THE EXTERNAL MALE GENITALIA AND THE PHYLOGENY OF BLATTARIA AND MANTODEA

by

KLAUS-DIETER KLASS

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CONTENTS

ABSTRACT

The external male genitalia of Blattaria and Mantodea (phallomeres, phallomere complex) are highly complicated structures, which are always extremely asymmetrical. They are provided with many sclerites and muscles. Their cuticular surface is complexly folded, and there are many distinct in- and evaginations (the formative elements), which may have the shape of spines, lobes, bulges, pouches, apodemes, tendons, etc.. The knowledge of phallomere morphology is extremely incomplete, and the potential for phylogenetic research inherent in these structures has so far hardly been used.

In 4 species of Mantodea and 10 species of Blattaria the sclerites, muscles, and formative elements of the phallomere complex and some other parts of the male postabdomen have been investigated in detail. Most of the subgroups of Blattaria (subfamilies in the system of McKittrick 1964) and four families of Mantodea (of the system of Beier 1968) are represented in this sample. Certain parts of the phallomeres are described for some further species of Blattaria.

A detailed homology hypothesis is presented for the sclerites, muscles, and formative elements of the phallomeres, which includes the homologies between Blattaria and Mantodea. The common ground-plan of Blattaria and Mantodea has been reconstructed. Phallomere characters have been evaluated in terms of phylogeny.

The resulting phylogenetic hypothesis is roughly as follows: In Mantodea, the basal dichotomy is between Mantoididae and the other families; the second one is between Chaeteessidae and the remaining families. In Blattaria, the basal dichotomy is between Blattinae + Polyzosteriinae and the remainder. These remaining Blattaria can be divided into three groups: The first consists of Tryonicinae only. The second contains Cryptocercidae as well as Lamproblattinae and Polyphaginae, the two latter taxa being especially closely related. The third group comprises Blattellidae and Blaberidae. Blattellidae are clearly paraphyletic, with Blaberidae as a rather subordinate subgroup. The first offshoot within Blattellidae (+ Blaberidae) are the Anaplectinae. The subsequent offshoots are various species of Plectopterinae, which is a paraphyletic taxon, too. Blaberidae, Nyctiborinae, Blattellinae and Ectobiinae together form a holophyletic group. Nyctiborinae and Blaberidae are possibly sister-groups.

Some other important results are:

(1) The asymmetry of the phallomere complex is homologous in Blattaria and Mantodea, and the morphology of each side is quite similar in the two groups. In Mantodea the hook-process hla (sclerite L3 of McKittrick 1964) is missing; this might be the consequence of a derived copulation procedure.

(2) In the common ground-plan of Blattaria and Mantodea asymmetry is already as extreme as in the extant species. The opinion of Mizukubo & Hirashima (1987) that the stem-species of Blattaria still had symmetrical phallomeres is refuted.

(3) The ground-plan morphology is most extensively retained in the Mantodea Mantoididae (left side) and Chaeteessidae (right side). In Blattaria, Blattinae have retained many ground-plan features, but in some other phallomere characters they are rather derived. The phallomeres of Cryptocercidae are not close to the Blattarian ground-plan as it is the opinion of McKittrick (1964).

(4) The hypothesis of Bohn (1987) that the side-reversed similarities of the phallomeres of Blaberidae on the one hand and of some subgroups of Blattellidae on the other are due to homology is highly supported. They are not due to parallel evolution as it is the view of Mizukubo & Hirashima (1987).

(5) Homologies between the left and the right side of the phallomere complex can be recognised in only very few respects. Probably, most of the complex morphology of the phallomeres has evolved when asymmetry had already been established. The concept of side-homologous subregions in Mizukubo & Hirashima (1987) and the assumptions of side-homologies in Grandcolas (1994) are refuted.

ZUSAMMENFASSUNG

Die äußeren männlichen Genitalien der Blattaria und Mantodea (Phallomeren, Phallomerenkomplex) sind äußerst komplizierte Strukturen. Sie sind mit vielen Skleriten und Muskeln ausgestattet und sind immer völlig asymmetrisch. Ihre Cuticula ist stark in sich verfaltet, und es finden sich viele markante Ein- und Ausstülpungen (formative Elemente), die die Form von Stacheln, Lappen, Beulen, Taschen, Apodemen, Sehnen o.ä. haben können. Die Phallomeren waren bislang noch kaum vergleichend-morphologisch bearbeitet, und die Möglichkeiten, die sie der Phylogenie-Forschung bieten könnten, wurden bislang noch kaum genutzt.

An 4 Arten der Mantodea und 10 Arten der Blattaria wurden die Sklerite, Muskeln und formativen Elemente des Phallomerenkomplexes sowie einige weitere Teile des Postabdomens eingehend untersucht. Die meisten höherrangigen Teilgruppen der Blattaria (Unterfamilien im System von McKittrick 1964) und vier Familien der Mantodea (nach dem System von Beier 1968) sind in dieser Auswahl vertreten. Teilbereiche der Phallomeren wurden an weiteren Arten der Blattaria untersucht.

Für die Sklerite, Muskeln und formativen Elemente der Phallomeren wird eine detaillierte Homologiehypothese vorgestellt, die auch die Homologiebeziehungen zwischen Blattaria und Mantodea einschließt. Der gemeinsame Grundbauplan der Blattaria und Mantodea konnte weitestgehend rekonstruiert werden. Die Phallomeren-Merkmale wurden in Hinblick auf die Phylogenie ausgewertet.

Aus den Merkmalsverteilungen ergibt sich die folgende Phylogenie-Hypothese: Innerhalb der Mantodea besteht die basalste Dichotomie zwischen Mantoididae und den restlichen Familien, die nächstfolgende zwischen Chaeteessidae und den verbleibenden Familien. Innerhalb der Blattaria ist eine basale Schwestergruppenbeziehung zwischen Blattinae + Polyzosteriinae und den ganzen restlichen Gruppen anzunehmen. Diese restlichen Blattaria lassen sich in drei Gruppen gliedern: Der ersten gehören nur die Tryonicinae an. Die zweite Gruppe umfaßt die Cryptocercidae, Polyphaginae und Lamproblattinae, wobei die beiden letzteren besonders enge Beziehungen zeigen. Der dritten Gruppe sind die Blattellidae und die Blaberidae zuzurechnen. Die Blattellidae sind eindeutig paraphyletisch: die Blaberidae sind eine untergeordnete Teilgruppe dieser Familie. Innerhalb der Blattellidae (+ Blaberidae) sind die Anaplectinae der basalste Seitenzweig. Die nachfolgenden Abzweigungen werden von verschiedenen Vertretern der Plectopterinae repräsentiert, womit auch dieses Taxon als paraphyletisch anzusehen ist. Blaberidae, Nyctiborinae, Blattellinae und Ectobiinae bilden gemeinsam eine holophyletische Gruppierung. Nyctiborinae und Blaberidae sind möglicherweise Schwestergruppen.

Weitere bedeutsame Ergebnisse sind:

(1) Die Asymmetrie des Phallomerenkomplexes ist bei Blattaria und Mantodea homolog, und die Morphologie jeder Seite ist ziemlich ähnlich. Bei Mantodea fehlt der Hakenfortsatz hla (L3-Sklerit in McKittrick 1964), was sich vielleicht als Folge eines apomorphen Kopulationsverhaltens interpretieren läßt.

(2) Im gemeinsamen Grundbauplan der Blattaria und Mantodea ist der Phallomerenkomplex bereits im selben Ausmaß (und in derselben Weise) asymmetrisch wie bei den rezenten Vertretern. Die Ansicht von Mizukubo & Hirashima (1987), die Phallomeren seien bei der letzten gemeinsamen Stammart der Blattaria noch symmetrisch gewesen, wird zurückgewiesen.

(3) Die Morphologie des Grundbauplans wird am umfangreichsten bei den Mantodea Mantoididae (linker Teil) und Chaeteessidae (rechter Teil) beibehalten. Innerhalb der Blattaria sind besonders bei den Blattinae viele Merkmale des Grundbauplans erhalten, in manchen Merkmalen der Phallomeren ist diese Gruppe allerdings bereits stark abgeleitet. Die Meinung von McKittrick (1964), daß die Phallomeren der Cryptocercidae dem Grundbauplan der Blattaria besonders nahestünden, ist abzulehnen.

(4) Die Hypothese von Bohn (1987), daß die seitenverkehrten Ähnlichkeiten der Phallomeren der Blaberidae und mancher Teilgruppen der Blattellidae als Homologien anzusehen sind, wird umfassend bestätigt. Eine Entstehung dieser Ähnlichkeiten durch parallele Evolution, wie sie Mizukubo & Hirashima (1987) annehmen, erscheint äußerst unwahrscheinlich.

(5) Homologien zwischen linker und rechter Seite des Phallomerenkomplexes lassen sich nur bezüglich sehr weniger Elemente begründen. Es ist zu vermuten, daß ein großer Teil der komplexen Phallomeren-Morphologie erst ausgebildet wurde, als bereits eine deutliche Asymmetrie etabliert war. Das Konzept seitenhomologer Subregionen von Mizukubo & Hirashima (1987) und auch die Annahmen von Seitenhomologien in Grandcolas (1994) lassen sich widerlegen.

1. INTRODUCTION

Blattaria, Mantodea, and Isoptera form a holophyletic group called Dictyoptera (s. lat.; Kristensen 1995) or Blattopteroidea (Hennig 1969). The relationships between the three groups are unresolved. Hennig (1969) regards Mantodea as the sister-group of Blattaria + Isoptera, and he points out the possibility that Isoptera might be a subgroup of Blattaria – closely related to the Blattarian family Cryptocercidae. These assumptions probably reflect the most parsimonious solution, but the arguments are scarce. Thorne & Carpenter (1992) assume that Isoptera are the sister-group of Blattaria + Mantodea. However, their results are not very convincing, since for many characters the assumed polarities are questionable (Kristensen 1995; Klass 1995).

Concerning the internal phylogeny of Blattaria and of Mantodea, the current ideas are based on the extensive investigations of McKittrick (1964) and McKittrick & Mackerras (1965) (Blattaria) and on the survey in Beier (1968) (Mantodea). In terms of systematics, these authors will be followed in this paper. In some aspects the ideas of these authors are well-founded, but many points are still debatable.

Beier (1968) divides the Mantodea into 8 families: Chaeteessidae, Metallyticidae, Mantoididae, Amorphoscelididae, Eremiaphilidae, Hymenopodidae, Mantidae, and Empusidae. These are not grouped into higher-ranked categories. Chaeteessidae are more primitive than all other families in that their hind-wings have a complete second anal-vein and in that their fore-legs are beset with stout setae rather than thorns. In Metallyticidae the second anal vein is vestigial, and in the other families the vein is completely missing. Hence, Chaeteessidae seem to be the first offshoot and Metallyticidae the second.

McKittrick (1964) divides the Blattaria into two sister-groups, Blattoidea and Blaberoidea. The Blattoidea, comprising Cryptocercidae and Blattidae, do not reveal a single feature that could be unambiguously regarded as a synapomorphy of the two families. The phylogenetic position of Cryptocercidae has been reanalysed by Grandcolas (1994), who assumes that they are a subgroup of Polyphaginae. However, this assignment is also not very convincing, since many of the homology assumptions upon which this assignment is based are debatable. The Blattidae of McKittrick, comprising Blattinae, Polyzosteriinae, Tryonicinae, and Lamproblattinae, are based on features most of which can be suspected to be plesiomorphic for Blattaria, and the family might be para- or even polyphyletic. The Blaberoidea of McKittrick, including Polyphagidae, Blattellidae, and Blaberidae are founded on the presence of a pair of special compound sclerites in the ovipositor, the crosspieces. However, crosspieces are simple gonangula strictly homologous with those of the other Blattaria (Klass 1995, in press), and the holophyly of Blaberoidea is thus highly questionable. McKittrick's assumption that Blattellidae and Blaberidae are closely related is well-founded. However, the exact relations between the two families are uncertain. Interpreting the morphological results of McKittrick (1964) concerning the male and female genitalia from the viewpoint of phylogenetic systematics and parsimony, the Blaberidae would have to be regarded as a rather subordinate subgroup of Blattellidae; however, not all features are consistently supporting this view. The relations between the various subgroups of Blattellidae, which are Anaplectinae, Plectopterinae, Blattellinae, Ectobiinae, and Nyctiborinae, are also rather unclear.

The external male genitalia of Blattaria and Mantodea (the phallomere complex composed of the phallomeres) have a highly complicated morphology. The knowledge of these structures is extremely scarce. However, a large potential for phylogenetic research can be supposed to be inherent in them, and this will be used in this paper to contribute to the solution of the basic problems of Blattarian and Mantodean phylogeny.

The phallomere complex, or at least its anterior part, is concealed within a genital pouch. Abdominal sternite 9 is a saucer-shaped subgenital plate, and the pouch is mainly formed from the intersternal membrane between the sternites 9 and 10, which is deeply invaginated anteriad. The ejaculatory duct opens into this pouch, and the phallomeres are evaginations surrounding the genital opening. The phallomere complex is provided with many sclerites and muscles, and with many distinct in- and evaginations of the cuticle (formative elements such as processes, lobes, pouches, apodemes, or tendons). The structure as a whole is always completely asymmetrical. Its morphology is quite variable within Mantodea (LaGreca 1954) and extremely so within Blattaria (McKittrick 1964). In Isoptera the phallomeres are said to be missing (Weidner 1970), a situation which is, according to Matsuda (1976), an element of the neotenic traits generally observable within this taxon.

The phallomere morphology of Mantodea has been studied by Snodgrass (1937) in *Tenodera sinensis*, by Levereault (1936, 1938) in *Stagmomantis carolina*, and by LaGreca & Rainone (1949) in *Mantis religiosa*. In each of these studies the cuticular elements and the musculature are described. The three species are closely related (Mantidae, Mantinae, Mantini in Beier 1968), and their phallomeres are rather similar. LaGreca (1954) compared the cuticular elements of the phallomeres of several Mantodea. In this selection all families of Beier (1968) are represented, except for those regarded as most primitive: Chaeteessidae, Metallyticidae, and Mantoididae.

Regarding the phallomeres of Blattaria, the paper of Snodgrass (1937) is the most important of the earlier contributions. The sclerotisations and – in part – the musculature of *Periplaneta americana*, *Blatta orientalis* (both: Blattidae, Blattinae), *Blattella germanica* (Blattellidae, Blattellinae), and *Ectobius lapponicus* (Blattellidae, Ectobiinae) are described. The phallomeres of Blattidae and Blattellidae are very different from each other, and assumptions on homology relations are made only to a very small extent.

McKittrick (1964) investigated the phallomere sclerites in 24 genera of Blattaria and gives a homology hypothesis. However, the descriptions are not very detailed, and the musculature has not been studied. Thus, this homology hypothesis is not very convincing in many points. McKittrick introduced a new terminology for the phallomere sclerites: The terms are composed of several letters and numbers, each giving some information about the position and the homology relations of the respective sclerite. McKittrick regards the phallomeres of *Cryptocercus* (Cryptocercidae) as primitive within Blattaria.

Grandcolas (1994) studied the phallomere sclerites of *Cryptocercus* and some Polyphaginae and Blattinae. He finds many synapomorphies for *Cryptocercus* and (subgroups of) Polyphaginae and assigns *Cryptocercus* to Polyphaginae. However, the homology relations assumed for the sclerites are disputable in many cases.

Mizukubo & Hirashima (1987) studied the phallomere sclerites and muscles of *Periplaneta* (various species; Blattinae), *Blattella* (various species; Blattellinae), and *Opisthoplatia orientalis* (Blaberidae). They use – with some modifications – the terminology of McKittrick. The authors homologise the phallomere sclerites according to their relative positions and their mutual relations. Furthermore, they introduce a new topic into the discussion: Homologies between elements of the left and of the right half of the phallomere complex are considered. In their analysis they dismiss the musculature as a valuable reference system for homologising. The phallomeres of the stem-species of Blattaria (excluding Mantodea) are supposed to be still symmetrical. Accepting this view, the asymmetry of the phallomere complex would have to be regarded as non-homologous in Blattaria and Mantodea. In the case of Blattellidae and Blaberidae, which families show obvious but side-reversed similarities in their phallomere morphology, Mizukubo &

Hirashima assume a parallel evolution of these similarities, and they also assume a still symmetrical morphology in the common stem-species of these two families. In McKittrick (1964), the same view is indicated through the designation of the sclerites. In contrast, Bohn (1987) supposes that the phallomeres of Blaberidae have undergone a change of their left-right-asymmetry and that the similarities concerned are homologous. The point of discussion is the same in the case of Plectopterinae, whose phallomeres also show side-reversed similarities with the other subfamilies of Blattellidae.

The knowledge of the morphology of the phallomeres and the other parts of the male postabdomen of Blattaria and Mantodea is extremely incomplete. The few hypotheses concerning homology relations (between species and between the left and right halves of the phallomere complex), the ground-plan, and the evolution of the phallomeres are not very convincing. Furthermore, nothing is known about homology relations between the phallomeres of Blattaria and Mantodea. Thus, there is compelling need for a large-scaled morphological investigation of the phallomere complex.

To do this is the intention of this paper. Phallomere morphology will be analysed in Blattarian and Mantodean species representing the various subgroups. This investigation should be as detailed as possible in order to avoid misinterpretations due to superficial observation and in order to get as many arguments as possible for assumptions and conclusions. The homology relations between the various species will be worked out in detail, and possible homologies between the left and the right side of the phallomere complex will be considered. The ground-plan features of the phallomeres will be reconstructed – focused on the common ground-plan of Blattaria and Mantodea, if there is one. The special condition of the phallomere elements in the various species and their evolution will be discussed in detail. The characters of the phallomeres will be evaluated in order to establish a phylogenetic hypothesis for Blattaria and Mantodea. The terminology for the phallomere elements will be based on the common ground-plan of Blattaria and Mantodea – in accordance with the homology relations assumed. A standardised, well-founded, and well-defined use of the terminology might also be valuable for taxonomic research and the description of species.

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2. MATERIAL AND METHODS

Species investigated

- Mantodea
  - Mantoididae *Mantoida schraderi* Rehn, 1951
  - Chaeteessidae *Chaeteessa caudata* Saussure, 1871
  - Metallyticidae *Metallyticus violaceus* Burmeister, 1838
  - Mantidae *Sphodromantis* Stal, 1871 (sp. indet.); *Mantis religiosa* (Linné, 1758)
- Blattaria
  - Blattoidea
    - Cryptocercidae *Cryptocercus punctulatus* Scudder, 1862
    - Blattidae
      - Blattinae *Archiblatta hoeveni* Sn. v. Vollenhoven, 1862; *Blatta orientalis* Linné, 1758; *Deropeltis* Burmeister, 1838 (sp. indet.); *Periplaneta americana* (Linné, 1758)
      - Polyzosteriinae *Eurycotis floridana* (Walker, 1868)
      - Tryonicinae *Tryonicus parvus* (Tepper, 1895); *Tryonicus angustus* (Chopard, 1924)
      - Lamproblattinae *Lamproblatta albipalpus* Hebard, 1919
  - Blaberoidea
    - Polyphagidae
      - Polyphaginae *Polyphaga aegyptiaca* (Linné, 1758); *Ergaula capensis* (Saussure, 1893); *Ergaula capucina* (Brunner v. W., 1893)
    - Blattellidae
      - Anaplectinae *Anaplecta* Burmeister, 1838 (sp. indet.)
      - Plectopterinae *Nahublattella* Bruijning, 1959 (sp. indet.); *Euphyllodromia angustata* (Latreille, 1811); *Supella longipalpa* (Fabricius, 1798)
      - Blattellinae *Parcoblatta lata* (Brunner v. W., 1865); *Loboptera decipiens* (Germar, 1817)
      - Ectobiinae *Ectobius sylvestris* (Poda, 1761)
      - Nyctiborinae *Nyctibora* Burmeister, 1838 (sp. indet.)
    - Blaberidae *Blaberus craniifer* Burmeister, 1838; *Byrsotria fumigata* (Guérin-Méneville, 1857); *Blaptica* Stal, 1874 (sp. indet.); *Nauphoeta cinerea* (Olivier, 1789)

The assignment of the respective genera to the various taxa is adopted from McKittrick (1964) and Beier (1968). The only exceptions are: The assignment of *Tryonicus* is taken from McKittrick & Mackerras (1965). *Polyphaga* and *Ergaula* are assigned to Polyphaginae according to Grandcolas (1994). *Euphyllodromia* is assigned to Plectopterinae by Roth (1967). *Archiblatta* is in its phallomere morphology rather close to *Deropeltis* (McKittrick 1964, fig.108), which is assigned to Blattinae by McKittrick (1964). *Nahublattella* is in its phallomere morphology very close to *Lophoblatta* (McKittrick 1964, fig.113), which is assigned to Plectopterinae by McKittrick (1964).

In the subsequent text these species will be named by their generic name alone. (*Tryonicus* is always *T. parvus*, *Ergaula* is always *E. capensis. T. angustus* and *E. capucina* will be addressed by their complete names).

Sphodromantis, Mantis, Deropeltis, Periplaneta, Blatta, Eurycotis, Supella, Parcoblatta, Loboptera, Blaberus, Nauphoeta, Blaptica, Byrsotria, Ergaula capucina, and *Polyphaga* have been reared in the laboratory and were available as freshly killed specimens. *Lamproblatta, Anaplecta, Nahublattella, Euphyllodromia, Nyctibora*, and *Mantoida* have been stored in 4% formaldehyde, *Cryptocercus* and *Ectobius* in 70% isopropanol. *Chaeteessa, Metallyticus, Archiblatta*, the two *Tryonicus*-species, and *Ergaula capensis* were dried specimens.

Preparation

For the examination of the musculature the abdomina were cut off and stored in 75% isopropanol for at least three days. For the study of cuticular elements the soft tissues were removed by treating the abdomina with 10% KOH for 4-20 hrs. at 40°C. The remaining cuticular structures were then washed in distilled water and stored in 75% isopropanol. Descriptions of morphological structures are always based on preparations of several specimens, with the exception of some species of which only one or two specimens were available (*Mantoida*, *Chaeteessa*, *Metallyticus*, both species of *Tryonicus, Ergaula capensis, Archiblatta*). Preparation was performed with sharp forceps and iris scissors. In the observation of small and weakly sclerotised structures it was sometimes useful to underlay the object with a piece of aluminium foil.

