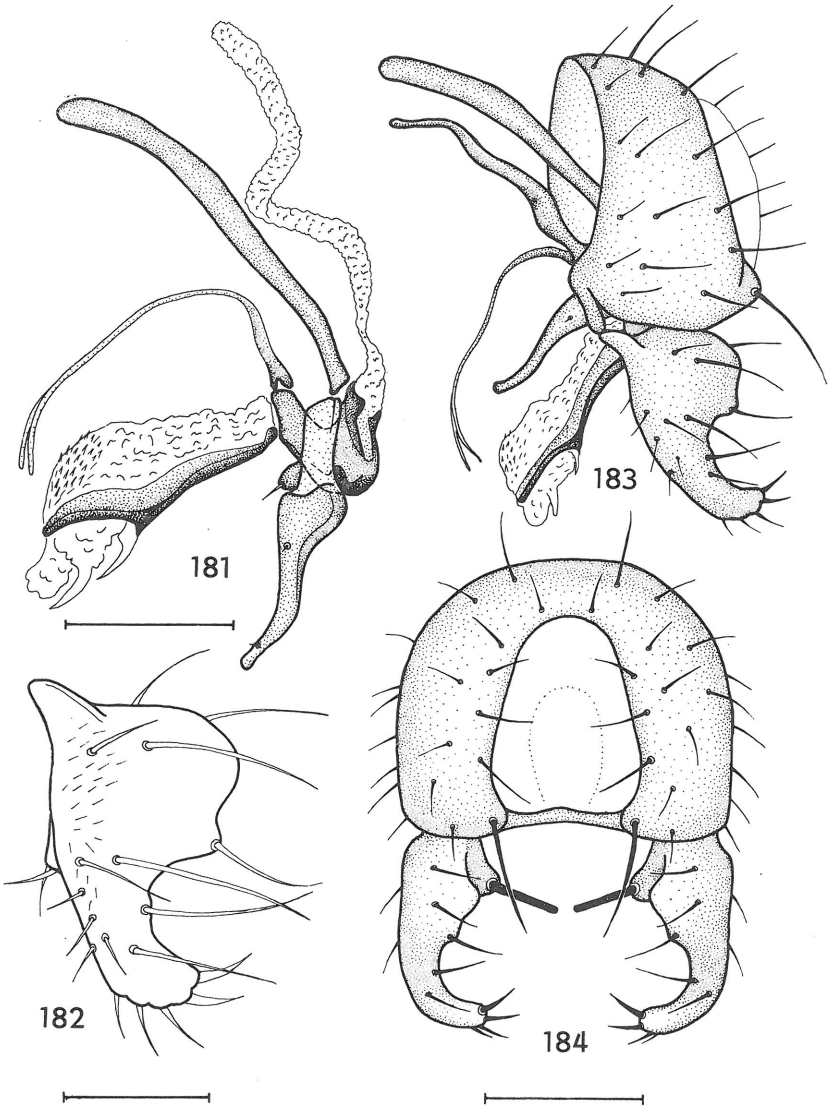

Figs. 181—184. *Minilimosina* (*S.*) *vitripennis* (ZETTERSTEDT) (♂, Austria). — 181 aedeagal complex laterally (only left postgonite figured); 182 — telomere; 183 — genitalia laterally; 184 — dtto caudally (aedeagal complex omitted). Scales: Figs. 181, 183,184 = 0.1 mm, Fig. 182 = 0.05 mm.

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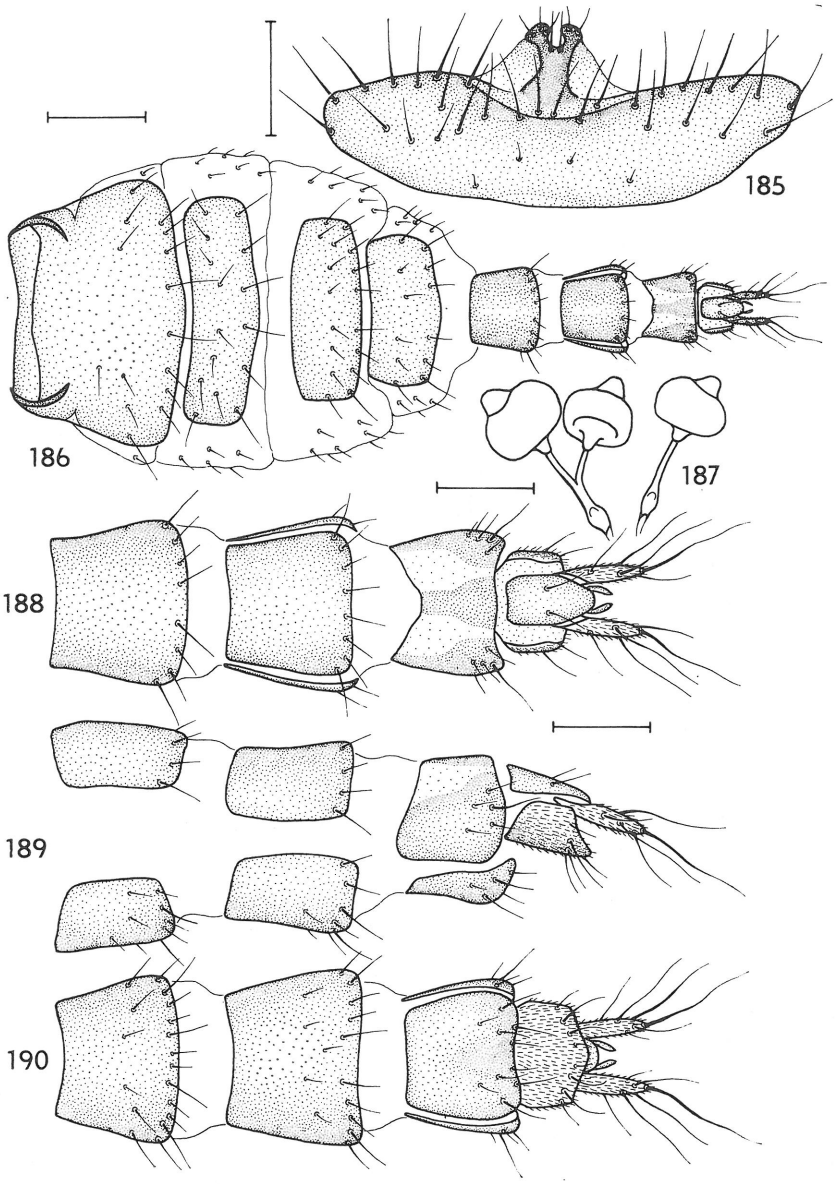
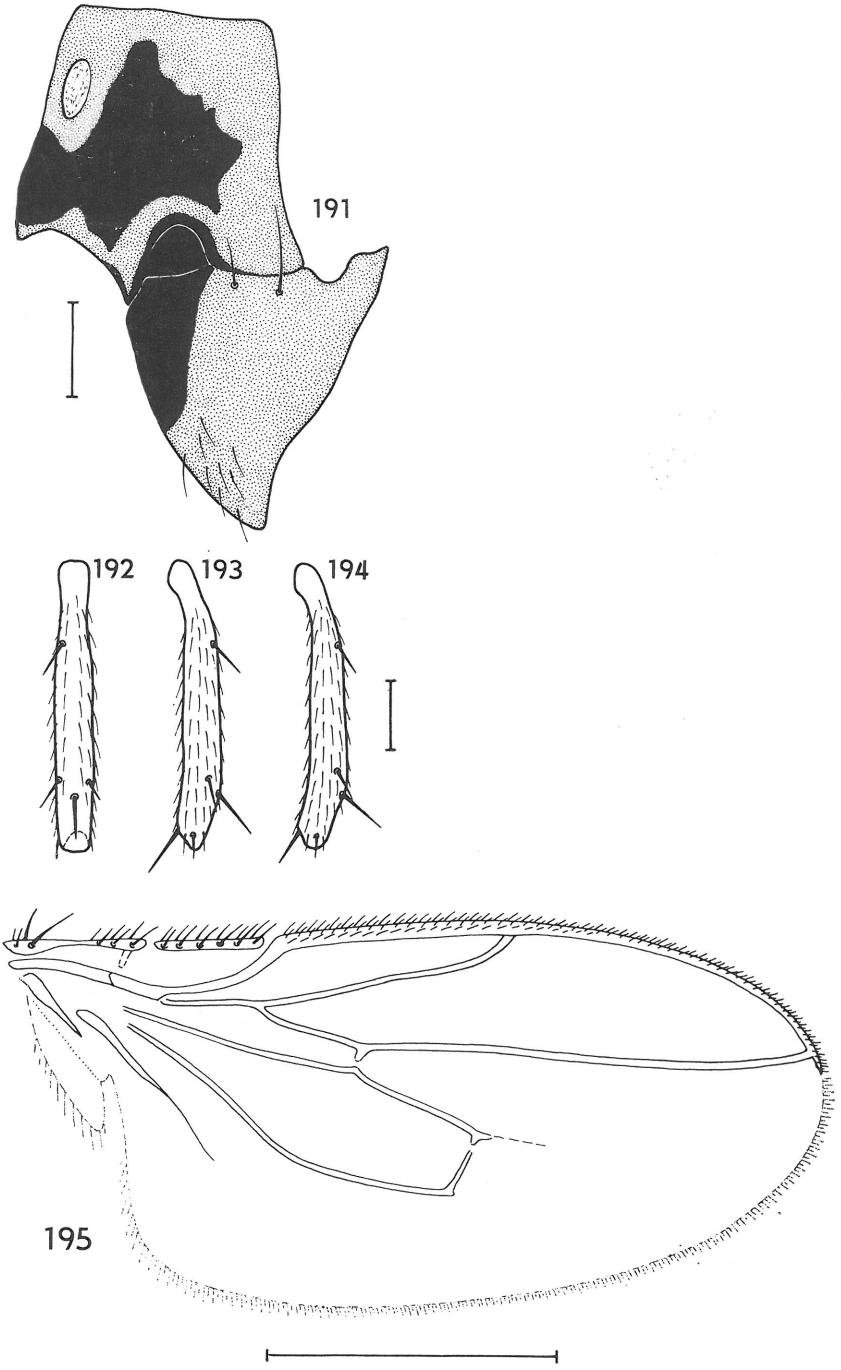