Remarks on the figures 1-319

- In all figures anterior is towards the top and posterior is towards the bottom of the sheet.
- The cuticle generally has an internal surface, which is in contact with the epidermis, and an external surface. In all figures the cuticle is partly seen from internally and partly from externally.
- Dark areas are sclerotised; white areas are membranous.
- Muscles are hatched longitudinally, in correspondence with the course of their fibers.
- In each figure only those structures are shown which can be directly seen by the observer and which are not covered by other structures. Thus, e.g. sclerites covered by membrane are not shown, even if they can be easily seen through the membrane in an original preparation.
- Mostly the cuticle is very thin, and in drawing it is regarded as a convoluted plane without thickness. Only in some cases when the cuticle is strongly thickened its thickness is considered in drawing.
- In drawing, the geometry of the cuticular foldings and of the other elements is strictly held to. Continuous black lines represent edges. Edges are understood throughout as lines along which the cuticle or the surface of a muscle curves beneath itself and thus vanishes from the observer's view. What appears as an edge is dependent on the angle of view. Edges of the cuticle can be external or internal: External edges are directed to the exterior, and along them the external surface of the cuticle is visible; internal edges are directed to the interior of the body, and along them the internal surface of the cuticle is visible. Edges beneath the visible surface are sometimes drawn as broken lines.

- The boundaries of the insertion areas of muscles are also shown by continuous black lines if they are directly visible. Parts of these boundary lines which are covered by the muscle itself or by other structures are drawn as broken lines. In some cases the insertion areas alone are drawn without the respective muscles (mainly in the figures showing the subgenital plates, e.g. fig.5); the boundary of the insertion area is again shown by a continuous black line.
- Undulate lines are cutting lines (through cuticle of normal thickness) or bound cut surfaces (of muscles or strongly thickened cuticle cut through).
- The series of figures pertaining to a certain species has as a whole been worked out with the intention of showing all relative positions of all elements of the phallomeres, including all the membranous foldings.
- The series of figures for the various species are designed for the best possible comparability. For example, in the overall views of the postabdomina (compare fig.1, 2, 3 and fig.58, 59, 60) the cutting lines have the same course in each species (their courses are, so to speak, homologous), and, if present, the same muscles are shown. Or, the right phallomeres of Blattaria are always shown in the same four aspects.

Remarks on homology

As a principle, elements regarded as homologous will be given the same name, and elements given the same name are regarded as homologous. Minor exceptions to this rule, mainly due to a not very high probability of homology, will be explicitly mentioned in the text.

Mainly the criteria of the relative position and of the special structure (1. and 2. major criteria of Remane 1952) will be used in this paper. These will be applied to the following kinds of structures, whose relative position and special structure will be comprehensively discussed in the homology analysis:

- Sclerotised areas of the cuticle (sclerites).
- Articulations or other special relations between sclerites.
- Formative elements: more or less distinct evaginations or invaginations of the cuticular surface of the phallomere complex (processes, ridges, pouches, tendons, apodemes, lobes, etc.).
- Insertion areas of muscles.
- The opening of the ejaculatory duct or genital opening.
- The opening of the phallomere-gland (a gland within the left part of the phallomere complex).

The sclerotisations of the phallomeres will be divided into areas which are strictly homologous in the different species. These areas are the main sclerites (or sclerite groups, if these main sclerites have split into several isolated sclerites) and – as their subunits – the sclerite regions. Some difficulties arise in this demarcation of homologous areas within the cuticular surface of different species and in the standardisation of this procedure. The following example shall illustrate these problems: Provided: In two compared species *A* and *B* homology is certain (as much as it can be) for a sclerite as well as for a muscle. In species *A* the muscle inserts on the sclerite, in species *B* the muscle inserts on the membrane next to the sclerite. The situation in *A* is primitive, the situation in *B* is derived. The derivation which *B* shows as compared with *A* can be interpreted in two different ways: (1) In *B* the insertion of the muscle has shifted from the sclerite to the membrane. (2) In *B* the sclerite has diminished and has "lost" the insertion of the muscle. According to (1) the sclerites of the two species are homologous in a strict sense. According to (2) they are homologous only in part, since in species *B* part of the sclerotisation has been lost. In one peculiar case the special circumstances can suggest an interpretation according to either (1) or (2). In many cases, however, an objective decision in favor of one of the two alternatives is hardly possible, and it is debatable whether a discussion of such a case is of importance at all. The interpretation will then be done in that way which seems to be more suitable for the explanation of homology relations.

3. GENERAL DESCRIPTION AND MORPHOLOGICAL DISCUSSION OF THE POSTABDOMEN AND OF THE MALE GENITAL REGION OF DICTYOPTERA

The postabdomen of male Dictyoptera comprises the abdominal segments 9-11 and the telson, which contains the anus (Snodgrass 1937). Matsuda (1976) postulates a twelfth segment for the ground-plan of insects, and this would also affect the interpretation of the Dictyopteran postabdomen. According to Matsuda himself, p.52, however, this "segment" contains neither mesoderm rudiments, nor ganglion rudiments, nor appendage rudiments. Thus, it does not fulfil either criterion to be regarded as a segment. This "twelfth segment" could be regarded as a (highly reduced) segment, if it is demonstrated to be homologous with a true segment (containing mesoderm) of another group of Arthropoda, having lost its segmental organs secondarily. This, however, has not been shown. Therefore, the twelve-segment-theory of Matsuda is not followed here.

Subsequently the general morphology of the postabdomen and the phallomeres of Blattaria and Mantodea will be described. This will essentially be a description of the common ground-plan of Blattaria and Mantodea, whose reconstruction will be substantiated step by step later on in this paper.

3.1. The cuticular elements

Abdominal segment 9

The sternite of segment 9 (subgenital plate, **S9** in fig.320, 321) always forms a large lobe-like extension to the posterior, which reaches or even exceeds the morphological posterior end of the body (with the anus **Af** in fig.320, 321c). Most species have a large membranous or only weakly sclerotised area in the anterior half of the subgenital plate (**M** in fig.320, 321b,d,k). The (heavier) sclerotisation is continuous in antero-posterior direction only in the lateralmost parts, to the left and to the right of area **M** (fig.321k). The lateral parts of the subgenital plate (**S9l** in fig.321k) curve upwards. The posterior edge of the subgenital plate bears styli (**S9s** in fig.320, 321b,d,k).

Along the anterior margin of the subgenital plate the intersternal membrane connecting sternites 8 and 9 adjoins and bends back sharply to the posterior margin of sternite 8 (compare fig.320). A more or less extensive anterior part of the subgenital plate is thus concealed by the posterior part of sternite 8 from ventrally and can be regarded as a broad apodeme or internal apophysis. The paired parts which project especially deeply anteriad (**S9a** in fig.321b,d,k) are the lateral sternal apodemes or apophyses; these paired parts will be designated as the apophyses of the subgenital plate subsequently. The summits of what I call apophyses can reasonably be regarded as homologous in the various species though they can take various positions from far lateral (like in fig.265) to far medial (like in fig.22). However, strict homology is certainly not true for the whole apophyses (= paired parts): The apophyses can be separated from each other to the far posterior (like in fig.265), the paired parts being very long, or the whole median part of the subgenital plate is produced far anteriad and only the anteriormost parts show the paired condition (like in fig.296). The apophyses present in the latter situation seem to correspond only to the anteriormost parts of the apophyses present in the former situation, and probably some median fusion has taken place in the posterior part. Hence, the term "apophysis" as used here is not intended to claim strict homology.

According to Walker (1922) and other authors, the subgenital plate is not the sternite of segment 9 only but is probably composed of: (1) the true sternite 9 (the part anterior to **M**); (2) the paired but medially fused coxites of segment 9 – probably serially homologous with the thoracic coxae or with more extensive basal parts of the thoracic appendages. If this composition is true, the subgenital plate is a coxosternite. The styli **S9s** sitting upon the coxites are probably serially homologous with distal parts of the thoracic legs.

The tergite of segment 9 (**T9** in fig.320, 321a) resembles the more anterior tergites, but like tergite 8 it is rather short. Its lateral parts (= paratergites, **T9p** in fig.321b) incline ventrad from the dorsal main part – often along a distinct edge. The ventral margins of the paratergites overlap in most cases, and to a varied extent, the lateral parts of **S9**.

The position of the phallomere complex

The intersternal membrane between sternites 9 and 10 is deeply invaginated anteriad to form the walls of the funnel-shaped genital pouch: The ventral wall of this pouch extends anteriad from the lateral and posterior edges of the subgenital plate (**Vw** in fig.321k, left half, fig.320). The dorsal wall extends anteriad from the anterior margins of the paraprocts **Pp** and **Pv**-sclerites (**Dw** in fig.320, 321b). The lateral walls extend anteriad from the posterior edge of the pleural membrane between tergite 9 and subgenital plate (**Sw** in fig.321b,d).

Deep in the genital pouch the cuticle turns posteriad again and forms the walls of the phallomere complex. The edge or line of turning, along which the walls of the genital pouch meet the walls of the phallomere complex, will be called the basal line (**Bl** in fig.320, 321b,d). Hence, the phallomere complex seems to be exclusively an elaboration of the intersternal area between sternites 9 and 10. The ejaculatory duct (**D** in fig.321b,d,e,g) opens on the phallomere complex.

In many Blattaria and Mantodea, the ventral wall of the genital pouch (**Vw** in fig.320, 321k), which covers the posterior part of the subgenital plate from dorsally, contains a sclerotisation (**S9d** in fig.320, 321b,d,k). **S9d** is regarded as a dorsal sclerotisation of the subgenital plate and is possibly the sclerotisation of the dorsal walls of the fused coxites and hence a part of the appendages of segment 9. This **S9d** can be either separated from or connected with the ventral main sclerotisation of the subgenital plate (around the lateral and posterior edges of the plate, as in fig.321k), and it may either occupy an extensive part of the ventral wall of the genital pouch or is restricted to the marginal areas close to the edges of the subgenital plate. The sclerotisations comprised in **S9d** are certainly not homologous in a strict sense throughout the species.

The phallomere complex

The phallomere complex will be divided into two main parts belonging to the left and to the right half of the body: left complex and right phallomere. This major division is shown in fig.321e and f, where the two parts are separated (compare fig.321d). Both are complicated structures with intensively folded cuticle and with sclerotised and membranous areas. Left complex and right phallomere are extremely asymmetrical in all Blattaria and Mantodea. The phallomere-gland (penis-gland, conglobate gland; **P** in fig.321e) opens on the left complex; at least its outlet channel is cuticulised. Since the morphology of the phallomere complex is highly variable within Blattaria and Mantodea, a description valid for all subgroups is impossible. The following description corresponds to the common ground-plan of Blattaria and Mantodea. In addition, some important derived states will be mentioned.

Left complex

Several left-lateral and ventral sclerites are designated **L4** (fig.321e,g,i): A large crescent-shaped **L4**-sclerite occupies the left edge of the left complex, including the adjacent margins of the dorsal and ventral walls, and the anteriormost ventral wall. Along most of this sclerite there runs an apodeme (**swe** in fig.321e,g), which is groove-like posteriorly but solid and beam-like anteriorly (the groove is filled in by the cuticle becoming thickened). The posteriormost part of the sclerite occupies a short process (**pda** in fig.321e,g). As a derived condition, the dorsal part of the sclerite can be strongly expanded to the right, and the dorsal and the ventral parts of the sclerite can be separated. A second, plate-like **L4**-sclerite lies in the right ventral wall. Another **L4**-sclerite in the anterior left ventral wall bears a node-like process (**nla** in fig.321i; present in Blattaria only). These three **L4**-sclerites can be separated from or connected with each other in the anterior ventral wall.

In the central and right parts of the left complex there are two pouches invaginated anteriad, which lie one above the other. The walls of the dorsal pouch (**pne** in fig.321e,n) are largely occupied by the hood-shaped sclerite **L1**. The phallomere-gland (**P** in fig.321e) opens into this **pne**-pouch. The ventral pouch (**lve** in fig.321e,g) contains the **L2**-sclerite, which is often restricted to the dorsal wall of the pouch and extends like an arch along its anterior and lateral margins. The left posterior part of sclerite **L2** leaves the **lve**-pouch and extends onto a process (**paa** in fig.321e,g) immediately to the right of the **pda**-process. The sclerotisations of **L4** and **L2** are connected in between the processes **pda** and **paa**. The right end of sclerite **L2** articulates with sclerite **L1** (articulation **A2** in fig.321e,n).

The ventral wall of the **lve**-pouch is almost completely membranous, and it is at the same time the left-anterior part of the dorsal wall of a large ventral lobe (**vla** in fig.321e,g,i). The ejaculatory duct (**D** in fig.320, 321g) opens into this wall. In some species this wall contains a small sclerite **L5** (fig.321e,g). The ventral wall of the **vla**-lobe is part of the ventral wall of the whole left complex and is largely occupied by the right-ventral **L4**-sclerite (fig.321g,i).

All Blattaria, but not Mantodea, have a large hook-like evagination from the left ventral wall of the left complex (**hla** in fig.321i). The **hla**-hook is largely occupied by sclerite **L3**, but a more or less extensive basal part is membranous (**30** in fig.321i). This membrane can be introverted, which procedure results in a more or less deep retraction of the hook into the left complex.

Right phallomere

The anteriormost ventral wall is occupied by the plate-like sclerite **R3** (fig.321f,h). Along the lateral and anterior margins of **R3** (parts of the basal line **Bl**) the sclerotisation of **R3** extends somewhat into the wall of the genital pouch, and these margins of sclerite **R3** form a groove- (as seen from externally) or fold-like (as seen from internally) apodeme **age** (fig.321f,h). Like in the **swe**-apodeme, parts of this **age**-apodeme can be filled in by the cuticle becoming thickened, and the respective parts of **age** are beam-like.

Behind the central part of **R3** the ventral wall is extensively invaginated dorsad and anteriad (**cbe** in fig.321f,h), and this invagination is partly sclerotised in its dorsal wall (anterior part of sclerite **R1** in fig.321f). Blattaria, but not Mantodea, have a sclerite **R2** left-ventral to the **cbe**-invagination (fig.321f,h), which articulates with the left posterior end of **R3** (articulation **A7** in fig.321f) and with the left end of **R1** (articulation **A6** in fig.321f). Sclerite **R2** and the posterior margin of the anterior part of **R1** often form tooth- or ridge-like cuticular evaginations (on **R1**: **pva** in fig.321h).

The part of the right phallomere posterodorsal to the **cbe**-invagination is composed of a large dorsal lobe (**fda** in fig.321f) and a ventral tooth (**pia** in fig.321h, which is in most species much smaller than the **fda**-lobe). The **fda**-lobe and the **pia**-tooth are confluent along the right edge of the right phallomere, and they diverge to the left. The dorsal wall of the **fda**-lobe – and often parts of its ventral wall, too – as well as the dorsal and ventral walls of the **pia**-tooth are occupied by the posterior part of sclerite **R1**. The sclerites **R1** and **R3** articulate with each other at the anterior right edge of the right phallomere (articulation **A3** in fig.321f,h). In the anteriormost dorsal wall of the **fda**-lobe, part of the cuticle is invaginated to form a hollow, long and narrow, membranous tendon (**tre** in e.g. fig.74; not shown in fig.321), which is present in some Blattaria only.

Discussion of the basic division of the phallomere complex

I propose this division of the phallomere complex into a left complex and a right phallomere. However, earlier suggestions for a basic division differ from this hypothesis: Snodgrass (1936, 1937) divides the phallomere complex of Blattinae into a ventral, a right, and a left phallomere. Beier (1970) follows Snodgrass regarding Blattaria as well as Mantodea, and he terms these main divisions hypophallus, right epiphallus, and left epiphallus. The ventral phallomere (= **vla**-lobe in the previous description) lies ventral to the genital opening (in a strict morphological sense anterior to it); i.e. the genital opening is in its anteriormost dorsal wall. The right phallomere (= right phallomere in the previous description) and the left phallomere (= left complex minus the **vla**-lobe) have their bases in the areas dorsal (in a strict sense: posterior) and lateral to the genital opening. Snodgrass (1937) deduces this basic division from his investigations of the ontogenetic stages of the phallomere complex in *Periplaneta americana* and *Blatta orientalis* (both: Blattinae): In medium-sized nymphs the phallomere complex consists of three distinct lobes, which hardly reveal any further elaborations. One lobe is situated medioventral to the prospective genital opening (prospective ventral phallomere), the other two take positions dorsolateral to the genital opening (prospective right and left phallomeres). Thus, a composition of a medioventral, a right-dorsal, and a left-dorsal basic element seems plausible, and according to Snodgrass (1937) the ventral phallomere is an unpaired medioventral element.

Quadri (1940) studied the ontogeny of the phallomere complex of *Blatta orientalis* in more detail. In first instar nymphs he finds one pair of lobes with an invagination between them (rudiment of ejaculatory duct). In the third instar each lobe is divided into a dorsal and a ventral secondary lobe, and thus four lobes surround the prospective genital opening. Later, the two left lobes form the left phallomere (more or less by fusion, without any clear border remaining). The ventral right lobe shifts to the left, into a position beneath the genital opening, and becomes the ventral phallomere. The dorsal right lobe maintains its position and becomes the right phallomere. Thus, according to Quadri, the ventral phallomere is a ventral part of the right half of the phallomere complex. Later Snodgrass (1957) took over the opinion of Quadri but still used the tripartite division in his terminology.

Concerning the assignment of the ventral phallomere, or ventral lobe **vla**, my own observations as well as the mode of innervation (Pipa 1988) are in conflict with the views of both Snodgrass (1937) and Quadri (1940):

In some aberrant specimens of Blattaria the phallomere complex is completely symmetrical. I could find two such specimens: (1) *Polyphaga aegyptiaca* (Polyphaginae) with two "right" phallomeres being mirror-images of each other; there was no trace of a ventral phallomere, which is present in normal specimens. Unfortunately, the specimen had been dried and macerated, and the relations to the internal genitalia and the presence of an ejaculatory duct could not be investigated. (2) *Deropeltis* sp. (Blattinae) with two "left" phallomeres and two complete ventral phallomeres, both pairs being mirror-images of each other. The phallomere-gland is paired. The ejaculatory duct is, as usual, unpaired. It opens in the median plane – in that area where the dorsal walls of the left and the right ventral phallomeres are confluent with each other. Thus, the location of the genital opening – in relation to the ventral phallomeres – is the same as in normal specimens, and the two ventral phallomeres are arranged in a way that this relative position is true of both of them.

Pipa (1988) studied the innervation of the male postabdomen in *Periplaneta americana*: From the posterior part of the last abdominal ganglion – a compound ganglion formed from the ganglion rudiments of abdominal segments 7 to 11 – one pair of nerves runs to the phallomeres (phallic nerve = nerve **5a** in Pipa). Their basal branchings are symmetrical. After entering the phallomeres, where the branches innervate the phallomere muscles, the branching pattern becomes completely asymmetrical. The ventral phallomere gets its innervations exclusively from branches coming from the left nerve.

The morphology of the two symmetrical specimens and the innervation pattern suggest that the ventral phallomere is neither an unpaired ventromedian element of the phallomere complex nor a part of its right half but a lobe-like part of its left half. I term it the **vla**-lobe, and the left and ventral phallomeres together I term the left complex. There is another, more practical (though not decisive) reason for this concept: The morphological relations between the left phallomere and the ventral phallomere are often very close, and the border between them is in many cases not very distinct. And this is with high probability the ground-plan situation (like in fig.321e,i). However, the question of the correct assignment of the ventral phallomere or **vla**-lobe is certainly not finally settled.

The homology relations between the phallomere elements of Blattaria and Mantodea on the one hand and the elements of the external genitalia of other Ectognathan taxa on the other are completely unclear. Only the earliest rudiments or primary phallic lobes can be reliably regarded as homologous.

The abdominal segments 10 and 11 and the telson

This morphologically posteriormost part of the body lies dorsal to the phallomere complex and covers it completely (Blattaria) or partly (Mantodea) (fig.320, 321a,b). For many sclerotisations of this region it is unclear whether they belong to abdominal segment 10 or 11 or to the telson, or to the segment 12 proposed by Matsuda (1976).

Description of morphology

The principal morphology of this area is in Blattaria and Mantodea always quite similar: Tergite 10 (**T10** in fig.320, 321a,b) is somewhat triangular by a more or less pronounced expansion of its median part to the posterior. Along the posterior edge of tergite 10 (**X** in fig.320, 321a,b) the cuticle bends sharply ventrad and anteriad, and the sclerotisation of **T10** often – and to a varied extent – follows this bend and forms the ventral sclerotisation of tergite 10 (**T10v** in fig.320, 321b). In some species tergite 10 is longitudinally divided along its midline by a stripe of membrane (a derived condition).

The cerci (**E11** in fig.321a,b) are the appendages of abdominal segment 11. They have their bases laterally beneath the posterior edge of tergite 10. The basal article of each cercus has at its dorsal basal margin a distinct articulation with a node-like thickening on the posterior margin of tergite 10 (articulations **A98** in fig.321b and e.g. fig.58). Median to the cercal bases there may be some further sclerotisations (three pairs at most; not shown in fig.321): The crescent-shaped **Ca**-sclerites (e.g. in fig.263) are close to the cercal bases and often lie upon distinct bulge-like evaginations. The **Cb**- and **Cc**-sclerites take more median positions (e.g. in fig.169, 170).

The anterolateral parts of tergite 10 curve ventrad and then mesad; these parts are the paratergites (**T10p** in fig.321b,c), which take a position posterolateral to the phallomere complex. The ventromedian ends of the paratergites **T10p** are in most species distinctly articulated with the lateral ends of the paraprocts **Pp** (articulations **A99** in fig.321b,c).

Median to the paratergites **T10p** and beneath the **T10v**-sclerotisation there is on each side a transverse (or oblique) bulge, the subanal lobe (**sbl** in fig.321b,c). The paraprocts **Pp** are always present as one pair of sclerites (fig.321b,c). From their lateral ends at the articulations **A99** they extend mesad and sclerotise more or less extensive parts of the subanal lobes **sbl**. Laterally the paraprocts are restricted to the ventral **sbl**-walls, medially they curve more and more into their dorsal walls (fig.321b,c). Consequently, the posterior parts of the paraprocts are curved upwards and back anteriad, and the paraprocts have a ventral anterior margin and a dorsal anterior margin. (The latter will subsequently be designated as the posterior margin, which is true in a strict morphological sense). The median tips of the subanal lobes (**Y** in fig.321b,c) lie on both sides of the anus (**Af** in fig.321c) and are either membranous or also sclerotised by the paraprocts. The median walls of the subanal lobes continue anteriad into the lateral walls of the rectum (**Re** in fig.321b,c).

In front of the (ventral) anterior margins of the paraprocts there is often another pair of ribbon-shaped sclerites (**Pv** in fig.320, 321b,c). These **Pv**-sclerites are either completely free (like in fig.321) or connected with the paraprocts laterally. In some species separate **Pv**-sclerites are missing, and in these cases they seem to have fused to the anterior margins of the paraprocts.

The membrane anterior to the ventral sclerotisation of tergite 10 (**T10v** in fig.321b) is evaginated to form an unpaired supraanal lobe (**spl** in fig.320, 321b,c), whose ventral wall continues anteriad into the dorsal wall of the rectum (**Re** in fig.320, 321b,c). In Mantodea the supraanal lobe bears a sclerotisation in its dorsal wall, the epiproct (**Ep** in fig.320, 321b,c). In many Blattaria the supraanal lobe is still distinct but never has a sclerotisation. In other Blattaria the supraanal lobe is no longer distinct from other small membranous foldings in the anal region, and its presence is questionable.

Discussion of morphology

Concerning all these elements, only the assignment of the anterior part of tergite 10 (**T10** including **T10p**) to abdominal segment 10 and the consideration of the cerci as the appendages of segment 11 is generally accepted. Regarding the other elements there are various opinions. Snodgrass (1933, 1936, 1937) regards the cerci and the subanal and supraanal lobes as elements of segment 11, the paraprocts being the medially divided sternite and the epiproct being the tergite of segment 11. Sternite 10 is assumed to be missing, tergite 10 is the true tergite 10, with no other elements incorporated, and the telson is only a small membranous ring surrounding the anus. Chopard (1917), Walker (1922), and Ford (1923) differ from Snodgrass only in assuming a participation of sternite 10 within the anterior margins of the paraprocts. This is said to be indicated by the articulations between the paraprocts and the paratergites of segment 10 (**A99** in fig.321b,c) and by some muscle insertions. In complete contrast to these authors, Heymons (1895) and Matsuda (1976) consider segment 11 as strongly reduced – the cerci being its only persisting products – and regard the subanal lobes and the paraprocts as well as the supraanal lobe and the epiproct as elements of the telson (Heymons) or of a twelfth segment (Matsuda; the only difference to Heymons is that Matsuda regards this posteriormost part of the body as a segment). Matsuda regards tergite 10 of Mantodea as a proper one, but tergite 10 of Blattaria is supposed to contain the epiproct.

These differences in the interpretation of the terminal elements are accompanied by a confused situation in the terminology for these structures. This concerns the usage of e.g. the terms subanal lobe, supraanal lobe, epiproct, paraproct, tergite 11, sternite 11, and telson. The comparison of the results of the various authors is thus rather difficult. For a correct interpretation of the elements concerned some clarifying investigations of ontogeny and morphology would be necessary. To do this is not the purpose of this paper, and the terminology for the respective elements subsequently practised is a descriptive one, not the morphologically correct one.

These controversial opinions, however, have to be discussed as far as homology relations within Dictyoptera are involved. This concerns the elements called tergite 10 **T10** and supraanal lobe **spl** in the above description (fig.320, 321), which are, according to Matsuda (1976), both not homologous in Mantodea on the one hand and in Blattaria and Isoptera on the other. (This difference is the same for females). Matsuda's opinion is as follows: Blattaria and Isoptera show in their ontogeny a very early differentiation of a supraanal lobe (meaning of supraanal lobe here: the dorsal part of the embryonic telson – Heymons – or segment 12 – Matsuda; not the structure called **spl**-lobe above!). By the extensive reduction of segment 11 during embryonic development this supraanal lobe comes into a position immediately behind abdominal tergum 10. The dorsal segmental border between supraanal lobe and tergum 10 then vanishes and these regions become fused. Thus, in the imago the sclerite called "tergite 10" **T10** above is regarded as a compound sclerite containing the true tergite 10 and the epiproct (the latter considered as the tergite of the telson or of the twelfth segment, respectively). In Mantodea, however, the differentiation of this supraanal lobe is delayed until postembryonic development. No fusion of supraanal lobe and tergum 10 takes place. Thus, in the Mantodean imago "tergite 10" **T10** is the true tergite 10, and the epiproct **Ep** is still situated behind it as a separate sclerite on an independent supraanal lobe.

If this is true, the element I call supraanal lobe **spl** (fig.321b) would be: (1) the supraanal lobe sensu Heymons and Matsuda in Mantodea (dorsum of telson or segment 12); (2) a posterior part of the supraanal lobe sensu Heymons and Matsuda in Blattaria / Isoptera (a lobe-like posterior part of the dorsum of the telson or segment 12). The condition in Mantodea, if not regarded as a neotenic trait, would be more primitive than the situation in Blattaria and Isoptera.

Matsuda (1976) refers to the results of earlier workers: Heymons (1895), Wheeler (1889), and Cholodkowsky (1891) for Blattaria; Graber (1890), Hagan (1917), Görg (1959), and Walker (1919, 1922) for Mantodea. From the data contained in these papers the following view results:

- Looking at the descriptions in Heymons, the fusion between tergum 10 and the dorsal part of the telson (or segment 12) really seems to take place in Blattaria.

- In Graber, Hagan, and Görg, however, I could not find any observation contradicting the same fusion in Mantodea: None of these authors treats the development of the region concerned in sufficient detail.
- Matsuda agrees with Walker and also Snodgrass (1933), p.73, and (1936), p.42, about Mantodea: Supraanal lobe and tergite 10 are not fused, and tergite 10 of the adults is a proper one. The two latter authors (the only ones from whom Matsuda could have adopted his assumption for Mantodea), however, make the same assumption for Blattaria, too. They regard – as I did in the above description – the membranous lobe (**spl** in fig.320, 321b) of Blattaria as homologous with the **spl**-lobe of Mantodea. Thus, the opinions of Walker and Snodgrass for Mantodea cannot – in a comparison with the results of Heymons for Blattaria – serve to state a difference between Blattaria / Isoptera and Mantodea.
- Accepting Heymons' results, in Blattaria the supraanal lobe sensu Walker and Snodgrass (= **spl**-lobe in my terminology) is posterior to or a posterior part of the supraanal lobe sensu Heymons. According to Matsuda, in Mantodea the former (**spl**-)lobe is differentiated in a postembryonic stage. Such a late elaboration of the **spl**-lobe is possibly also true of Blattaria (and Isoptera?); at least, to my knowledge, an embryonic rudiment of this lobe is not mentioned in the literature.
- Thus, no argument comes from the data used by Matsuda to contradict the homology of the **spl**-lobes of Blattaria and Mantodea. The assumption of a difference between Blattaria and Mantodea is based upon a comparison of non-comparable data.

Hence, the elements I call supraanal lobe **spl** and tergite of segment 10 **T10** might both be regarded as homologous in Blattaria and Mantodea – whatever structures these may be in a strict morphological sense. Moreover, there are some arguments supporting these homologies: (1) The supraanal lobe of Mantodea and the membranous lobe found in many Blattaria (**spl**) show exactly the same relations to surrounding elements – namely those shown in fig.320, 321b,c. (2) My own investigations of the musculature of the respective region in *Sphodromantis* (Mantodea), *Lamproblatta, Eurycotis*, and *Cryptocercus* (Blattaria) had the result that muscle insertions are present neither on the lobe of *Sphodromantis* nor on that of the Blattarian species, and the relations of these lobes to the surrounding muscles are the same in both groups. (3) Investigations in the same species show that the tergites 10 are provided with the same sets of muscle insertions. An unpaired muscle running from the posterior part of tergite 10 to the rectum (present in all these species) could be the musculus epiprocto-analis (Weidner 1982). The position of its dorsal insertion might support the view that the true epiproct has been incorporated into tergite 10 in both Blattaria and Mantodea.

3.2. The musculature

Most muscles are compact, and the insertion areas are well-defined. Some others, however, are rather diffuse, and it is not possible to exactly demarcate their insertion areas. (Such a diffuse condition will be mentioned in the muscle lists in chapter 5.). The data given in the figures must be considered with these reservations.

According to their morphological arrangement, the following groups of muscles can be distinguished:

Phallomere muscles: Intrinsic muscles of the phallomere complex. All muscles of this group will be studied. Three subgroups will be distinguished:
a) Intrinsic muscles of the left complex.
b) Intrinsic muscles of the right phallomere.
c) Muscles connecting the left complex and the right phallomere.

Phallomero-sternal muscles: Muscles connecting parts of the phallomere complex or the ventral and lateral walls of the genital pouch with the subgenital plate. All muscles of this group will be studied.

Ventral muscles: Muscles connecting successive sternites (mainly the respective anterior margins). These muscles are, compared with the more anterior segments, quite reduced in the postabdomen. Only the muscles belonging to abdominal segment 9 (running from sternite 9 to the – possibly obsolete – sternite 10) will be studied.

Dorsal muscles: Muscles connecting successive tergites. In some species lateral parts of the dorsal muscles of segment 9 have shifted in a way that they can hardly be recognised as dorsal muscles but seem to be muscles from the tergite to the phallomere complex. Only these parts of the dorsal muscles will be studied.

Dorsoventral muscles: Muscles connecting tergite and sternite of the same segment. If there really are vestiges of appendages contained in the subgenital plate, some of the muscles included here might be muscles from the tergite to the appendages. These muscles will be considered only in part.

Rectal muscles: Muscles from the ectodermal rectum to e.g. the anterior margin of the subgenital plate, the tergite 10, or the paraprocts, which function as dilators or suspensors of the rectum. These have in most cases clearly demarcated insertion areas on the respective parts of the exoskeleton, but the fibers diverge like a fan on their way to the rectum, and the rectal insertions are composed of many small insertion areas, which are often widely separated from each other. Only those muscles inserting on the subgenital plate will be considered.

Muscles of the ejaculatory duct: The ejaculatory duct is covered by a mat of fibers showing a ring-like, spiral, or longitudinal arrangement. This musculature will not be investigated in detail.

4. TERMINOLOGIES AND ABBREVIATIONS

4.1. The terminology for the sclerites of the phallomere complex

Mantodea

The most elaborate terminology is that of LaGreca (1954). It is the only one that is based on quite detailed investigations of phallomere morphology and that has already been applied to a broader sample of species. However, some disadvantage lies in the fact that LaGreca uses some names for sclerites as well as for the formative elements of the cuticle (e.g. processes or pouches) on or in which these sclerites are situated. For example, lamina ventrale (= lv) designates the sclerite I call **L2** and, at the same time, the pouch **lve**, which contains sclerite **L2** (fig.321g). This ambiguity makes LaGreca's terminology rather impractical. The other terminologies put forward (e.g. Beier 1968) are not very handy because of their long terms, and they are by far not detailed enough for my purposes.

Blattaria

McKittrick (1964) has developed a new, very simple and handy terminology, which has been adopted by most of the subsequent workers. Mizukubo & Hirashima (1987) also employ it but propose some changes. In both terminologies, the names for sclerites are short sequences of letters and numbers, each position containing certain information. Some of these terms have already been applied in the description of the phallomeres in 3.1., e.g. **L2, R3**.

McKittrick regards the phallomere complex of *Cryptocercus punctulatus* as the most primitive and takes it as the reference type for her terminology. She adopts the tripartition of Snodgrass (1936) into left, right and ventral phallomeres, and according to this major division McKittrick basically distinguishes left, right and ventral sclerites, which get **L**, **R**, or **V**, respectively, in the first position of their names. Then, on the left and on the right phallomere, the sclerites are numbered separately. The ventral phallomere has only one sclerite. In this way seven main sclerites are distinguished (**L1, L2, L3, V, R1, R2, R3**). No assumptions concerning side-homologies are intended in this terminology. What McKittrick – starting fom this situation in *Cryptocercus* – regards as a product of a secondary "subdivision" or as a special region or "elaboration" of a main sclerite is expressed by the addition of one or two small letters (**d** = dorsal, **v** = ventral, **l** = lateral, **m** = median, **vm** = ventromedian). Sclerites of certain species regarded as completely new elements not present in *Cryptocercus* are given the next free number of the respective phallomere. This terminology is very handy and clear and contains a lot of information.

Mizukubo & Hirashima state side-homologies for the elements of the left and of the right half of the phallomere complex and integrate these assumptions in their terminology. For that purpose, they modify the terminology of McKittrick in two ways:

(1) According to the assumption of a plane of symmetry, they basically distinguish right and left elements (**R** or **L** in first position); then both **R** and **L** are grouped into dorsal and ventral elements (**D** or **V** in second position). The left-dorsal elements **LD** and the left-ventral elements **LV** compose the left phallomere. The right-ventral elements **RV** correspond to the ventral phallomere (**vla**-lobe in my terminology). The right-dorsal elements **RD** correspond to the right phallomere. Thus, the basic division into **LD, LV, RV**, and **RD** essentially conforms with the division of the phallomere-complex proposed by Quadri (1940).

(2) As regards the numbers and small letters, Mizukubo & Hirashima adopt the terminology of McKittrick, but changes are made in order to get side-homologous elements provided with the same names – except for **R** or **L** in the first position. These changes are, compared with McKittrick, not very extensive.

The terminology for Blattaria and Mantodea used in this paper

The terminology of Mizukubo & Hirashima will not be employed since I do not agree with the assumptions of these authors (discussion in chapter 8.). I will use a modified version of McKittrick's terminology and apply it to both Blattaria and Mantodea. There are three reasons why the terminology of McKittrick is not adopted unchanged, and I will procede in the following way:

1. Reason: The tripartition in McKittrick's terminology (**L, V, R**) reflects the earlier view of Snodgrass (1936) that the ventral phallomere is a medioventral basic element of the phallomere complex. In my view the ventral phallomere = ventral lobe **vla** is a ventral part of the left half of the phallomere complex (= left complex).

1. Procedure: All sclerites of the left complex will get **L**, all sclerites of the right phallomere will get **R** in the first position of their names.

2. Reason: Like Mizukubo & Hirashima (1987), I cannot accept the view of McKittrick that the phallomeres of *Cryptocercus* are closest to the primitive Blattarian type and should be used as a reference type. I have taken the common ground-plan of the phallomeres of Blattaria and Mantodea (compare in 3.1.) as the basis of my terminology. The ground-plan pattern I assume for the phallomere sclerites is rather different from that proposed by McKittrick (compare fig.321e-i and McKittrick 1964, fig.106).

2. Procedure: Each sclerotisation that is assumed to be present as one isolated and undivided sclerite in its most primitive condition within the taxon comprising all Blattaria and Mantodea and their last common stem-species is designated as a main sclerite. Hence, these main sclerites can be (1) sclerites of the common ground-plan of Blattaria and Mantodea or (2) sclerites formed de novo (not by the division of sclerites already present before) in any subgroup of Blattaria or Mantodea. Each main sclerite will get its own number in the second position of its name. In the description in 3.1. these are the sclerites **L1, L2, L3, L4, L5, R1, R2**, and **R3**. Numbering is arbitrary. If any of these main sclerites becomes divided, the whole of its descendants is called sclerite group **L1, L2**, etc..

Unfortunately, for many sclerotisations the most primitive condition and the evolution are not completely clear, and there is in many cases, and to various extents, some uncertainty about whether a certain sclerotisation fulfils the definition of a main sclerite. As regards the sclerotisations shown in fig.321, **L1, R1**, and **R3** are assumed to be isolated and undivided sclerites in the common ground-plan of Blattaria and Mantodea (fig.321e-i). **L3, L5**, and **R2** are also isolated and undivided in their most primitive states, but they are possibly not yet present in this ground-plan; however, if a later origin is really true for them, they can be at least assumed to be new sclerotisations, not split off descendants of ground-plan sclerites. To regard **L2** and **L4** as two main sclerites is somewhat subjective: (1) **L2** and **L4** are primitively connected in between the processes **paa** and **pda** (fig.321e,g); the interspace between **paa** and **pda** is here defined as the border between **L2** and **L4**. (2) For **L4** it is not clear whether it has been present as one, two, or three sclerites in the ground-plan (the latter alternative is shown in fig.321e,g,i). Apart from these early evolved sclerites, there are several main sclerites which are undoubtedly apomorphic for certain subgroups (**L6...., R4....**).

3. Reason: McKittrick names certain parts of her main sclerites with small letters in the third position, no matter whether these parts are (1) products of a complete division or (2) only certain regions of a main sclerite. However, these two situations represent two different aspects of a sclerotisation and its evolution: (1) On the one hand, a main sclerite is composed of one or more separate individual sclerites. Since divisions or fusions of sclerites can take place, the state of subdivision of a main sclerite is subjected to evolutionary changes. (2) On the other hand, a main sclerite, irrespective of its state of subdivision, consists of several regions each of which is characterised by taking a certain position, by having a certain shape, by occupying certain in- or evaginations of the cuticle, or by bearing certain muscle insertions or articulations. The properties of these regions undergo evolutionary changes, too. The special state of subdivision (1) and the special properties of the regions (2) of a main sclerite are largely independent of each other, and evolution works on both these aspects and has to be considered from both viewpoints.

3. Procedure: I strictly separate these two aspects (1) and (2) in my terminology, and for the designation of different parts of main sclerites two terminologies completely independent of each other will be used:

The **first terminology** serves to designate **individual sclerites** having originated by a division of a main sclerite: If any main sclerite is divided into two or more sclerites completely separated from each other by membrane, each of the sclerites will get one **capital letter** in the third position of its name (e.g. **L2D, R1C**). (The main sclerite has become a sclerite group. An individual sclerite as defined here may, however, be connected with parts of another main sclerite). If any of these individual sclerites undergoes a further division or a fusion, all resulting sclerites involved in this process will get a new capital letter. Equal designation of sclerites of different species means the assumption of homology. Different designation, however, does not always mean complete non-homology: Some small sclerites of one species can as a whole be homologous with one large sclerite of another species, and none of the sclerites will have the same letter. In the third position of these terms, I, O, and Q will not be used (danger of confusion with "1" and "0" in the figures); R will not be used on the right side, L on the left side. Among other things, this terminology serves for a clear reference between the text and the figures.

The meaning of a term designating a certain individual sclerite, e.g. **L2D**, is hence as follows:

L	**2**	**D**
a sclerotisation of the **L**eft side,	belonging to main sclerite **2,**	being the individual sclerite **D**

The **second terminology** serves to designate **certain regions** of the main sclerites or sclerite groups: This regioning is essentially independent of any natural sub-division of the respective sclerotisations. To name these regions one **small letter** will be added in the third position (e.g. **L2d, R1c**). Equal designation of sclerotisations of different species means the assumption of homology. Different designation means complete non-homology. These names mainly serve for the demarcation of homologous areas on the main sclerites / sclerite groups of different species and for a description of their evolution as regards the properties listed above in **3. problem** (2). Therefore, this dividing into regions, or regioning, will be performed with practicability as the main point of interest (the best possible way to explain homology relations). It is in general arbitrary. (The definition of the regions, however, will in some cases be done in correspondence with a concrete division of the respective main sclerite into smaller sclerites in a certain, arbitrarily selected species). Only the more complicated main sclerites will be divided into regions. The small letters are in most cases abbreviations of typical attitudes (e.g. position) of the regions. These abbreviations and the definition of the various regions will be given in the homology discussion of the respective main sclerites (chapter 6.).

The meaning of a term designating a certain sclerite region, e.g. **R1c**, is hence as follows:

R	**1**	**c**
a sclerotisation of the **R**ight side,	belonging to main sclerite **1**,	being the region **c**, which takes a rather **c**entral position

In Blattellidae Plectopterinae, some other Blattellidae, and Blaberidae the phallomere complex is side-reversed (Bohn 1987), being essentially a mirror-image of the phallomere complex of the other Blattarian subgroups. In the terminology for the sclerites, this fact will be taken into account by adding ' at the end of the term. This will be done in the terms for individual sclerites as well as in the terms for sclerite regions. (For example, **L4U'** is a **L4U** on a side-reversed phallomere complex, and it is on the right side). This procedure is different from Bohn (1987), who adds ' after the first letter (**L4U'** would be **L'4U**), but the meaning is the same. (Of course, since homology should be the basis of the terminology, the left complex will still have this name, if it is, after a reversal of the phallomere complex, on the right side of the body; the same practice will be applied to the right phallomere.)

4.2. Abbreviations for other sclerites of the postabdomen

The terminology for the sclerites of the postabdomen is largely pre-set by the earlier literature. Abbreviating is done according to the same principle as in the phallomere sclerites. A capital letter in the first position designates the category (**S** = sternite; **T** = tergite; **E** = sclerotisation of an appendage = extremity). A number in the second position designates the abdominal segment the sclerite belongs to. A small letter in the third position (not obligatory) serves to designate a special region. As discussed in 3.1., there are many problems concerning the correct morphological assignment and designation of postabdominal sclerotisations. In such problematical cases neutral abbreviations will be used (e.g. **Pp** = paraproct; **Ep** = epiproct; all elements of the subgenital plate are called **S9** despite the possibility of true appendages being involved).

4.3. The terminology for the formative elements

The phallomere complex contains many areas where the cuticular body wall forms pouches, apodemes, tendons, hook-, spine-, tooth-, or lobe-like processes, or comparable structures. These more or less distinct invaginations (or infoldings) and evaginations (or outfoldings) of the cuticle are responsible for the shape of the phallomere complex, and I will designate them as the formative elements. These will receive special names serving for a clear and practicable reference and for a clear presentation of homology relations. The terms are composed of three small letters. The first two letters are the individual name of the respective formative element, the third letter stands for one of the two possible categories (**a** = evagination, German "**A**usstülpung"; **e** = invagination, German "**E**instülpung"). A certain area of the cuticle can belong to two or more neighboring formative elements, and, in such a case, the respective terms "overlap" each other. For example, a certain area of the cuticle can be e.g. the dorsal wall of a specific evagination and the ventral wall of an immediately adjacent invagination at the same time, or a large evagination can fork into smaller ones in its distal part.

The first two letters are essentially selected arbitrarily but are mostly abbreviations for characteristic attitudes (e.g. **vla** = ventral lobe, evagination). In other cases the abbreviations of the terms of LaGreca (1954) have been used (e.g. **lve** = lamina ventrale, invagination; LaGreca's name for sclerite **L2** and for the pouch containing **L2**; compare fig.321g). The formative elements of the phallomere complex termed in this paper are listed in 4.7.

Similar terms are used for formative elements outside the phallomere complex (e.g. **sbl** = subanal lobe), but the letter in third position is part of the abbreviation and does not stand for a category.

4.4. The terminology for the muscles

Muscles are named by a small letter determining the category, followed by a number for the individual muscle. Numbering is arbitrary. The categories are as follows:

l	Intrinsic muscles of the left complex	(**l**eft)
r	Intrinsic muscles of the right phallomere	(**r**ight)
b	Muscles connecting the left complex and the right phallomere	(**b**etween)
s	Phallomero-sternal muscles	(**s**ternal)
p	Muscles not inserted on the phallomere complex but taken into account (some ventral, dorsal, dorsoventral, and rectal muscles)	(**p**eripheral)

In some cases it can be reliably assumed that a muscle has divided. In other cases homology can be assumed for groups of muscles of different species, without the possibility to ascertain the homology relations for the single muscles of the group. In both these situations all muscles of the group get the same number, and the single muscles are distinguished by adding a small letter in the third position. In these cases equal letters do not mean homology of the respective muscles by principle; which homologies are assumed will be explicitly mentioned in the text.