Figs. 185—190. *Minilimosina* (*S.*) *vitripennis* (ZETTERSTEDT). 185 — male *S5* (based on specimen from Austria); 186 — female abdomen dorsally; 187 — spermathecae; 188 — female postabdomen dorsally; 189 — dtto laterally; 190 — dtto ventrally (all based on specimens from Denmark). Scales: Figs. 185, 188—190 = 0.1 mm, Fig. 186 = 0.2 mm, Fig. 187 = 0.05 mm.

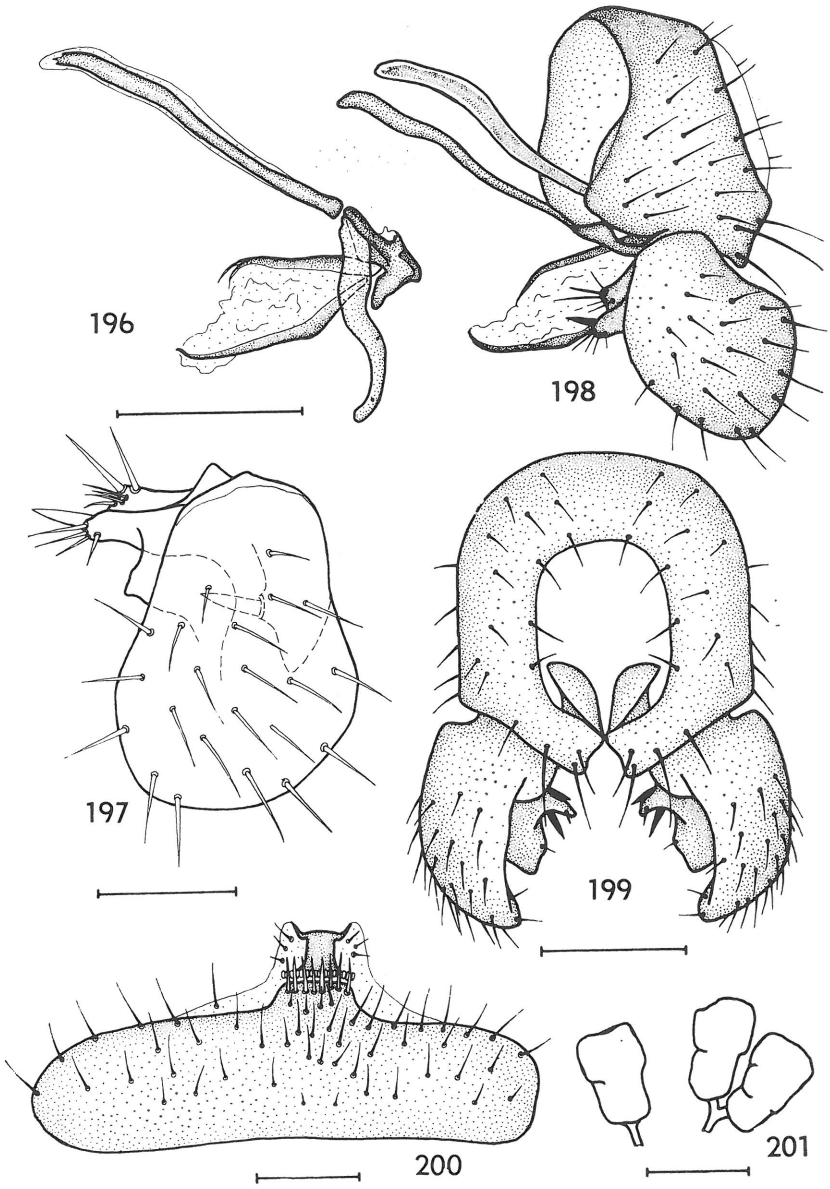
DOI: 10.21248/contrib.entomol.32.2.195-282



Figs. 191—194. *Minilimosina* (*S.*) *splendens* (DUDA) (Czechoslovakia). 191 — mesopleuron and sternopleuron (♂, pruinose area dotted); 192 — female t_2 dorsally; 193 — dtto anteriorly; 194 — male t_2 anteriorly. Scales = 0.1 mm.