For the muscles of the categories **l** and **r** it is not clear which of them have originally been pairs or if there are pairs at all. The muscles of category **b** are probably unpaired transverse muscles. The phallomero-sternal muscles **s** will be separately numbered on the left and on the right side, though pairs can be identified in many cases; those inserting on the left half of the subgenital plate are given odd numbers, those inserting on the right half are given even numbers. (In species having side-reversed phallomeres the reverse is true). Only the "peripheral" muscles **p** will be designated pairwise.

4.5. The terminology for the articulations

Articulations between sclerites are named by **A** ("Articulation") and an added number (e.g. **A5**, **A98**). The numbers 1-79 are reserved for the articulations within the phallomere complex, the numbers 80-99 for the articulations outside the phallomere complex. Numbering is arbitrary. The term articulation is taken in its widest sense: each case of close contact between two sclerites. Even if the contact has become looser by evolutionary changes, the remaining vicinity of the sclerites will in many cases still be designated as an articulation (in order to designate the assumed homology of the respective vicinity). Places where articulations have been lost by a fusion of the sclerites concerned are often given the name of the respective articulation, but * is added (e.g. **A99***).

4.6. Survey of the terminologies used

Main sclerites / sclerite groups of the phallomere complex:

L	2
Capital letter	Number
(side: L, R)	(main sclerite)

Regions of the main sclerites / sclerite groups of the phallomere complex:

L	2	d
Capital letter	Number	Small letter
(side: L, R)	(main sclerite)	(specific region)

Individual sclerites of the main sclerites / sclerite groups of the phallomere complex:

L	2	D
Capital letter	Number	Capital letter
(side: L, R)	(main sclerite)	(individual sclerite)

Postabdominal sclerites outside the phallomere complex:

S	9	d
Capital letter	Number	Small letter
(category: S, T, E)	(abdominal segment)	(specific region)

Formative elements of the phallomere complex:

p	n	e
Small letter	Small letter	Small letter
(part of individual name)	(part of individual name)	(category: a, e)

Muscles:

r	4	b
Small letter	Number	Small letter
(category: l, r, b, s, p)	(individual muscle)	(separate part of the muscle)

Articulations:

A	6
Capital letter A	Number
(articulation)	(individual articulation)

4.7. Abbreviations in the figures 1-321

CL = Capital letter; SL = Small letter; NR = Number; facultative parts of the terms are put in brackets; the abbreviations for the formative elements are listed separately.

A + NR	Articulation
Af	Anus
b + NR (+ SL)	Muscle between left complex and right phallomere (or part of it)
Bl	Basal line
D	Ejaculatory duct
Dw	Dorsal wall of genital pouch
E + NR (+ SL)	Sclerotisation of an appendage (or part of it)
E11	Sclerotisation of cerci
Ep	Epiproct
L + NR	Main sclerite / sclerite group of left complex
L + NR + CL	Separate sclerite of main sclerite / sclerite group of left complex
L + NR + SL	Region of main sclerite / sclerite group of left complex
l + NR (+ SL)	Muscle of left complex (or part of it)
M	Membranous or weaker sclerotised field of subgenital plate
P	Phallomere-gland
p + NR (+ SL)	Muscles not inserted on phallomere complex
Pp	Paraproct
Pv	Ribbon-like sclerotisation anterior to paraproct
R + NR	Main sclerite / sclerite group of right phallomere
R + NR + CL	Separate sclerite of main sclerite / sclerite group of right phallomere
R + NR + SL	Region of main sclerite / sclerite group of right phallomere
r + NR (+ SL)	Muscle of right phallomere (or part of it)
Re	Rectum
S + NR (+ SL)	(Coxo-) Sternite (or part of it)
S9a	Apophysis of subgenital plate
S9d	Dorsal sclerotisation of subgenital plate
S9l	Anterolateral part of subgenital plate
S9s	Stylus on subgenital plate
s + NR (+ SL)	Phallomero-sternal muscle (or part of it)
sbl	Subanal lobe
spl	Supraanal lobe
Sw	Lateral wall of genital pouch
T + NR (+ SL)	Tergite (or part of it)
T9p	Paratergite of abdominal segment 9

T10p	Paratergite of abdominal segment 10
T10v	Ventral sclerotisation of abdominal tergite 10
U	Pleura between abdominal tergite 9 and sternite 9
Vw	Ventral wall of genital pouch
X	Posterior edge of abdominal tergite 10
Y	Median part of subanal lobe

Formative elements of the phallomere complex

Column 2: LG = term derived from LaGreca (1954). Column 3: left = left complex; right = right phallomere. Column 4: If the formative element is sclerotised entirely or partly, the respective sclerotisation is given; if it is membranous, memb is listed; if both situations occur in different species, the more primitive situation is listed first.

Term	Meaning of term	Position	Sclerotisation	Shape
afa	apofisi falloide = af (LG)	left	memb, L1m	lobe, process
age	anterior groove	right	R3	fold/beam-like apodeme
are	apodeme, right	right	R3	fold-like apodeme
ate	anterior tendon	left	memb, L4n?	tendon
boe	bulb, opposite	left	L2d	hood-shaped apodeme
cbe	central bulge	right	R1t	large, shallow invagination
cla	central lobe	left	memb	lobe
cwe	cleft "Wulst"	right	R1t	curved cuticular thickening
dca	dorsal cushion	left	memb, L1	1-more cushions, processes
dla	dorsal lobe	right	memb, R4	lobe
dte	dorsal trough	left	L2d + L4l	shallow invagination
fda	fallomero dorsale di destra = fd (LG)	right	R1	lobe
fpe	fence, posterior	left	memb	fold-like invagination
goa	genital opening	left	memb	1-2 cushions, lobes
gta	—	left	L2p	process
hge	hook groove	left	L3	groove
hla	hook, left	left	L3	hook
ipe	inter, phallomere-glands	left	memb	fold-like invagination
lba	lobe, between	left	L7	lobe
loa	lobo membranoso = lo (LG)	left	L1m	slender process
lve	lamina ventrale = lv (LG)	left	L2	flat pouch
mla	median lobe	left	memb	lobe
nla	node, left	left	L4n	node, bulge
paa	processo apicale = pa (LG)	left	L2d	process

pbe	**p**ouch, **b**etween	left	memb	flat pouch
pda	**p**rocesso **d**istale = pd (LG)	left	L4l	process
pia	**pi**astra ventrale = pi (LG)	right	R1v	tooth, ridge
pne	**p**rocesso a**n**teriore = pn (LG)	left	L1a	pouch
pra	**p**rong, **r**ight	right	R1d	process
psa	**p**osterior **s**ting	left	L2m	bifid process
pva	**p**rocesso **v**entrale sclerificato = pv (LG)	right	R1t	tooth, ridge
rge	**r**ight **g**roove	right	R1c	groove
sbe	**s**ting **b**ulb	left	L4l	bulb + channel
sla	**s**ting, **l**eft	left	L4d	sting-like process
sra	**st**ing, **r**ight	right	R1d	sting-like process
swe	**s**clerotised “**W**ulst”	left	L4l	fold/beam-like apodeme
tre	**t**endon, **r**ight	right	memb	long, narrow tendon
tve	**t**endon, **v**irga	left	L4l	tendon, apodeme
vfa	**v**entral **f**old	left	memb	broad lobe
vge	**v**irga **g**roove	left	L4l	groove
via	**vi**rga	left	L2d + L4l	process
vla	**v**entral **l**obe	left	L4v	lobe
vpe	**v**entral **p**ouch	left	memb	broad, flat pouch
vsa	**v**entral **s**ting	left	L4l	sting-like process
vte	**v**entral **t**endon	left	memb	broad, flat tendon
xla	—-	left	L2m	short process

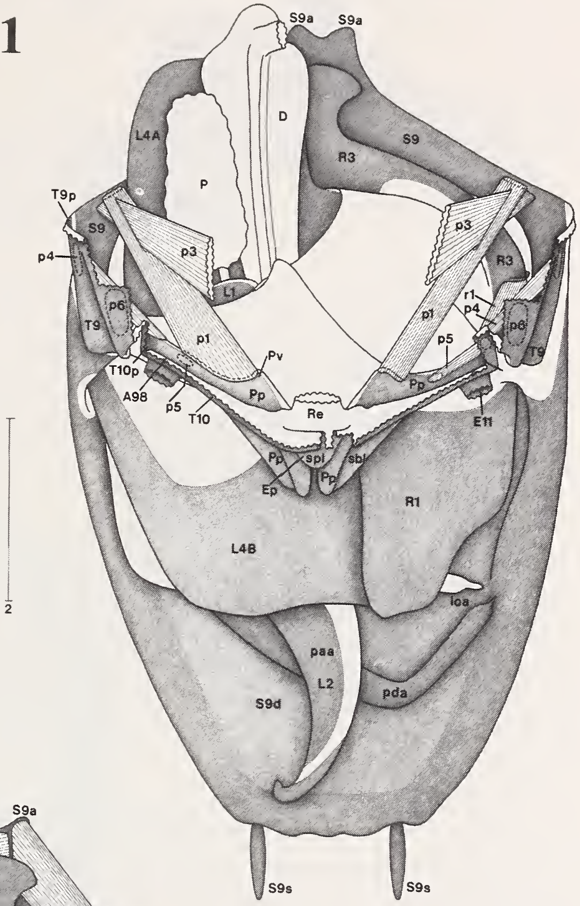
5. DESCRIPTIONS OF PHALLOMERES AND POSTABDOMINA

The complicated morphology of the phallomere complex and the courses of all investigated muscles will be described in detail. The morphology of the subgenital plate and of the posteriormost part of the abdomen can be largely seen from the figures and from the general descriptions in 3.1.. Only the condition of the following elements will be mentioned: **Pv**-sclerites; sclerites **Ca, Cb**, and **Cc** median to the cercal base; ventral sclerotisation of tergite 10 **T10v**; articulations **A98** (cercal base – posterior margin of tergite 10) and **A99** (paratergite 10 – paraproct); some peculiarities will also be pointed out.

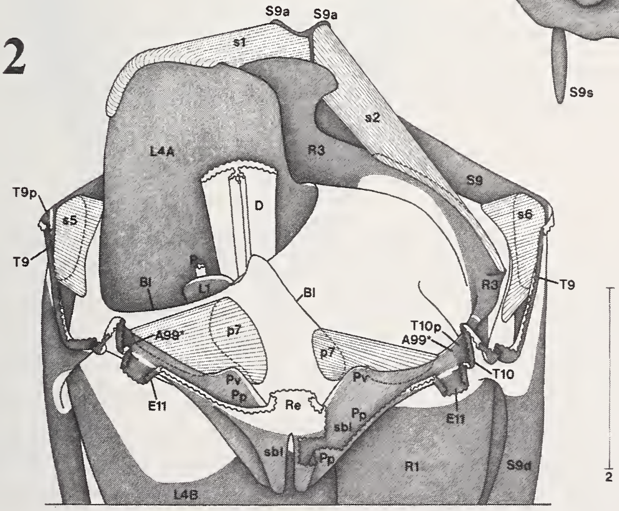
Figs.1,2: *Sphodromantis* sp. (Mantodea, Mantidae) – **1:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, epiproct, subanal lobes, paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. – **2:** Same as in fig.1, after removal of further parts of abdominal tergites 9 and 10, parts of right paraproct, and supraanal lobe with epiproct. Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. Posterior to transverse line: like in fig.1. – Scale: 2mm.

Sphodromantis sp.

1



2



5.1. *Sphodromantis* sp. (Mantodea, Mantidae)

Left complex

The dorsal wall is largely occupied by sclerite **L4B** (fig.9), the ventral wall by the large plate-like sclerite **L4A** (fig.6, 9-11). **L4A** extends posteriorly onto the process **pda** (fig.6, 12). On the left edge of the left complex **L4A** and **L4B** articulate (**A1** in fig.6, 10). **L4B** has a solid keel-like apodeme (**swe** in fig.10; cross-section in fig.11) at its anterior left margin.

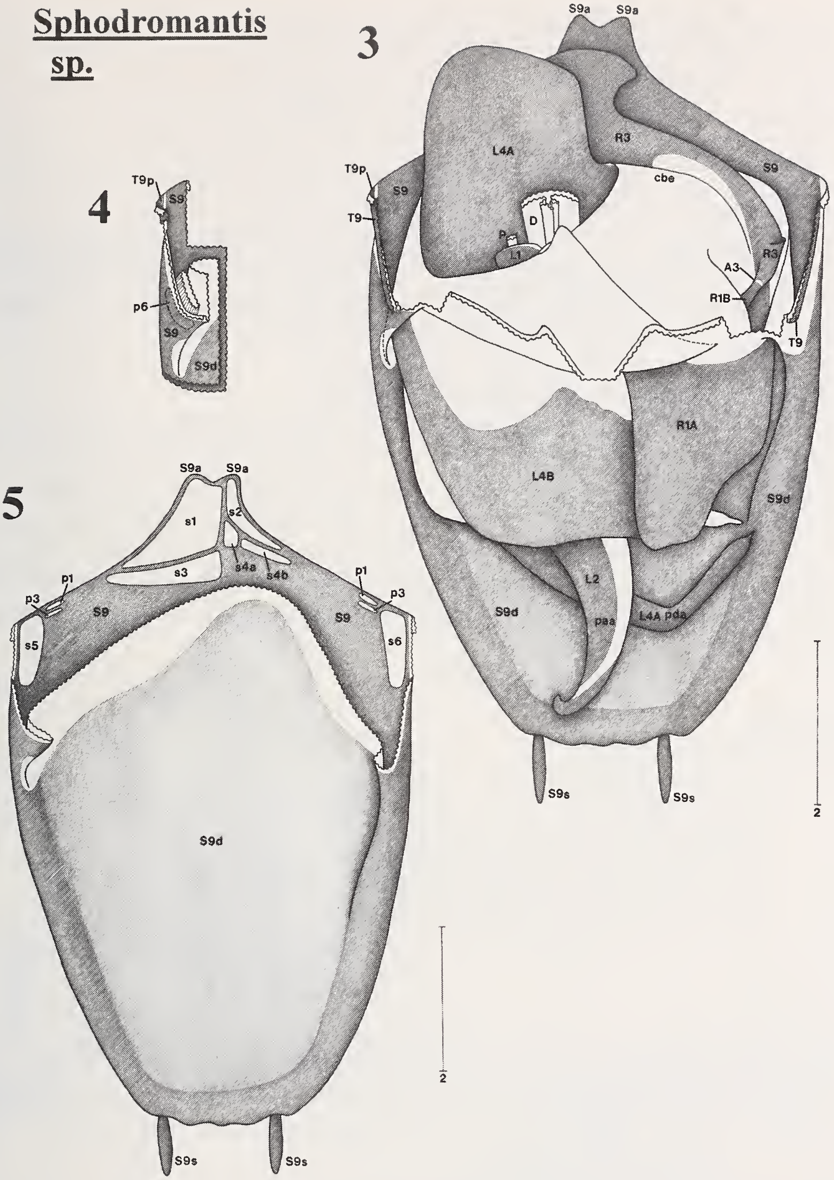
From beneath the posterior and right margins of **L4B**, two deep pouches invaginate to the left and anteriad and lie one above the other (**pne** and **lve** in fig.10, 11). The dorsal pouch **pne** (fig.10) is largely occupied by sclerite **L1A** (fig.10), which lies mainly in the ventral wall but bends anteriorly into the dorsal wall around the left edge of the pouch. The phallomere-gland (**P** in fig.10) opens into the membranous anteriormost ventral wall of the **pne**-pouch. The ventral pouch **lve** (fig.10-12) deepens extensively to the left. (The edge along the bottom of the **lve**-pouch is labelled **7** in fig.11). Its dorsal wall is occupied by sclerite **L2**. The ejaculatory duct (**D** in fig.11, 12) opens into its membranous ventral wall. The edge between the pouches **pne** and **lve** (**1** in fig.10, 11) bears three processes: most anteriorly a hammer-shaped one (**afa** in fig.9-11); far behind this a long and narrow lobe (**loa** in fig.10); immediately behind the latter a stout hook (**paa** in fig.10). The anterior part of this edge **1** is occupied by sclerite **L1B** (fig.10, 11), which is separated from both **L1A** and **L2** by narrow stripes of membrane (**2** in fig.10, **A2** in fig.11). **L1B** also sclerotises the **afa**-process and has a strip-like posterior extension into the dorsal wall of the **loa**-process. The posterior part of sclerite **L2** extends onto the **paa**-process (fig.11) and occupies most of its surface.

The membranous ventral wall of the **lve**-pouch with the genital opening is at the same time the dorsal wall of the large ventral lobe **vla** (= ventral phallomere; fig.10-12). Close to the genital opening there are two small membranous lobes (**goa** in fig.12). The ventral wall of the **vla**-lobe is part of the ventral wall of the left complex and is largely sclerotised by **L4A** (fig.6).

Right phallomere

The anterior ventral wall is occupied by sclerite **R3** (fig.6, 13): Its left part is expanded, its narrow right part curves posteriad and articulates (**A3** in fig.6, 8, 14) with the posteroventral sclerite **R1B**. The ventral wall behind the left and central parts of **R3** is broadly invaginated dorsad and anteriad (**cbe** in fig.13). The ventral wall behind the right part of **R3** bears two teeth, which are both sclerotised by **R1B**: the anterior **pva** and the posterior **pia** (fig.6, 14). **pia** and **pva** are both on the crest of a leftward projecting evagination of the ventral wall (fig.8, 14). The posterior part of the right phallomere is a large lobe (**fda** in fig.6, 13), with its dorsal wall completely occupied by sclerite **R1A**. Around the anterior right edge of the right phallomere **R1A** curves into the ventral wall, where it is connected with **R1B** by a stripe of very weak sclerotisation (**4** in fig.6, 14).

Sphodromantis sp.



Figs.3-5: *Sphodromantis* sp. (Mantodea, Mantidae) – **3:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **4:** Left margin of subgenital plate (compare fig.3); with insertion of muscle p6. – **5:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6). – Scale: 2mm.

The whole anterior and right margins of **R3** form a groove-like apodeme **age** (fig.6; cross-section in fig.8, 14). The cuticle along the bottom of the **age**-groove is thickened. In the left part of **R3** the **age**-groove abruptly deepens and, in addition, curves posteriad and finally back to the right (fig.6, 8, 13, 14). By this deepening and curving the left part of the **age**-apodeme is a crescent-shaped plate, which is sclerotised dorsally and ventrally (fig.6-8, 13, 14). The ventral wall of the genital pouch becomes evaginated by the posterior part of the crescent and forms a membranous pouch (**5** in fig.6, 7, 8, 13, 14). In the right posterior part of **R3** the **age**-apodeme bears an additional apodeme fold **are** (fig.6; cross-section in fig.8), which bears another small keel-like apodeme (**3** in fig.6, 13). The groove-like shape of the sclerotisation extends posteriad beyond articulation **A3** (where **R3** ends and the groove is no longer called **age**) onto sclerite **R1B** (fig.6, 8, 13).

Subgenital plate and posterior abdominal segments

Fig.1,2 (posterior segments); fig.5 (subgenital plate **S9**). The paraprocts **Pp** and the epiproct **Ep** are just weakly sclerotised and do not have distinct boundaries to the surrounding membranes; it is therefore not possible to determine the exact outlines of these sclerotisations, the presence of articulations **A99** (**A99*** in fig.2), and the presence of separate **Pv**-sclerites (compare fig.321b,c). The data given in fig.1, 2 must be considered with these reservations. A ventral sclerotisation of tergite 10 **T10v** was not found. The sclerites **Ca, Cb**, and **Cc** are missing (or strongly obsolete?). The articulations **A98** are well-developed.

Musculature

Muscles	Positions of insertions	in fig.
l1	**L1A** (anteriorly on **pne**-pouch) – right anterior dorsal wall of left complex	17
l2	**L1A** (dorsally on **pne**-pouch) – **L4B** (right part)	15
l3	**L1A** (posteroventrally on **pne**- pouch) – **L2** (left part)	16
l4	**L2** (left-posterior part) – **L4B** (central part)	15
l5	**L4A** (left-anterior part) – **L2** (left-anterior part)	15

⟶ p.37

Figs.6-8: *Sphodromantis* sp. (Mantodea, Mantidae) – **6:** Phallomere complex in ventral view. – **7:** Anterior part of phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.6; left anterior part of sclerite R3 removed. – **8:** Right phallomere with transition to left complex in ventral view; some ventral parts removed. – Scale: 2mm.

⟶ p.38

Figs.9,10: *Sphodromantis* sp. (Mantodea, Mantidae) – **9:** Left complex in dorsal view. – **10:** Left complex in dorsal view; some dorsal parts removed. – Scale: 2mm.

⟶ p.39

Figs.11-14: *Sphodromantis* sp. (Mantodea, Mantidae) – **11,12:** Left complex in dorsal view; with further removal of its parts (mainly of dorsal ones). – **13:** Right phallomere in dorsal view. – **14:** Right phallomere in dorsal view; some parts removed (mainly dorsal ones). – Scale: 2mm.

Sphodromantis sp.

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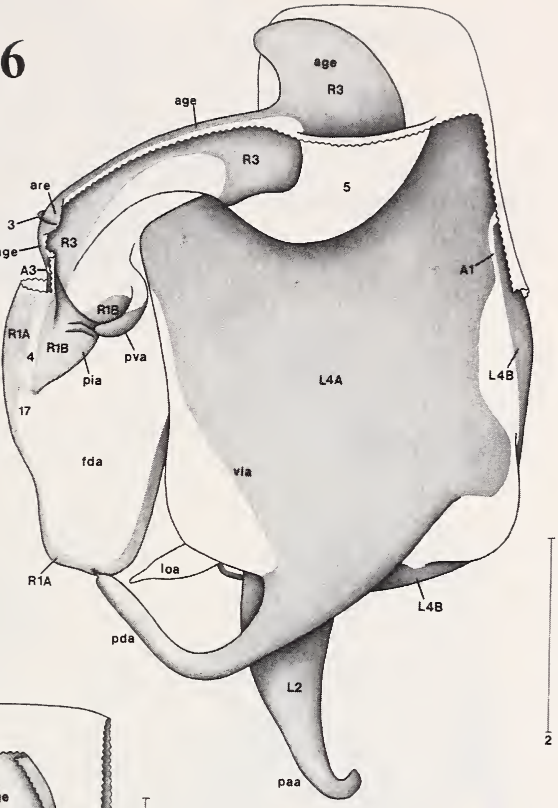

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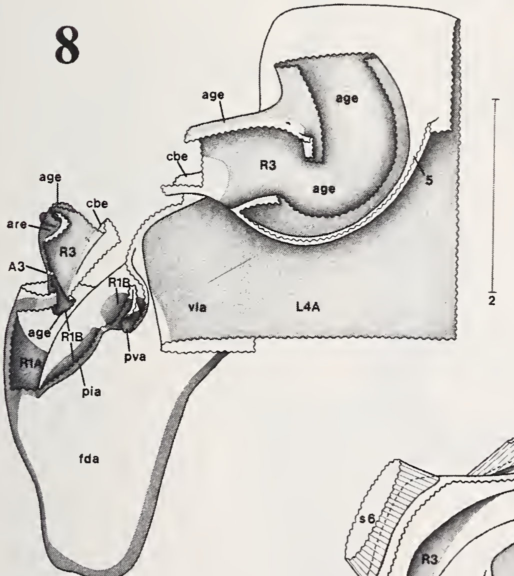

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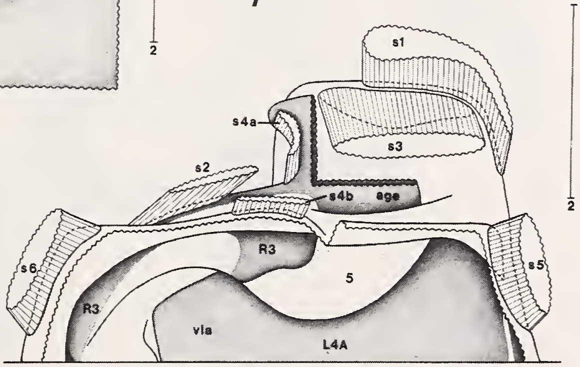

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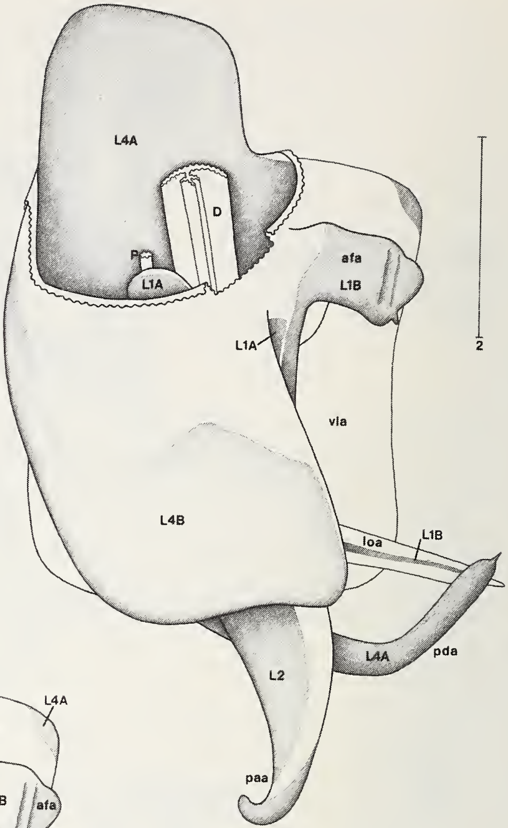
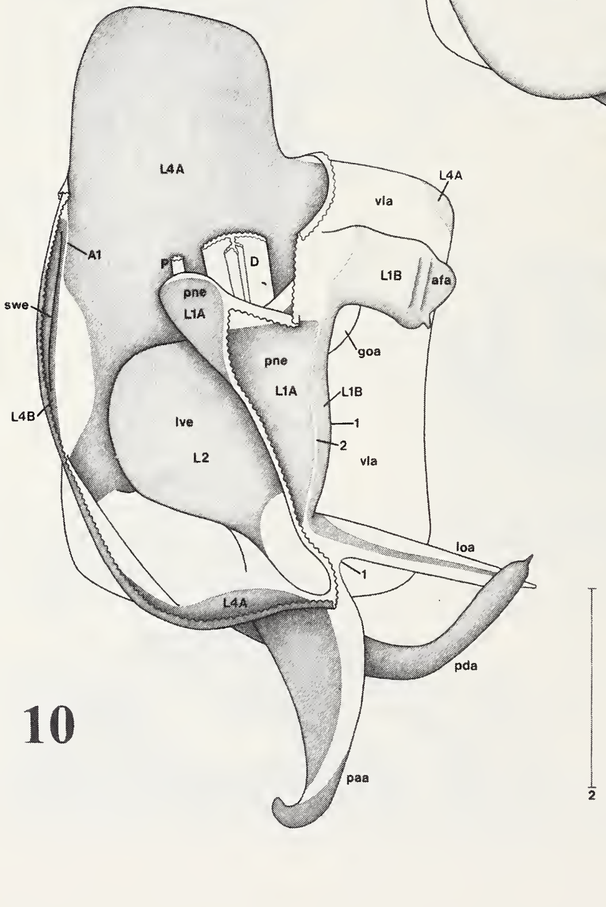


<u>Sphodromantis sp.</u>



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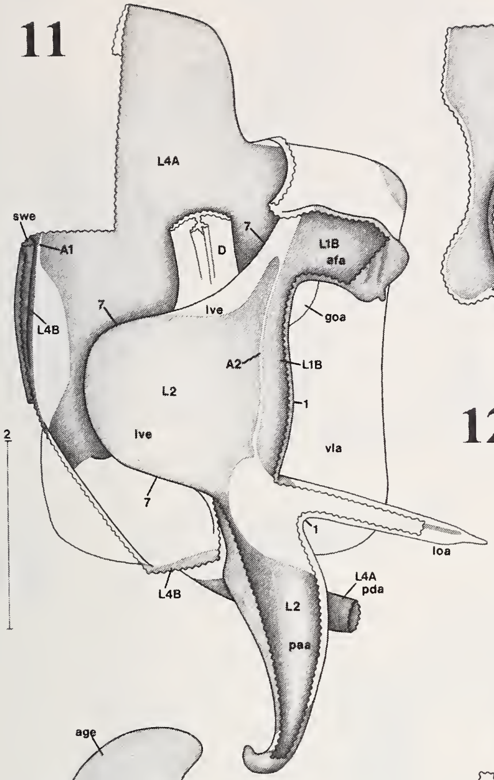

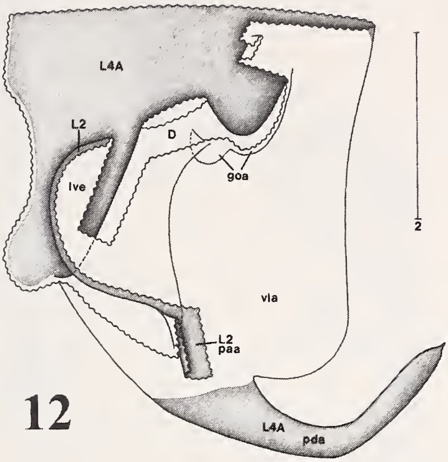

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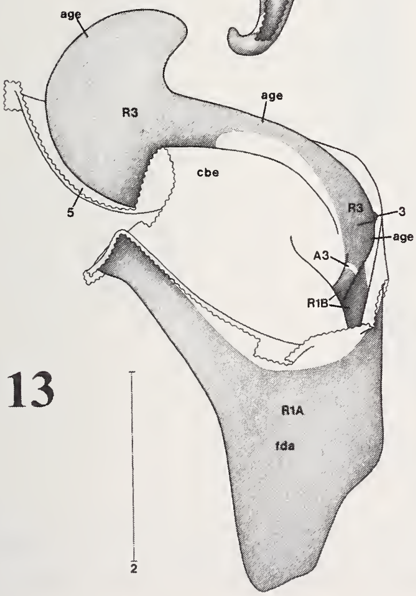

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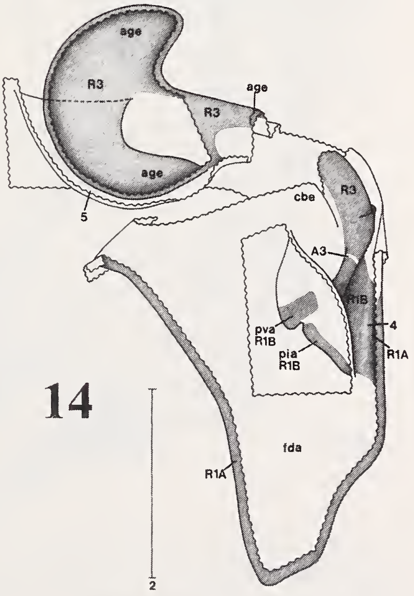

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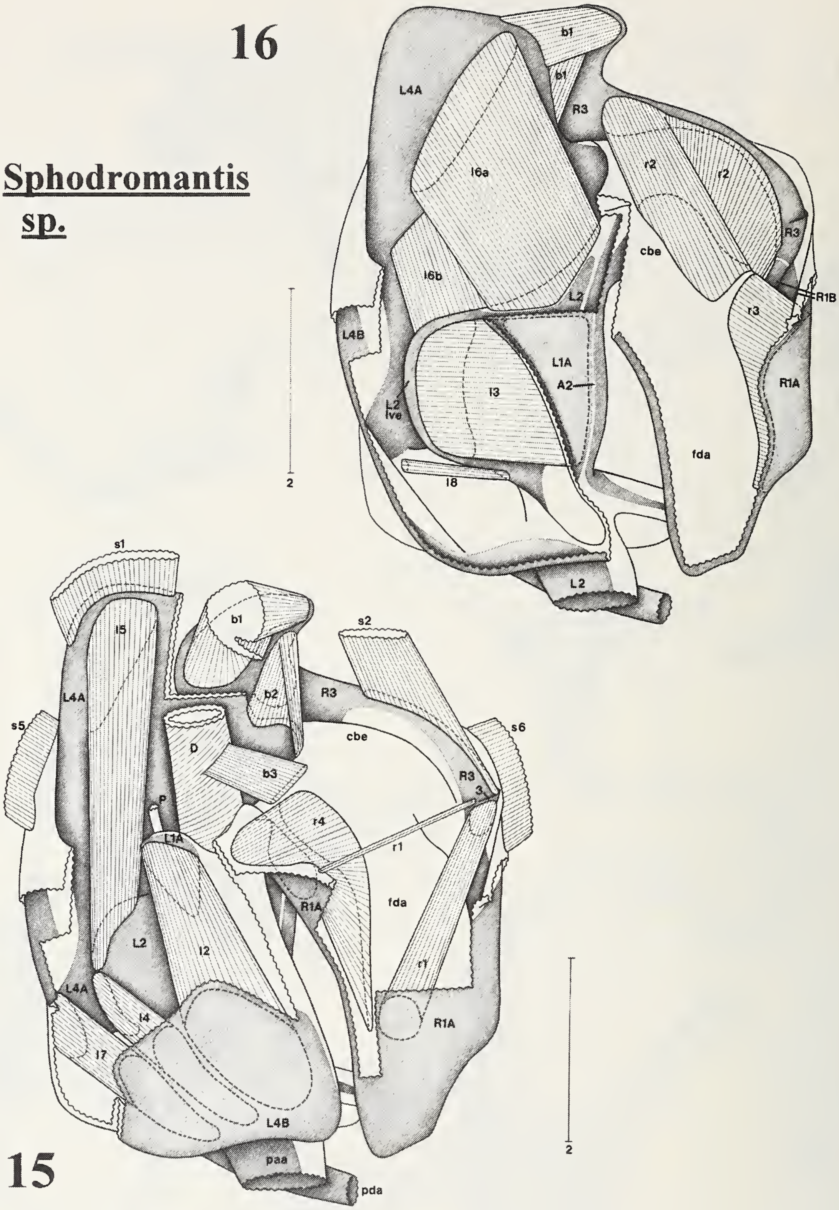
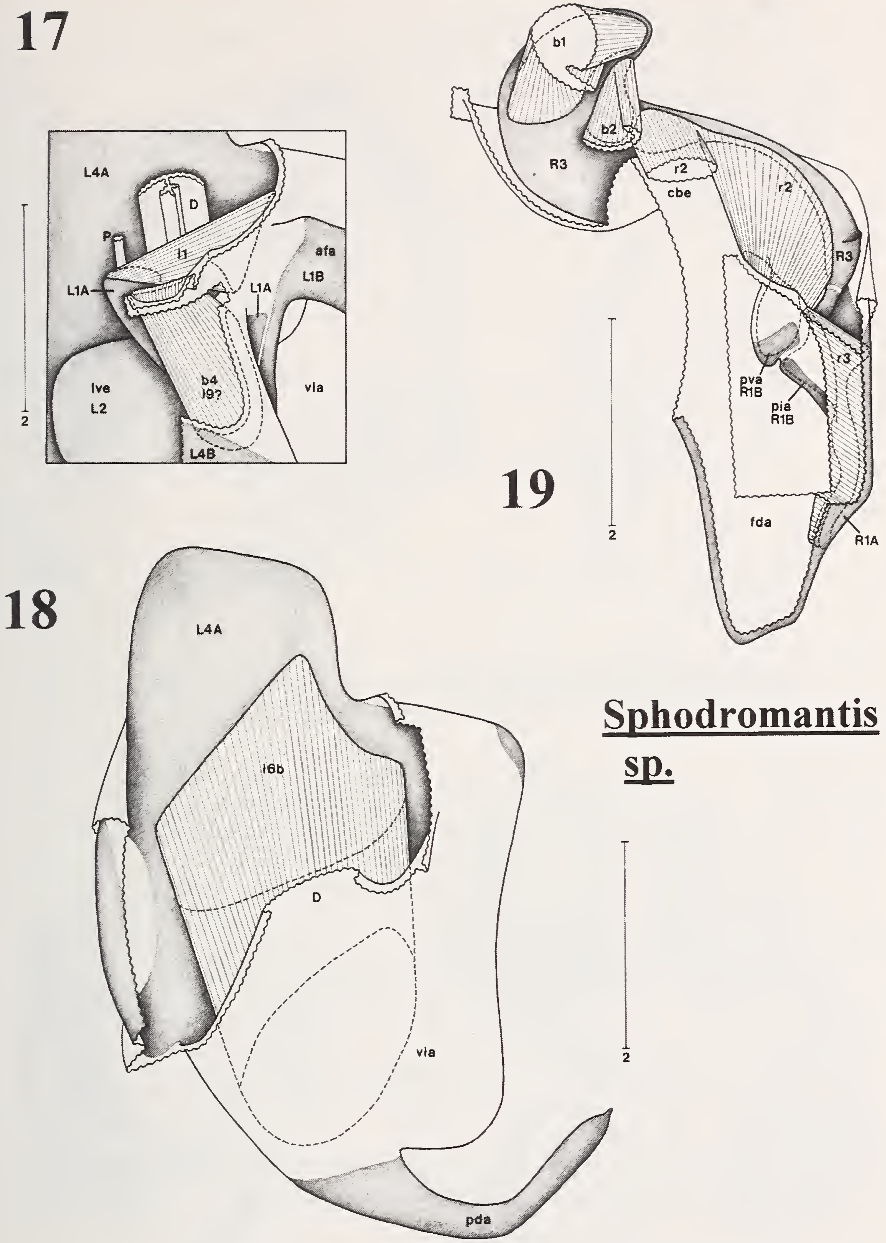


Figs.15,16: *Sphodromantis* sp. (Mantodea, Mantidae) – Left complex and right phallomere in dorsal view; each figure with some muscles; parts of phallomere complex removed to various extents. – Scale: 2mm.



Figs.17-19: *Sphodromantis* sp. (Mantodea, Mantidae) – **17:** Detail of left complex in dorsal view (compare fig.10); with some muscles. – **18:** Left complex in dorsal view; with muscle l6b; dorsal parts largely removed. – **19:** Right phallomere in dorsal view; with some muscles; dorsal parts largely removed. – Scale: 2mm.

l6a	**L4A** (anterior part) – **L2** (right-anterior part)	16
l6b	**L4A** (central part) – dorsal wall of **vla**-lobe behind genital opening	16, 18
l7	**L4A** (left-posterior part) – **L4B** (left-posterior part)	15
l8	Membrane behind left posterior end of **L4A** – **L2** (posterior part); only very few fibers; completely missing in some specimens	16
r1	**R3** (right margin) – **R1A** (dorsal wall of **fda**-lobe)	1, 15
r2	**R3** – **R1B** on **pva**-tooth and membrane of **cbe**-invagination	16, 19
r3	**R1A** (right part) – **R1B** on **pia**-tooth and right ventral wall of **fda**-lobe	16, 19
r4	**R1A** (left-anterior part) and membrane behind it – left ventral wall of **fda**-lobe	15
b1	**L4A** (anterior margin) – **R3** (left anterior part)	15, 16, 19
b2	**L4A** (anterior margin) and **vla**-lobe (anteriormost part) – **R3** (left-anterior part)	15, 19
b3	Ejaculatory duct **D** – left ventral wall of right phallomere	15
b4 (l9?)	Longitudinally within right dorsal wall of left complex	17
s1	**S9** left side (medially and most anteriorly) – **L4A** (anterior margin)	2, 5, 7, 15
s2	**S9** right side (medially and most anteriorly) – **R3** (lateral anterior margin)	2, 5, 7, 15
s3	**S9** left side (medially and anteriorly) – anteriormost left ventral wall of genital pouch	5, 7
s4a	**S9** right side (medially and anteriorly) – **R3** (left ventral wall of **age**-apodeme)	5, 7
s4b	**S9** right side (medially and anteriorly) – anteriormost median ventral wall of genital pouch	5, 7
s5	**S9** left side (laterally and anteriorly) – anterior left wall of genital pouch	2, 5, 7, 15
s6	**S9** right side (laterally and anteriorly) – anterior right wall of genital pouch	2, 5, 7, 15
p1 (pair)	**S9** – paraproct **Pp** (anterior margin, corresponding to **Pv**-sclerotisation)	1, 5
p3 (pair)	**S9** – rectum (ventral wall); in most specimens **p3** penetrates **p1**.	1, 5
p4 (pair)	**T9** (lateralmost anterior margin, possibly corresponding to paratergite **T9p**) – anterior margin of paratergite **T10p**	1
p5 (pair)	**T10** (lateralmost anterior margin) – paraproct **Pp** (lateral anterior margin, corresponding to **Pv**-sclerotisation)	1
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin)	1, 4
p7 (pair)	Membrane anterior to paraproct **Pp** – anterior margin of paraproct **Pp** and paratergite **T10p** (border between **Pp** and **T10p** not clear)	2

5.2. *Metallyticus violaceus* (Mantodea, Metallyticidae)

Left complex

The left complex resembles that of *Sphodromantis*. However, sclerite **L4B** (fig.23) is ribbon-shaped and restricted to the anterior dorsal wall. The ventral sclerite **L4A** extends

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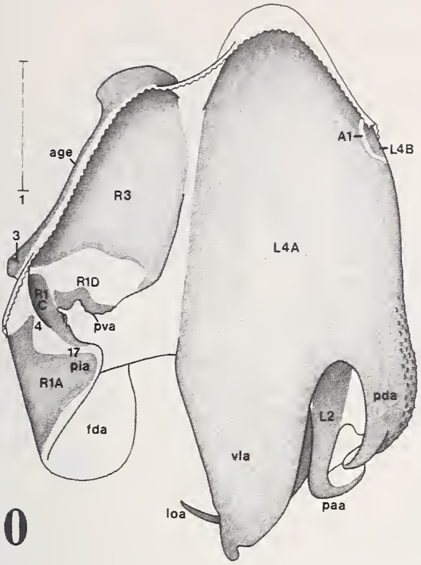
Figs.20-23: *Metallyticus violaceus* (Mantodea, Metallyticidae) – **20:** Phallomere complex in ventral view. – **21:** Right phallomere with transition to left complex in ventral view; some ventral parts removed. – **22:** Subgenital plate in dorsal view; left stylus missing. – **23:** Left complex and right phallomere in dorsal view. – Scale: 1mm.



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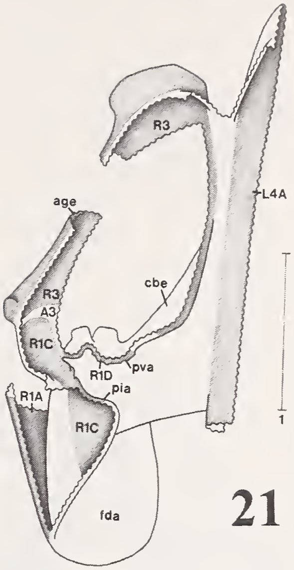

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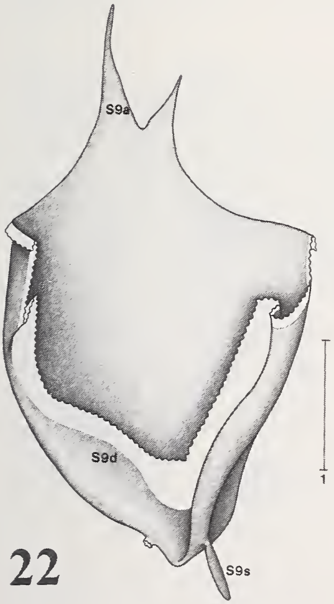
Metallyticus violaceus



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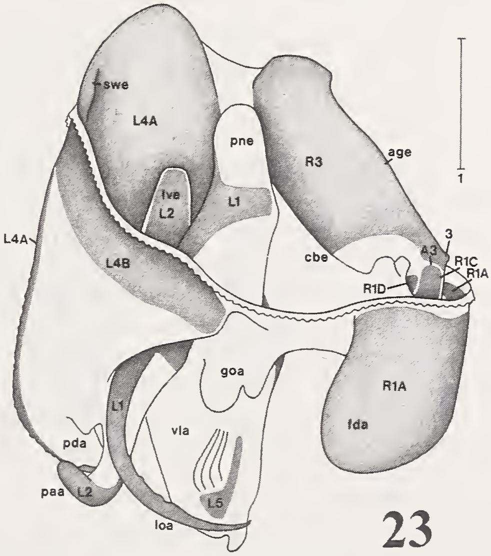

23

posteriorly onto two processes (fig.20, 27): the left **pda**-process and the right **vla**-lobe. **L4A** and **L4B** articulate on the left edge of the left complex (**A1** in fig.20, 24). **L4A** bears, anterior to **A1**, a small keel-like apodeme (**swe** in fig.23, 24; cross-section in fig.25).