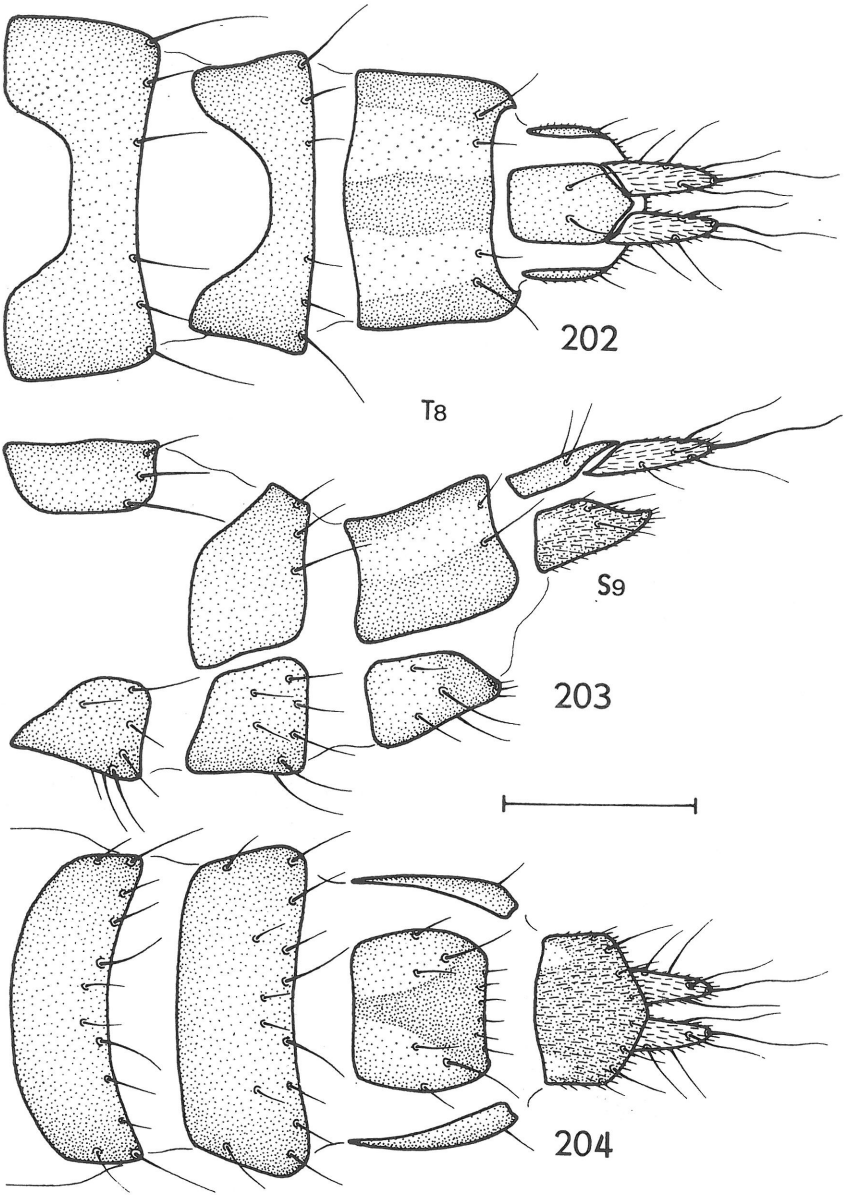
Fig. 195. *Minilimosina* (*S.*) *splendens* (DUDA) (♀, Czechoslovakia), wing. Scale = 0.5 mm.

DOI: 10.21248/contrib.entomol.32.2.195-282



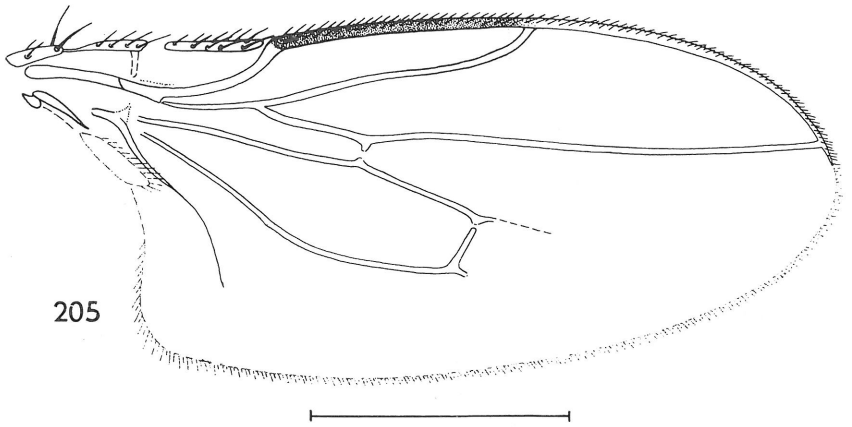
Figs. 196–201. *Minilimosina* (*S.*) *splendens* (DUDA) (Czechoslovakia). 196 – aedeagal complex laterally (only left postgonite figured); 197 – telomere; 198 – male genitalia laterally; 199 – dtto caudally (aedeagal complex omitted); 200 – male *S5*; 201 – spermathecae. Scales: Figs. 196, 198–200 = 0.1 mm, Figs. 197, 201 = 0.05 mm.