Like *Sphodromantis*, *Metallyticus* has a dorsal pouch **pne** and a ventral pouch **lve**, which contain the sclerites **L1** and **L2** (fig.23-25). Within the **pne**-pouch (fig.24, 25) **L1** occupies the ventral wall and parts of the dorsal wall. In the ventral wall **L1** is partly divided by a stripe of membrane (**2** in fig.25). A phallomere-gland, whose opening were to be expected within the **pne**-pouch, was not found. The ventral pouch **lve** (fig.26) deepens strongly anteriad. Its dorsal wall is occupied by the ribbon-shaped **L2**-sclerite. The edge between the pouches **pne** and **lve** (**1** in fig.25, 26) has its anterior starting point in the ventral wall of the **pne**-pouch. The anteriormost part of edge **1** bulges to the right (**afa** in fig.25, 26). Most posteriorly edge **1** bears a somewhat hook-like process **paa**, whose ventral wall is sclerotised by a posterior extension of **L2** (fig.20, 25, 26). Another sclerotised process **loa** (fig.23-25) arises from the posterior ventral wall of the **pne**-pouch (fig.25). Anterior to the **loa**-process, in the area of the bulge **afa**, **L1** bends around the edge **1** into the dorsal wall of the **lve**-pouch, where it has a hinge-like articulation with the right margin of **L2** (**A2** in fig.26).

The membranous ventral wall of the **lve**-pouch is at the same time the left part of the dorsal wall of the ventral lobe **vla** (= ventral phallomere; fig.27). The ejaculatory duct (**D** in fig.26, 27) opens into the anterior ventral wall of the **vla**-lobe. Dorsal to the genital opening there are two membranous lobes (**goa** in fig.25, 26). Posterior to the genital opening the dorsal **vla**-wall contains a small sclerite **L5**, with some small but distinct folds to the left of it. The ventral **vla**-wall is completely sclerotised by a part of **L4A** (fig.20).

Right phallomere

Sclerite **R3** occupies the anterior ventral wall (fig.20, 24). The left end of **R3** has a short extension to the posterior (fig.20, 26). The anterior and right margins of **R3** form a groove-like apodeme **age**, which deepens abruptly in its left part but does not curve like in *Sphodromantis* (fig.20, 24; cross-section in fig.21). Next to its right-posterior end the **age**-apodeme bears a small keel-like apodeme (**3** in fig.20, 24). The right posterior end of **R3** articulates (**A3** in fig.21, 24, 26) with the posteroventral sclerite **R1C**. Sclerite **R1D** is situated to the left of **R1C** and posterior to **R3**; it is in close contact with **R1C** and bears a dental ridge (**pva** in fig.20, 25, 26). The ventral wall of the right phallomere posterior to **R3** and **R1D** is extensively invaginated dorsad and anteriad (**cbe** in fig.21, 24). Sclerite **R1C** extends from articulation **A3** posteriad onto a large ventral tooth (**pia** in fig.20, 26), occupying mainly its dorsal wall. Like in *Sphodromantis*, the area of articulation **A3** and the adjacent part of **R1C** are somewhat groove-like – a posterior extension of the **age**-apodeme on **R3**. The posterior part of the right phallomere is composed of a large dorsal lobe (**fda** in fig.23, 24) and of the ventral **pia**-tooth. The dorsal wall of the **fda**-lobe is

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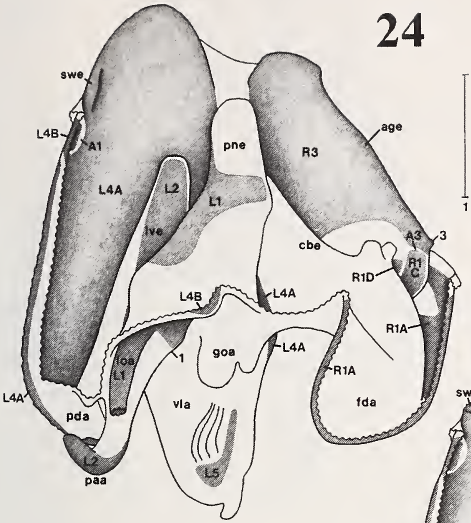
Figs.24-27: *Metallyticus violaceus* (Mantodea, Metallyticidae) – Left complex and right phallomere in dorsal view; with successive removal of their parts (mainly of dorsal ones); fig.27: all parts of right phallomere removed. – Scale: 1mm.

Metallyticus violaceus

24



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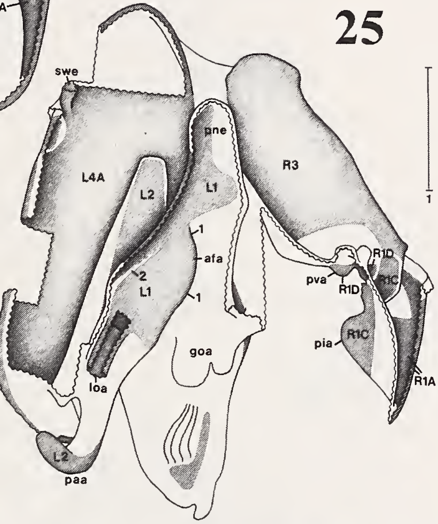

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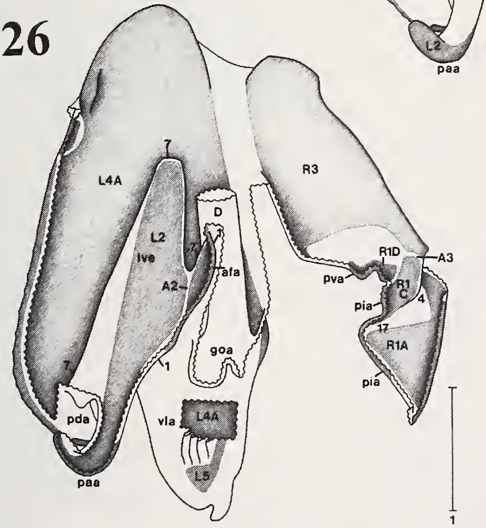

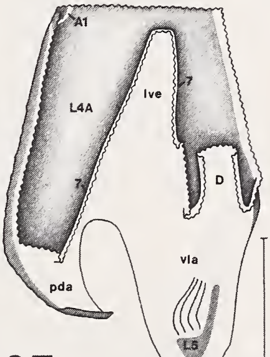

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completely occupied by sclerite **R1A**. Around the right edge of the right phallomere **R1A** curves ventrad and sclerotises the ventral wall of the **pia**-tooth (fig.20, 26). **R1A** is completely separated from **R1C**.

Subgenital plate

Fig.22. In the specimen examined only the right stylus **S9s** was preserved.

5.3. *Chaeteessa caudata* (Mantodea, Chaeteessidae)

Left complex

Sclerite **L4** occupies the whole ventral and dorsal walls (fig.28, 31). The dorsal and ventral parts of **L4** are firmly connected along the left edge of the left complex. Within the ventral part of **L4**, the left, right, and anterior margins as well as an anterior transverse bridge are distinctly heavier sclerotised (fig.28, 32).

A dorsal **pne**-pouch and a ventral **lve**-pouch invaginate from beneath the right margin of the dorsal **L4** and take a position in the center of the left complex. These pouches contain the sclerites **L1** and **L2** (fig.32, 34). The **pne**-pouch has its anterior part deeply invaginated anteriad, its posterior part has the shape of a groove open to the right. **L1** occupies the whole ventral wall of the **pne**-pouch; only within the anterior part of **pne L1** curves around the left edge of the pouch into the dorsal wall; here it has a short extension directed right-posteriad (fig.32). The phallomere-gland (**P** in fig.32, 34) opens into the membranous right wall of the **pne**-pouch. The ventral pouch **lve** deepens strongly anteriad. The ribbon-shaped sclerite **L2** occupies most of its dorsal wall (fig.34). The edge **1** (fig.34) between the pouches **pne** and **lve** bears in its posterior part a long process **paa**, whose ventral wall is sclerotised by a posterior extension of **L2** (fig.28, 34). Immediately anterior to the **paa**-base, **L1** curves from the ventral wall of the **pne**-pouch into the dorsal wall of the **lve**-pouch (around edge **1** in fig.34, 35), where it articulates with **L2** (**A2** in fig.34, 35). Anterior to this **L1**-curvature edge **1** bears a membranous process **afa**. Edge **1** forks immediately anterior to **afa**. Between the two branches the small membranous pouch **pbe** deepens to the left. **pbe** is situated between the pouches **pne** and **lve**.

The membranous ventral wall of the **lve**-pouch is at the same time the left dorsal wall of a large ventral lobe **vla** (= ventral phallomere; fig.28, 32). The ejaculatory duct (**D** in fig.32, 35) opens into the anterior dorsal wall of the **vla**-lobe – far on the right side and outside the **lve**-pouch. The ventral wall of the **vla**-lobe is sclerotised by a part of the ventral **L4** (fig.28).

Figs.28-31: *Chaeteessa caudata* (Mantodea, Chaeteessidae) – **28:** Phallomere complex in ventral view. – **29a:** Right phallomere with transition to left complex in ventral view; some ventral parts removed. – **29b:** Detail of right phallomere in ventral view (compare fig.29a); with sclerite R1B and tooth pva. – **30:** Subgenital plate in dorsal view; styli missing. – **31:** Left complex and right phallomere in dorsal view. – Scale: 0.5mm.

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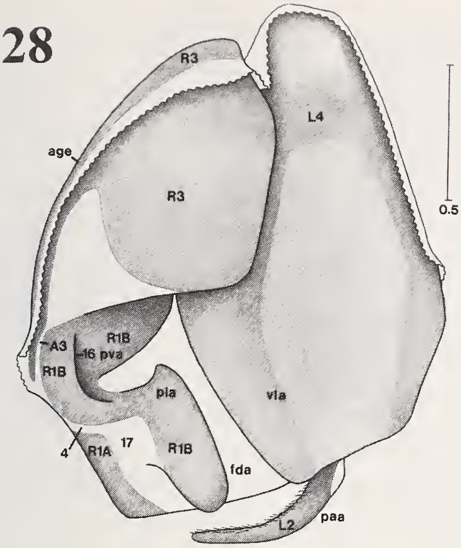

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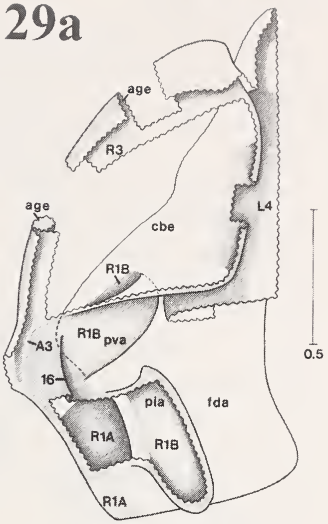

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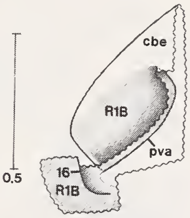

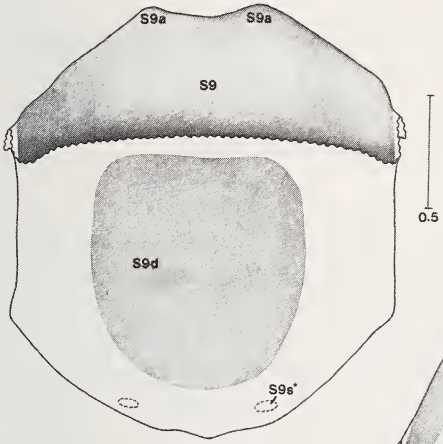

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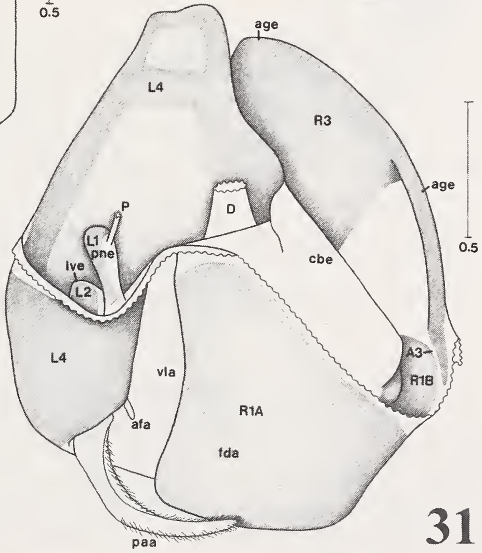

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Chaeteessa caudata

Right phallomere

Sclerite **R3** in the anterior ventral wall is hatchet-shaped (fig.28, 31). Its anterior and right margins form an apodeme **age** (fig.28, 32). The left part of **age** is groove-like, the right part is beam-like (the groove is filled in by the cuticle being thickened; cross-section through **age** in fig.29a, 33). The leftmost part of **R3** bends back to the right (fig.29a, 32, 33).

Posterior to the left part of **R3** the ventral wall of the right phallomere is invaginated dorsad and anteriad (**cbe** in fig.29a, 32). The right posterior end of **R3** has a broad articulation **A3** with the posteroventral sclerite **R1B**. From **A3** sclerite **R1B** extends to the left onto the anterior tooth **pva**, on which way it bends dorsad along the edge **16** (fig.28, 29a), as well as onto the posteroventral tooth **pia**. The dorsal and ventral walls of **pva** and **pia** are completely sclerotised by **R1B** (fig.28, 29a, 33).

The posterior part of the right phallomere is composed of the large dorsal lobe **fda** (fig.31, 32) and the ventral tooth **pia**. The dorsal wall of **fda** is occupied by sclerite **R1A**. Around the right edge of the right phallomere **R1A** curves into the ventral wall, where it is restricted to the right margin and completely separated from **R1B** by membrane (**4** and **17** in fig.28, 32).

Subgenital plate

Fig.30. The styli **S9s** have been lost in the examined specimen; only their points of insertion are shown (**S9s***).

5.4. *Mantoida schraderi* (Mantodea, Mantoididae)

Left complex

Sclerite **L4** extends along the left, anterior, and right margins of the ventral wall (fig.41, 44). Along the whole left edge of the left complex **L4** also curves into the dorsal wall (fig.44, 45), where it is restricted to the left margin. Only a very distinct part of **L4** in the anterior dorsal wall extends farther to the right (**L4d** in fig.44). An apodeme **swe** runs along the whole left arm of **L4** (fig.44, 45). The anterior part of **swe** is beam-like by the cuticle being thickened (cross-section of **swe** in fig.46). To the posterior this thickening decreases, and **swe** is groove-shaped (cross-section in fig.45).

To the right of the dorsal part of **L4**, a dorsal pouch **pne** (fig.44, 45) and a ventral pouch **lve** (fig.45, 46) are invaginated anteriad, which contain the sclerites **L1** and **L2**. Within

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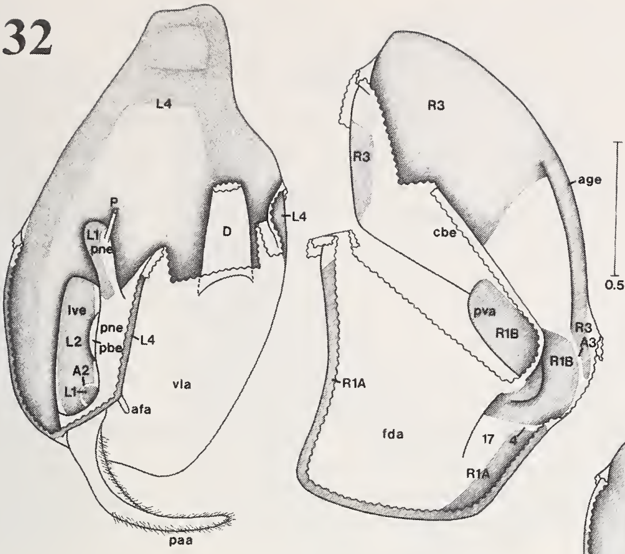
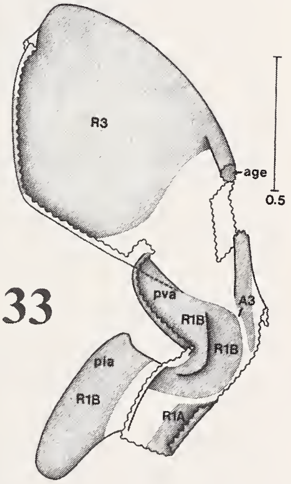
Figs.32-35: *Chaeteessa caudata* (Mantodea, Chaeteessidae) – **32:** Left complex and right phallomere (separated from each other) in dorsal view; some parts removed (mainly dorsal ones; compare fig.31). – **33:** Right phallomere in dorsal view; further parts removed (mainly dorsal ones; compare fig.32). – **34:** Left posterior part of left complex in dorsal view; further parts removed (mainly dorsal ones; compare fig.32). – **35:** Posterior part of left complex in dorsal view; right posterior part of left complex with genital opening retained; further parts removed in the left half (mainly dorsal ones; compare fig.34). – Scale: 0.5mm.

32



Chaeteessa caudata



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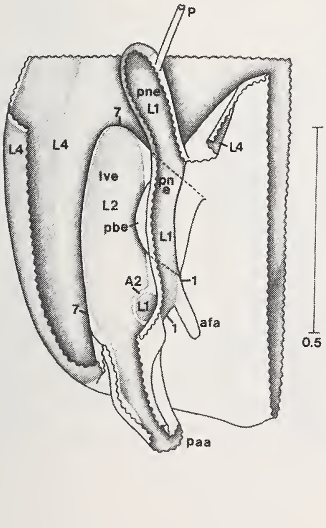

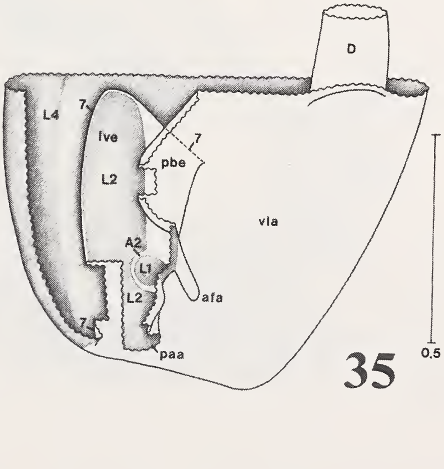

35

the **pne**-pouch, the hood-shaped **L1** occupies most of the ventral wall and the left margin of the dorsal wall (fig.45). The left-dorsal posterior margin of **L1** articulates with a small sclerite on the process **loa** (fig.45). The right posterior margin of **L1** has a ribbon-like extension. The phallomere-gland (**P** in fig.44, 45) opens into the anteriormost membranous part of the **pne**-wall. The ventral pouch **lve** (fig.46) is more tranversely extended (and less antero-posteriorly as in *Metallyticus* and *Chaeteessa*). The edge along the bottom of the **lve**-pouch is labelled **7** in fig.46, 47. The ejaculatory duct (**D** in fig.46) opens into the right part of **lve**. Sclerite **L2** extends like an arch along the margins of the dorsal wall of **lve**. In the anteriormost left edge of the pouch, however, it bends into the ventral wall of **lve** (fig.47), and from here it extends posteriad to join the left posterior end of **L4**. The area where these posterior ends of **L2** and **L4** are interconnected is as a whole upcurved (fig.45) and bears two short processes: the right, somewhat pointed **paa**, whose sclerotisation belongs to **L2**, and the left, bulge-like **pda**, whose sclerotisation is part of **L4**. The edge **1** (fig.45, 46) between the pouches **pne** and **lve** is transversely orientated, not longitudinally as in the previous species. Far to the right of **paa** the right posterior ends of **L1** and **L2** contact each other (articulation **A2** in fig.45, 46) – exactly in the edge **1**. Immediately to the right of **A2** the invagination of the **lve**-pouch – and thus also the edge **1** – ends (fig.46), and immediately to the right of this point the membranous lobe **afa** has its base.

The membranous ventral wall of the **lve**-pouch is at the same time the anterior dorsal wall of the ventral lobe **vla** (= ventral phallomere; fig.46, 47). The ejaculatory duct (**D** in fig.46, 47) opens most anteriorly, and quite far to the right, into this membrane. The ventral wall of the **vla**-lobe is partly sclerotised by the right posterior part of **L4** (fig.41, 47).

Right phallomere

Sclerite **R3** in the anterior ventral wall is hatched-shaped (fig.41, 44). Its anterior and right margins form an **age**-apodeme (fig.41, 44, 45), which is distinctly groove-like in its left part but more beam-like in its right part (cross-section through **age** in fig.43, 45). In its left part **age** is deeper. On the utmost right posterior part of **R3** the **age**-apodeme bears a small keel-like apodeme (**3** in fig.43, 44).

The horseshoe-shaped sclerite **R1D** lies in the ventral wall posterior to the central part of **R3** and sclerotises the tooth **pva** (fig.41, 43, 45). Posterior to the left and central parts of **R3** and posterior to **R1D** the ventral wall of the right phallomere is invaginated dorsad and anteriad (**cbe** in fig.43-45). The right posterior end of **R3** articulates (**A3** in fig.41, 44) with the ventral part of sclerite **R1E**. The groove called **age** on **R3** extends beyond

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Figs.36,37: *Mantoida schraderi* (Mantodea, Mantoididae) – **36:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, epiproct, subanal lobes, paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. – **37:** Same as in fig.36, after removal of further parts of abdominal tergites 9 and 10, parts of right paraproct, and supraanal lobe with epiproct. Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. Posterior to transverse line: like in fig.36. – Scale: 1mm.

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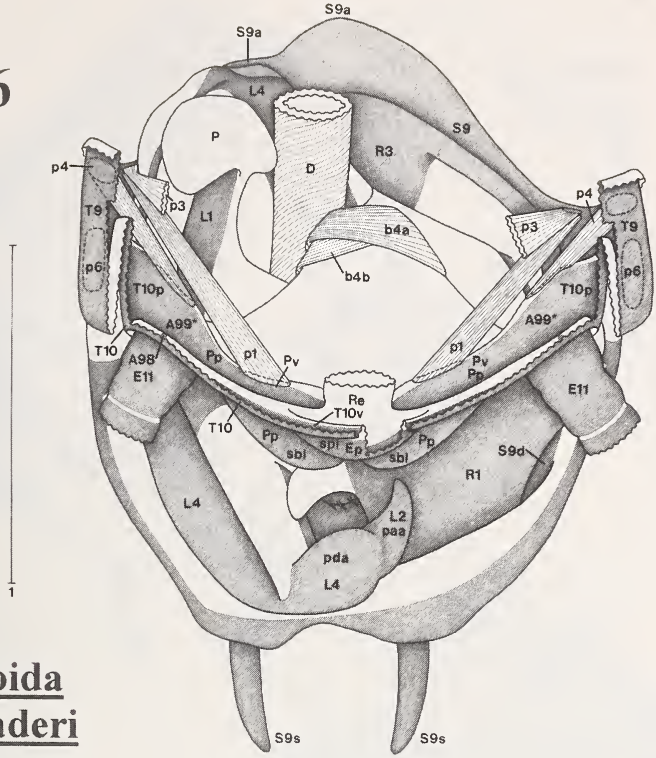

Mantoida schraderi

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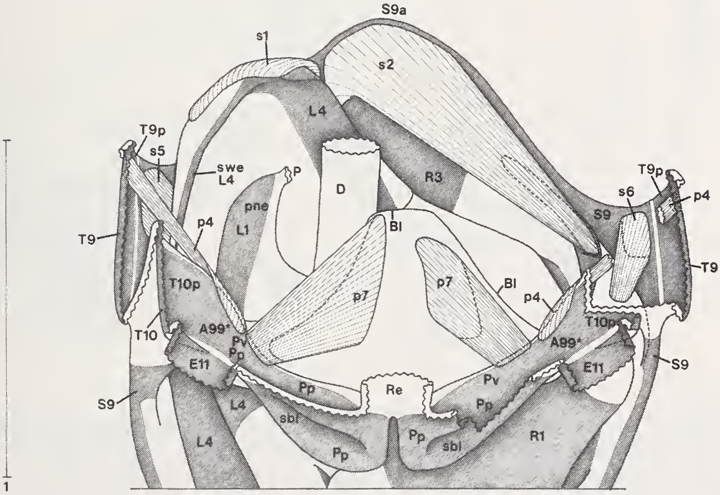

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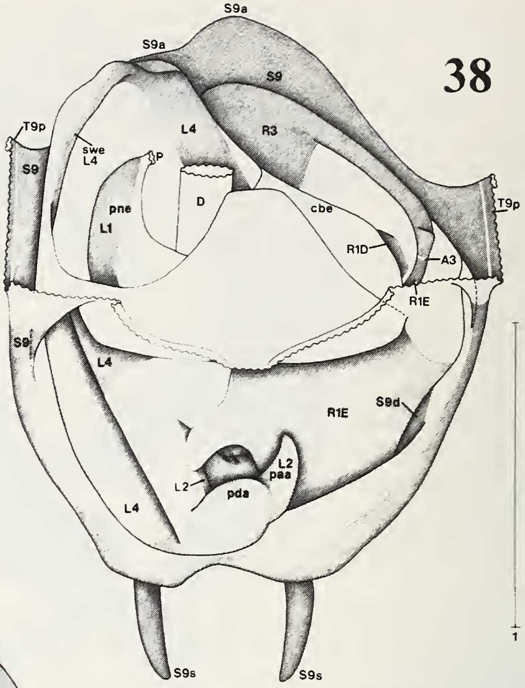
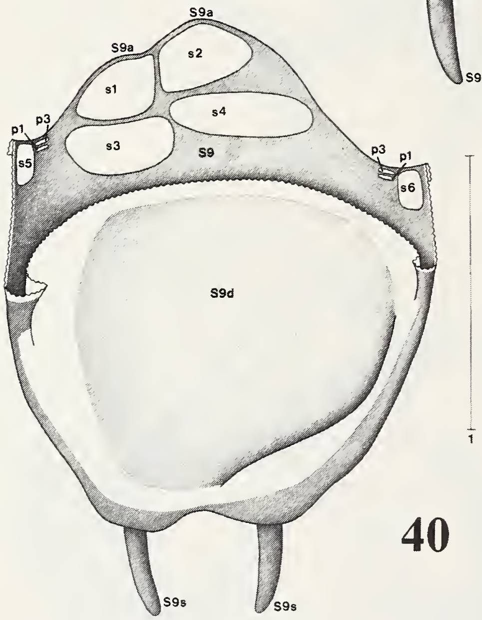


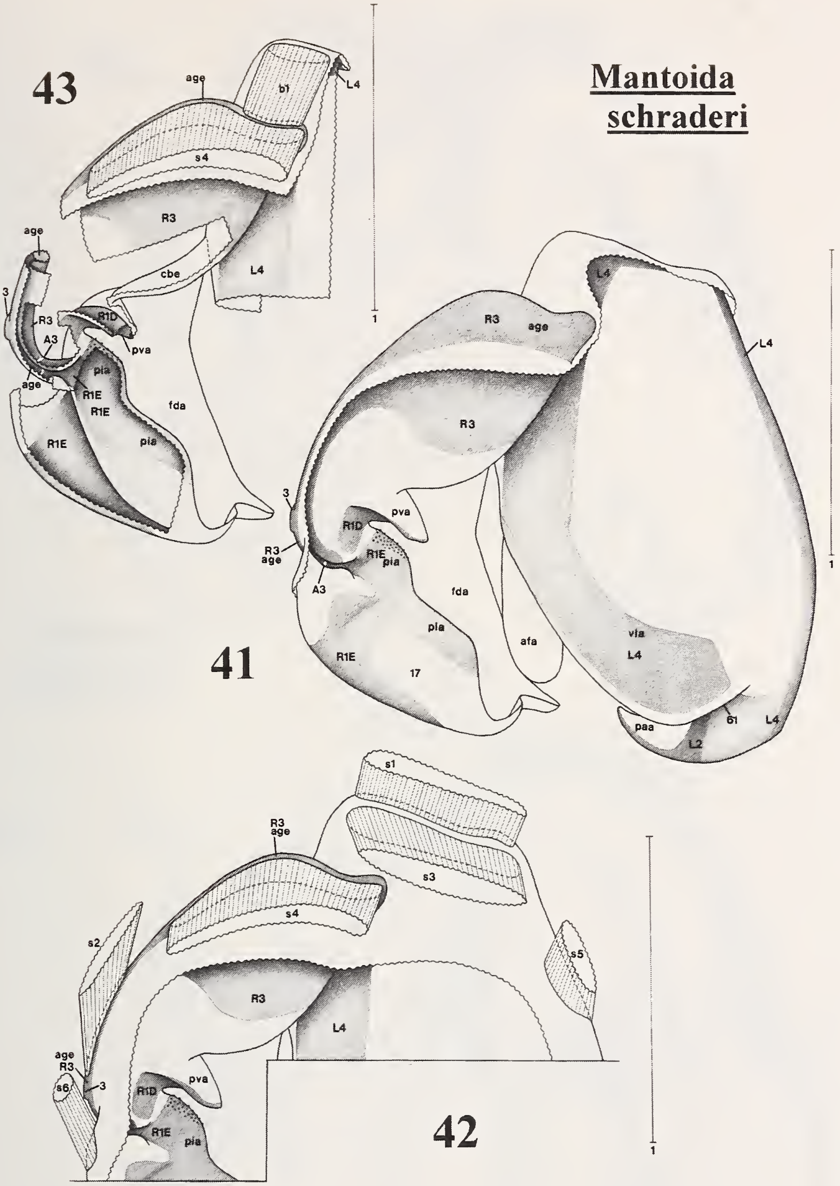


40

Mantoida schraderi

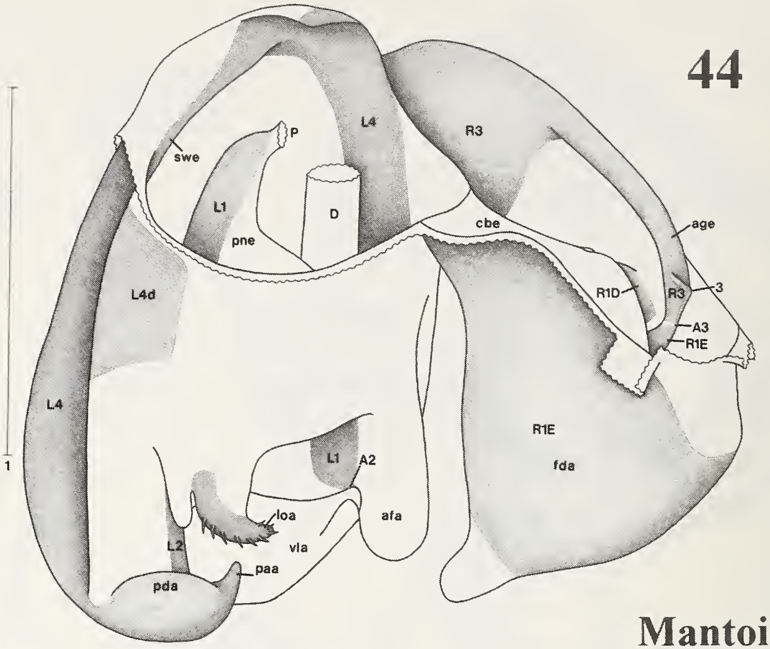
Figs.38-40: *Mantoida schraderi* (Mantodea, Mantoididae) – **38:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **39:** Left margin of subgenital plate (compare fig.38); with insertion of muscle p6. – **40:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6). – Scale: 1mm.

Mantoida schraderi



Figs.41-43: *Mantoida schraderi* (Mantodea, Mantoididae) – **41:** Phallomere complex in ventral view. – **42:** Anterior part of phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.41. – **43:** Right phallomere with transition to left complex in ventral view; with some muscles; some ventral parts removed. – Scale: 1mm.

44



Mantoida schraderi

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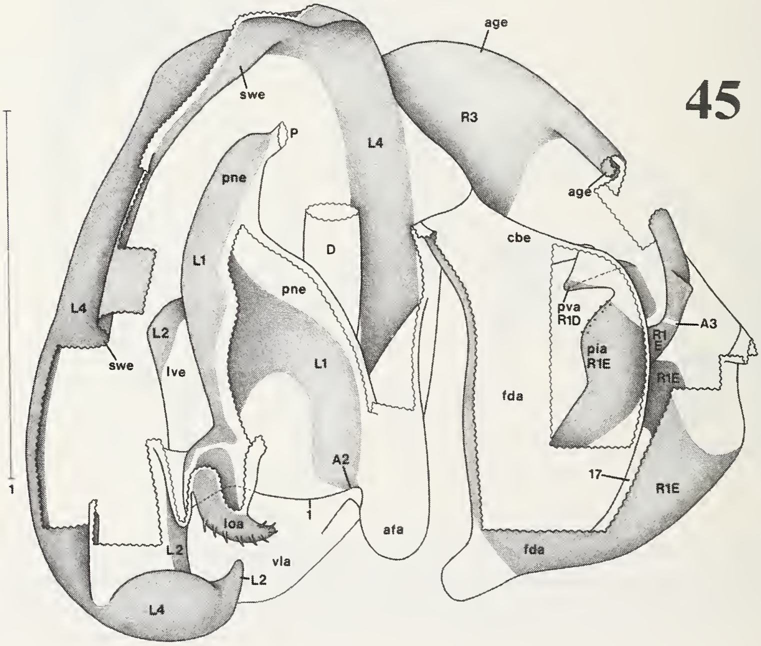

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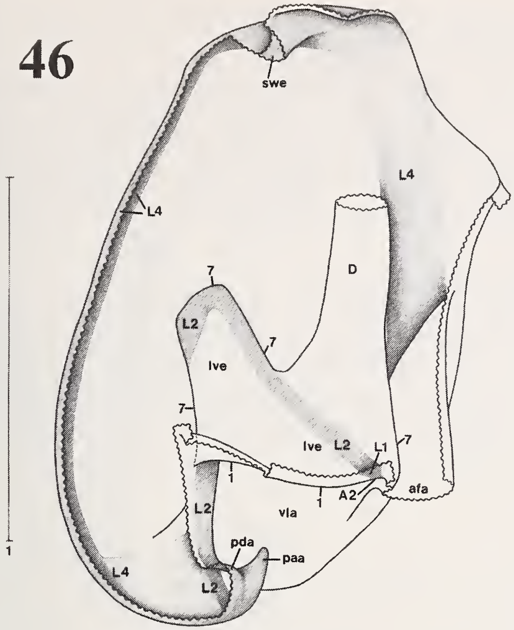

Mantoida schraderi

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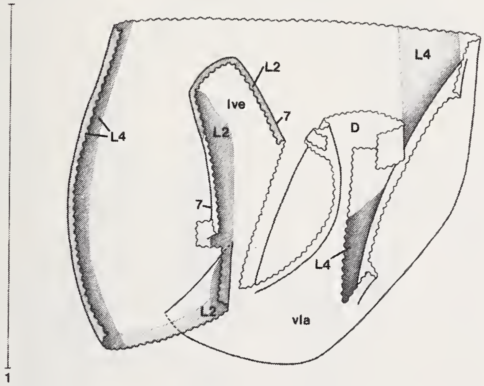


Figs.46,47: *Mantoida schraderi* (Mantodea, Mantoididae) – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.

Figs.44,45: *Mantoida schraderi* (Mantodea, Mantoididae) – **44:** Left complex and right phallomere in dorsal view. – **45:** Left complex and right phallomere in dorsal view; some parts removed (mainly dorsal ones). – Scale: 1mm.

articulation **A3** (where it is no longer called **age**) onto **R1E** (fig.41). The anterior margin of **R1E** is in close contact with **R1D** (fig.41).

The posterior part of the right phallomere is composed of the large dorsal lobe **fda** (fig.44, 45), with **R1E** in its dorsal wall, and the ventral tooth **pia**. Sclerite **R1E** extends from articulation **A3** left-posteriad onto the **pia**-tooth and occupies most of its dorsal and ventral walls (fig.41, 43, 45). Another part of **R1E** extends narrowly to the right edge of the phallomere, curves dorsad, and, becoming broader again, occupies most of the dorsal wall of the **fda**-lobe (fig.41, 44).

Subgenital plate and posterior abdominal segments

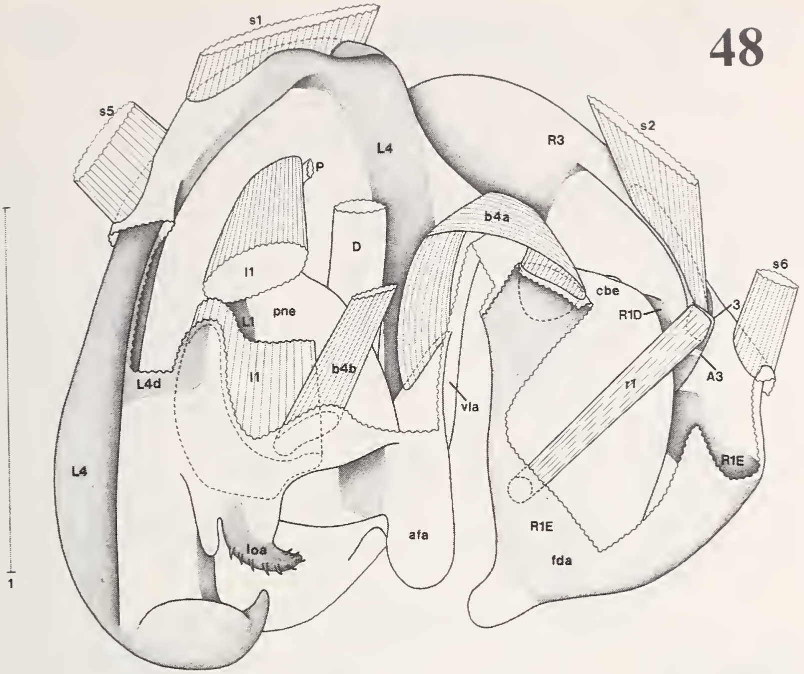
Fig.36, 37 (posterior segments); fig.40 (subgenital plate **S9**). The ventral part of tergite 10 **T10v** is very narrow but distinct. Separate **Pv**-sclerites are missing; they are assumed to have been incorporated into the anterior margins of the paraprocts **Pp**. The sclerites **Ca, Cb**, and **Cc** are missing. The articulations **A99** are missing (**A99***: paratergites **T10p** and paraprocts **Pp** have fused). The articulations **A98** are well-developed.

Musculature

Muscles	Positions of insertions	in fig.
l1	**L1** (anteriorly on **pne**-pouch) – central dorsal wall of left complex near right end of **L4d**	48
l2	**L1** (left-ventrally on **pne**-pouch) – **L4** (dorsally on left arm, on **swe**-apodeme)	49
l3	**L1** (posteroventrally on **pne**-pouch) – **L2** (left-anterior part)	50
l4	**L2** (left-anterior part) – **L4** (dorsally on left arm, on **swe**-apodeme)	50, 51
l5	Left anterior membranous ventral wall of left complex – **L2** (left-anterior part)	50, 51
l6	Right anterior membranous ventral wall of left complex – **L2** (right part) and dorsal wall of **vla**-lobe around genital opening	50, 52
l7	Left posterior membranous ventral wall of left complex – **L4** (posterior ventral part of left arm)	52
l9	Transversely within right dorsal wall of left complex	49
r1	**R3** (right margin) – **R1E** (dorsal wall of **fda**-lobe)	48
r2	**R3** – **R1D** on **pva**-tooth and membrane of **cbe**-invagination	49, 50
r3	**R1E** (right part) – **R1E** on **pia**-tooth and right ventral wall of **fda**-lobe	49, 50
r4	**R1E** (left-anterior part) – left ventral wall of **fda**-lobe	49
b1	Membrane behind right anterior margin of **L4** – **R3** (left anterior margin)	43
b2	Dorsal wall of **vla**-lobe (right-anterior part) – **R3** (left anterior margin)	49
b4a	Dorsal wall of **vla**-lobe (right-anterior part) – **R1E** (left anterior margin)	36, 48
b4b	Central dorsal wall of left complex – membrane posterior to anterior margin of **R1E** (in fig.36 the insertion is beneath muscle **b4a**)	36, 48

Figs.48,49: *Mantoida schraderi* (Mantodea, Mantoididae) – Left complex and right phallomere in dorsal view; each figure with some muscles; parts of phallomere complex removed to various extents. – Scale: 1 mm.

48



Mantoida schraderi

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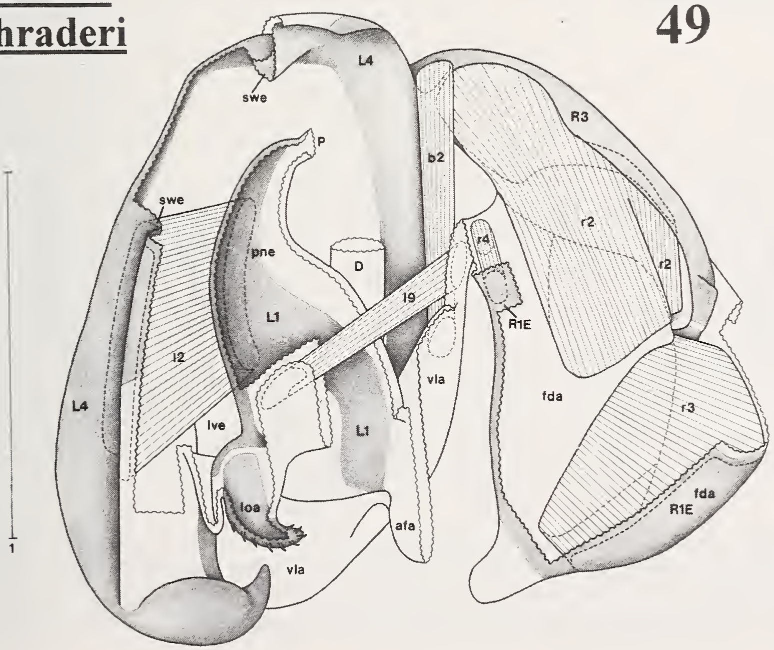

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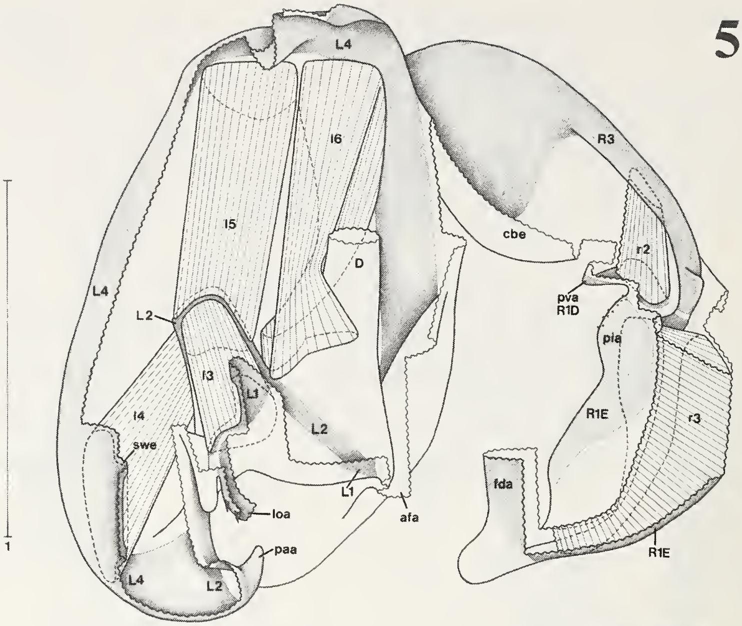

Mantoida schraderi

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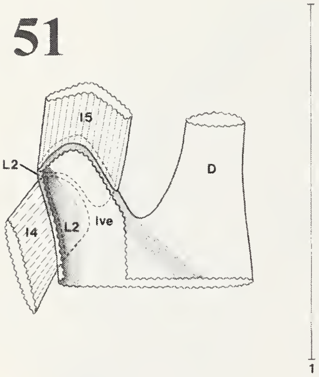
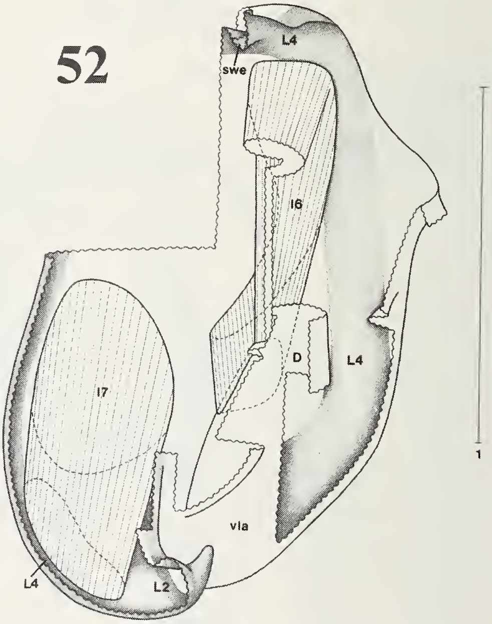




Figs.50-52: *Mantoida schraderi* (Mantodea, Mantoididae) – **50:** Left complex and right phallomere in dorsal view; each figure with some muscles; parts of phallomere complex removed. – **51:** Detail of left complex in dorsal view (compare fig.46); with some muscles. – **52:** Left complex in dorsal view; with some muscles; parts of left complex removed (mainly dorsal ones). – Scale: 1mm.

s1	**S9** left side (medially and most anteriorly) – **L4** (anterior margin)	37, 40, 42, 48
s2	**S9** right side (medially and most anteriorly) – **R3** (lateral anterior margin)	37, 40, 42, 48
s3	**S9** left side (medially and anteriorly) – anteriormost left ventral wall of genital pouch	40, 42
s4	**S9** right side (medially and anteriorly) – **R3** (left ventral wall of **age**-apodeme)	40, 42, 43
s5	**S9** left side (laterally and anteriorly) – anterior left wall of genital pouch	37, 40, 42, 48
s6	**S9** right side (laterally and anteriorly) – anterior right wall of genital pouch	37, 40, 42, 48
p1 (pair)	**S9** – paraproct **Pp** (anterior margin, corresponding to **Pv**-sclerotisation)	36, 40
p3 (pair)	**S9** – rectum (ventral wall)	36, 40
p4 (pair)	**T9** (lateralmost anterior margin, also extending onto paratergite **T9p**) – anterior margin of paratergite **T10p** (far medially); on both sides completely divided into a dorsal (fig.36: on **T9**) and a ventral (fig.37: on **T9p**) bundle	36, 37
p5 (pair)	Not investigated; presence highly probable	—
p6 (pair)	**T9** (lateralmost part) – membrane immediately above lateral margin of **S9**	36, 39
p7 (pair)	Membrane anterior to paraproct **Pp** – anterior margin of paraproct **Pp** and paratergite **T10p** (border between **Pp** and **T10p** not clear)	37

5.5. *Archiblatta hoeveni* (Blattaria, Blattidae, Blattinae)

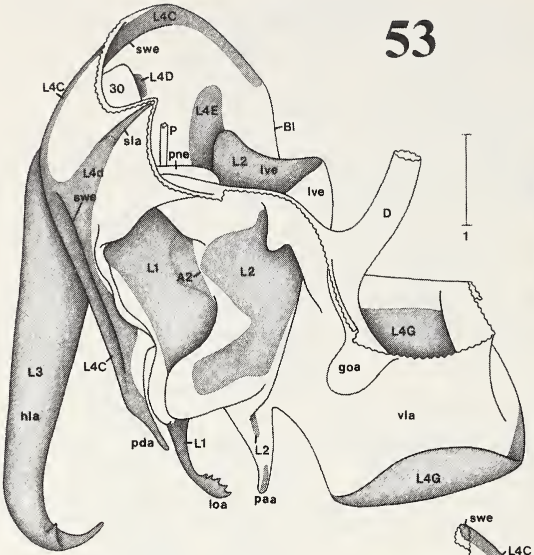
Left complex

L4 is a group of five sclerites: The crescent-shaped **L4C** occupies the whole left edge and the anteriormost left ventral wall of the left complex (fig.53). That part along the left edge has a distinct dorsal extension to the right (**L4d** in fig.53), the end of which forms a spine **sla**. Along the whole of **L4C** there runs an apodeme **swe** (fig.53-56), whose anterior part is beam-like by the cuticle being thickened (anterior cross-section of **swe** in fig.54); to the posterior this thickening decreases, and **swe** becomes more and more groove-shaped (posterior cross-section of **swe** in fig.54). The sclerites **L4D, L4E, L4F**, and **L4G** lie in the ventral wall of the left complex. **L4D** bears a node-like process **nla** (fig.56, 57). **L4E** and **L4F** are simple plates. **L4G** occupies the ventral wall of a large ventral lobe **vla** (= ventral phallomere; fig.53, 54, 57), and its posterior part is upcurved.