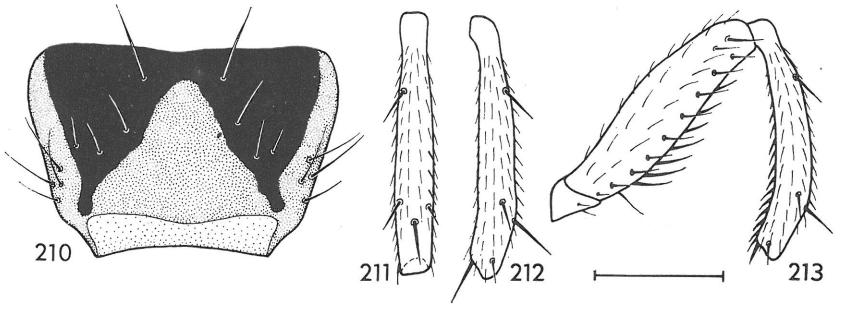
DOI: 10.21248/contrib.entomol.32.2.195-282



Figs. 202—204. *Minilimosina* (*S.*) *splendens* (DUDA) (♀, paralectotype). 202 — postabdomen dorsally; 203 — dtto laterally; 204 — dtto ventrally. Scale = 0.1 mm. Abbreviations: see p. 198.

DOI: 10.21248/contrib.entomol.32.2.195-282





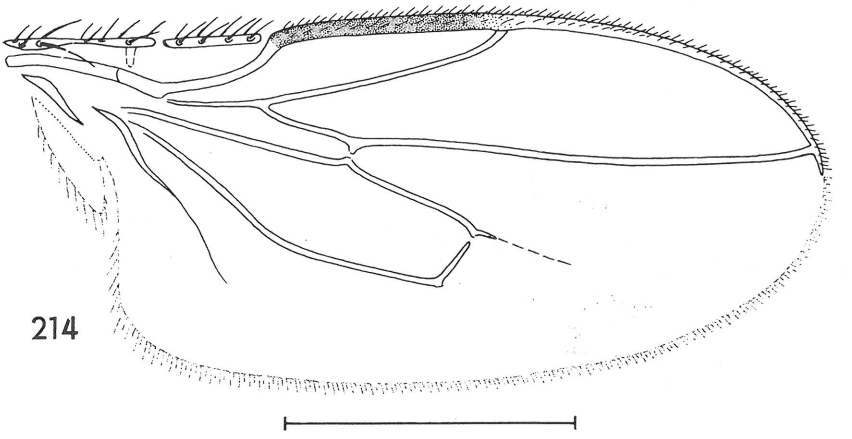


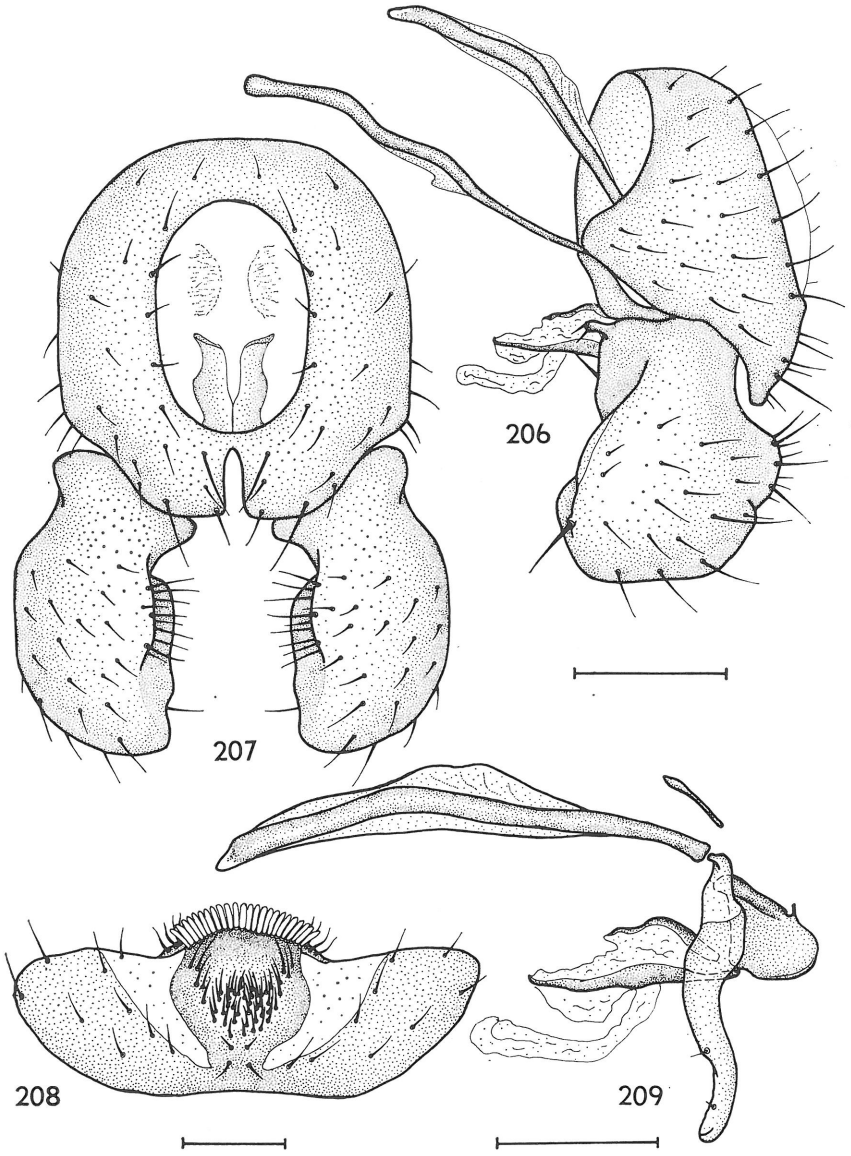
Fig. 205. *Minilimosina* (*S.*) *hackmani* (ROHÁČEK) (♂, holotype), wing. Scale = 0.5 mm.

Fig. 206—209 see page 282.

Figs. 210—213. *Minilimosina* (*S.*) *v-atrum* (VILLENEUVE). 210 — *T1+2* dorsally (based on ♂ lectotype of *L. guestphalica*; pruinose area dotted); 211 — female t_2 dorsally; 212 — dtto anteriorly (based on ♀ paralectotype of *L. guestphalica*); 213 — male mid trochanter, f_2 and t_2 anteriorly (based on ♂ from Czechoslovakia). Scale = 0.2 mm.

Fig. 214. *Minilimosina* (*S.*) *v-atrum* (VILLENEUVE) (♀, Czechoslovakia), wing. Scale = 0.5 mm.

DOI: 10.21248/contrib.entomol.32.2.195-282



Figs. 206–209. *Minilimosina* (*S.*) *hackmani* (ROHÁČEK) (♂, holotype). 206 – genitalia laterally; 207 – dtto caudally (aedeagal complex omitted); 208 – *S5*; 209 – aedeagal complex laterally (only left postgonite figured). Scales = 0.1 mm.

Part II (Systematic part) in the following issue.

DOI: 10.21248/contrib.entomol.32.2.195-282