In the center of the left complex there are two pouches **pne** and **lve** (fig.53-56), which contain the sclerites **L1** and **L2**. The anterior part of **L1** lies in the ventral wall of the small and flat **pne**-pouch (fig.53, 54). The posterior part of **L1** extends onto a broad lobe, which is divided into three processes posteriorly (fig.54, 55): the two short, membranous **dca** (left side) and the long, sclerotised **loa** (right side). Along the lateral and posterior edges of this lobe the cuticle bends ventrad and anteriad (fig.55) as far as to the edge **6**, where it turns posteriad again. The phallomere-gland (**P** in fig.55, 56) opens immediately posterior to edge **6**.

The large sclerite **L2** adjoins to the right of **L1** (fig.53, 54), and the two sclerites articulate (**A2** in fig.53, 54). From **A2** sclerite **L2** extends to the right, curves ventrad and – becoming narrower – back to the left; then it bends posteriad and runs to the posterior edge of the

53



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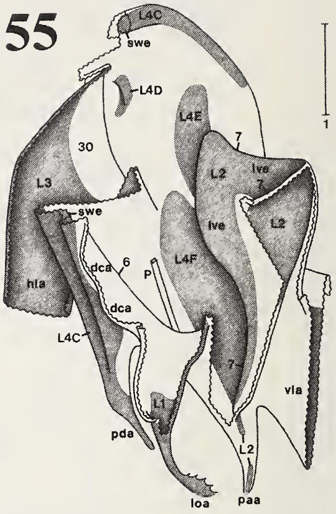

Archiblatta hoeveni

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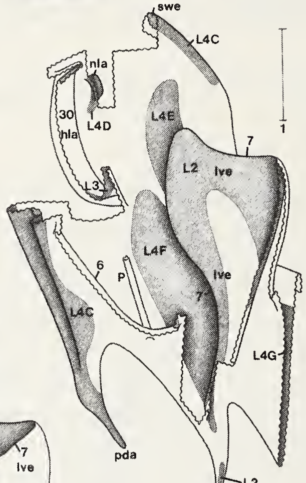

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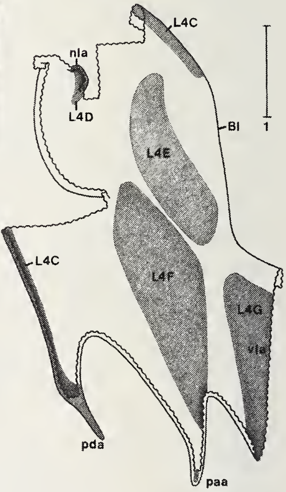

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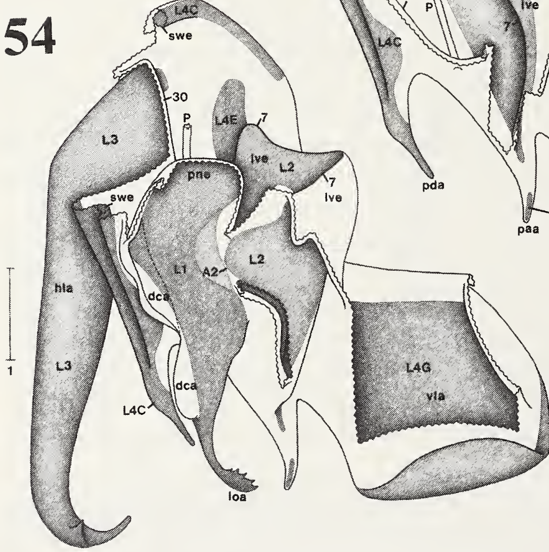

left complex; here it ends at the base of a small process **paa** (fig.56). This arch-like course of **L2** extends along the margins of a pouch **lve**, which is, like **L2** itself, curved dorsoventrally (in contrast to Mantodea, whose **lve**-pouches extend within one plane). Thus, the left parts of the **lve**-pouch and of **L2** lie beneath the **pne**-pouch as in Mantodea, but their right parts curve upwards into the same plane which also contains sclerite **L1**. The edge along the bottom of this **lve**-pouch is labelled **7** in fig.54, 55. The invagination of the **lve**-pouch starts immediately anterior to the **paa**-process (posterior end of **7** in fig.55), and it ends in the anterior dorsal wall of the left complex (dorsal part of **7** in fig.54), where **L2** leaves the pouch and approaches **L1**. According to the curvature of the **lve**-pouch, it is preferable to name that wall of **lve** containing sclerite **L2** the inner one (instead of dorsal) and the opposite wall the outer one (instead of ventral). **L2** is restricted to the inner **lve**-wall; only most posteriorly it bends into the outer (or ventral) **lve**-wall. Then it leaves the pouch and ends on the **paa**-process (fig.55, 56). **paa** is, except for another small distal sclerite (probably a split off part of **L2**), membranous (fig.55-57).

The membranous outer (or ventral) wall of the **lve**-pouch is at the same time the dorsal wall of the **vla**-lobe (fig.53-56; in the figures **vla** is pulled to the right). The ejaculatory duct (**D** in fig.53) opens into this wall. Dorsal to the genital opening there is a small membranous lobe **goa**. The ventral wall of the **vla**-lobe is sclerotised by **L4G**. The posterior edge of the **vla**-lobe continues leftward into the posterior edge of the remaining left complex, where the **paa**-process follows (fig.53, 57).

The large hook **hla** is evaginated from the left anterior ventral wall of the left complex. **hla** is, except for its basalmost walls (**30** in fig.54-56), completely sclerotised by **L3** (fig.53-55). **hla** is retractable for a very short distance, since the basal membranous walls **30** can be introverted (this state is shown in the figures).

Right phallomere

The right phallomere is only schematically shown in fig.330f. Differences to *Eurycotis* (following species) will be explained in 6.7.4., 6.7.5., and 6.7.6.

5.6. *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae)

Left complex

The left complex resembles that of *Archiblatta*. **L4** is a group of three sclerites: The crescent-shaped **L4H** occupies the left edge and the left anterior ventral wall of the left complex (fig.65, 66). That part of **L4H** in the left edge broadens in its posterior half. A beam-like apodeme **swe** (fig.65, 66; anterior and posterior cross-section in fig.66) runs along **L4H**. At the anterior end of the **swe**-apodeme **L4H** bends abruptly posteriad and broadens into a plate bearing the node-like process **nla** (fig.68, 69) in its left half. The

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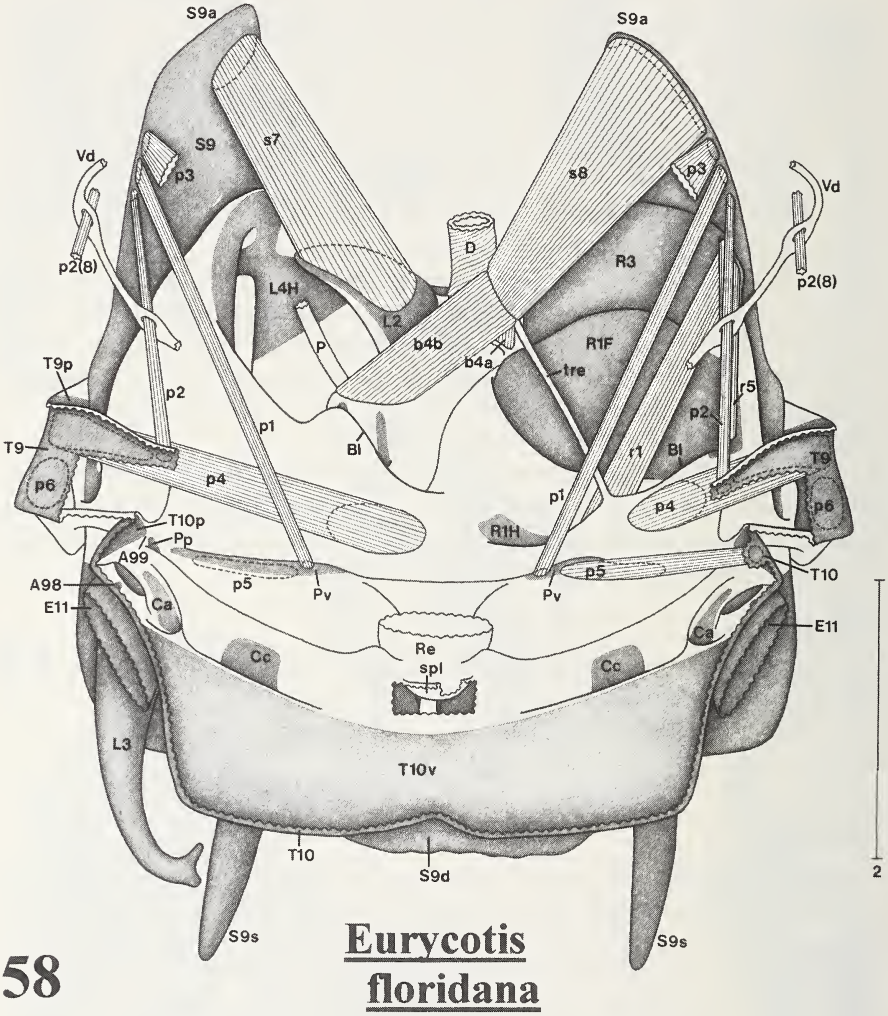
Figs.53-57: *Archiblatta hoeveni* (Blattaria, Blattidae, Blattinae) – **53:** Left complex in dorsal view. – **54-57:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.

plate **L4F** lies in the posterior ventral wall. Along its anterior margin the membrane is evaginated posteroventrad to form the broad lobe **mla** (fig.63, 69). **L4G** occupies most of the ventral and right walls of a large ventral lobe **vla** (= ventral phallomere; fig.63, 65, 66).



58

Fig.58: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, subanal lobes (covered), paraprocts (mostly covered), Pv-sclerites, distal part of rectum, basal parts of cerci, parts of vasa deferentia, and part of musculature. Supraanal lobe shown through a window cut into the membrane anterior to ventral sclerotisation of abdominal tergite 10 T10v. – Scale: 2mm.

Sclerite **L1** lies in the central dorsal wall of the left complex (fig.65-67). Its anterior part occupies the ventral wall of a pouch-like invagination (**pne** in fig.65-67). Its posterior part has a longitudinal furrow (**8** in fig.67) and extends onto two processes (**dca** in fig.67, 68). The phallomere-gland (**P** in fig.68) opens into the ventral wall of the right **dca**-process. Two small sclerites **L6A** and **L6B** lie in the left-dorsal wall of the **pne**-pouch; each bears

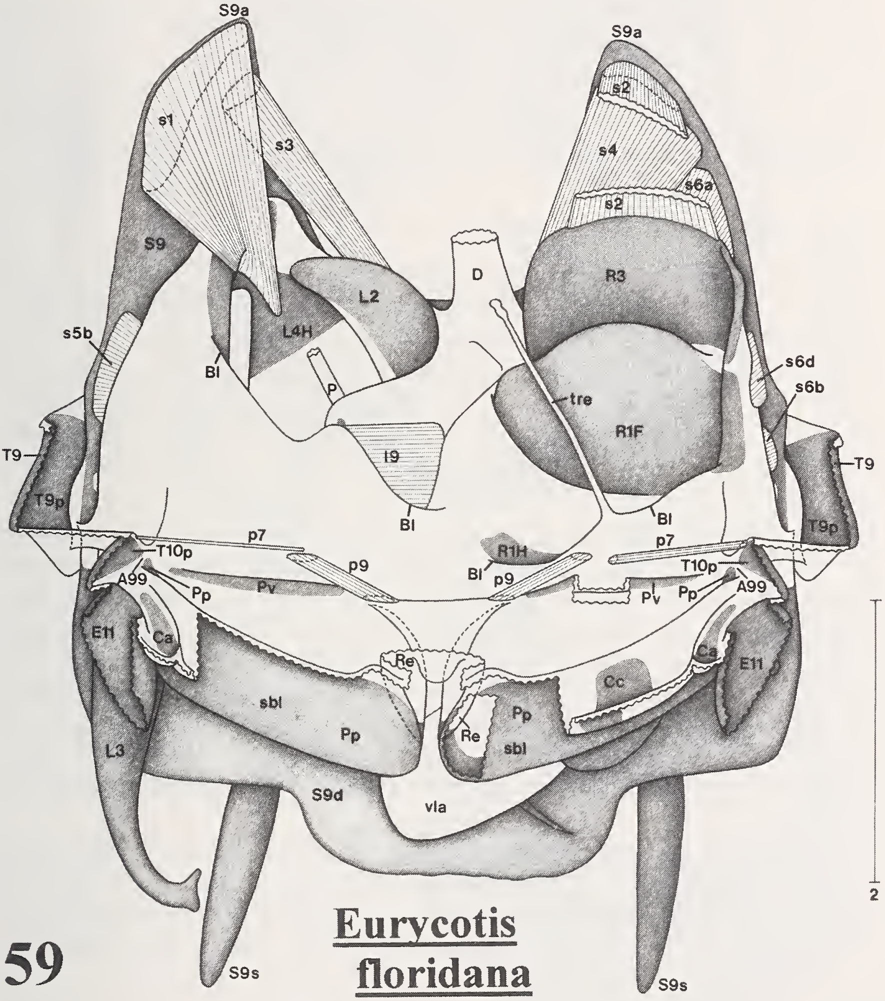


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Fig.59: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – Male postabdomen as in fig.58, after removal of further parts of abdominal tergites 9 and 10 (especially T10v) and supraanal lobe. Distal part of rectum, basal parts of cerci, and dorsal wall of right subanal lobe cut open. Another part of musculature shown. – Scale: 2mm.

a spine (fig.65, 66). Sclerite **L2** adjoins to the right of **L1** (fig.67), and the two sclerites articulate (**A2** in fig.67). Like in *Archiblatta*, **L2** is dorsoventrally curved (fig.67, 68), and the anterior part of **L2** lies in the inner wall of a large pouch (**lve** in fig.65-68; the edge along the bottom of the **lve**-pouch is labelled **7** in fig.66-68). The anteroventral parts of **L2** and **lve** deepen strongly to the left to form a tongue-like apodeme (**lve** in fig.67). At the posterior margin of **L2** there are three processes, the largest of which is the completely sclerotised **paa** (fig.67).

The outer wall of the **lve**-pouch is completely membranous and is at the same time the dorsal wall of the **vla**-lobe (fig.65-67; in the figures **vla** is pulled to the right). The ejaculatory duct (**D** in fig.65, 66) opens into the anterior part of this wall. Dorsal to the genital opening there is a membranous lobe **goa** (fig.66). In contrast to *Archiblatta*, the main part of the **vla**-lobe is separated by a deep notch (**9** in fig.63) from the remaining ventral parts of the left complex. The **hla**-hook (fig.65-67) is like in *Archiblatta*.

Right phallomere

Sclerite **R3** in the anterior (right-)ventral wall is a curved plate (fig.74-77). The right and the right anterior margins of **R3** form a groove-like apodeme **age** (fig.74, 77; cross-section through **age** in fig.78). The right part of **age** bears a keel-like apodeme (**3** in fig.74, 77).

Posterior to the left part of **R3** sclerite **R2** adjoins, and the two sclerites articulate (**A7** in fig.75-77). **R2** forms a dental ridge (fig.74-77). Posterior to the central part of **R3** the ventral wall of the right phallomere is extensively invaginated dorsad and anteriad (**cbe** in fig.74-76; compare fig.77 and 78). This **cbe**-invagination takes a position in the center of the right phallomere.

Posterior to the right end of **R3** sclerite **R1F** adjoins, and the two sclerites are articulated (**A3** in fig.74, 75, 77). **R1F** extends from its central part behind **A3** in three directions: The first arm bends left-dorsad (along edge **16**, fig.77, 78) and occupies the whole right-dorsal wall of the **cbe**-invagination (fig.74, 75, 78). This arm forms a dental ridge (**pva** in fig.75, 78, 80) at its posterior margin and articulates with the left-dorsal end of **R2** (**A6** in fig.75, 76) at its median end. The second arm of **R1F** extends posteriad and sclerotises the anterior part of a two-pointed ventral tooth (**pia** in fig.77). The third arm of **R1F** extends posterodorsad (fig.74); its dorsal margin folds back to the right to form a sclerotised groove (**rge** in fig.74); the **rge**-groove is a posterior continuation of the **age**-groove on **R3**.

The posterior part of the right phallomere is composed of the dorsal lobe **fda** (fig.74) and the ventral tooth **pia** (fig.77, 78). **fda** and **pia** are confluent along the right edge of the right phallomere and diverge towards the left. The dorsal wall of the **fda**-lobe and parts of its ventral wall are occupied by sclerite **R1H** (fig.74, 76). The left part of **R1H** scle-

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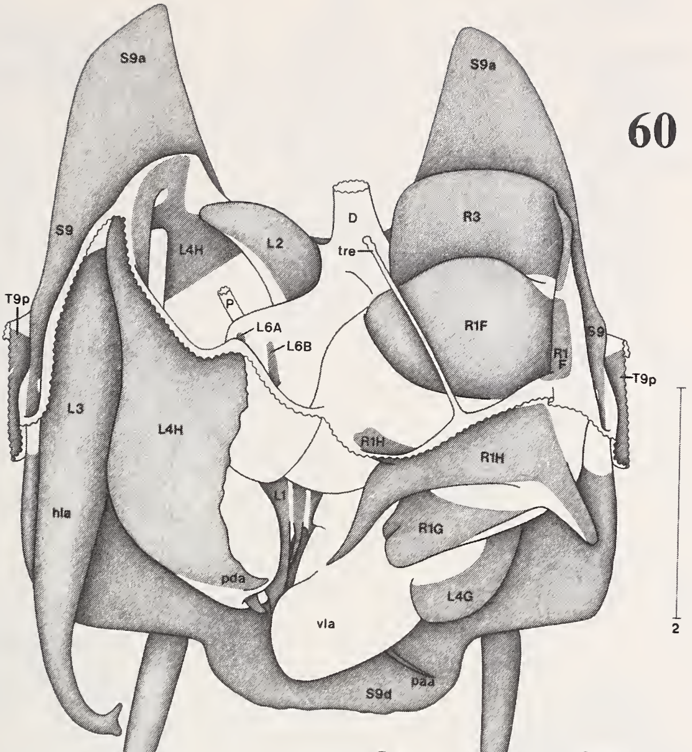
Figs.60-62: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – **60:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **61:** Left margin of subgenital plate (compare fig.60); with insertion of muscle p6. – **62:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6). – Scale: 2mm.



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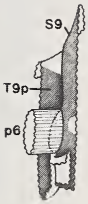

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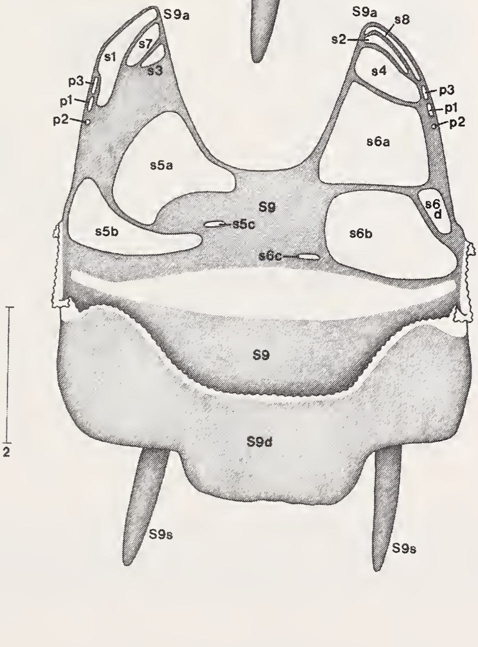
Eurycotis floridana



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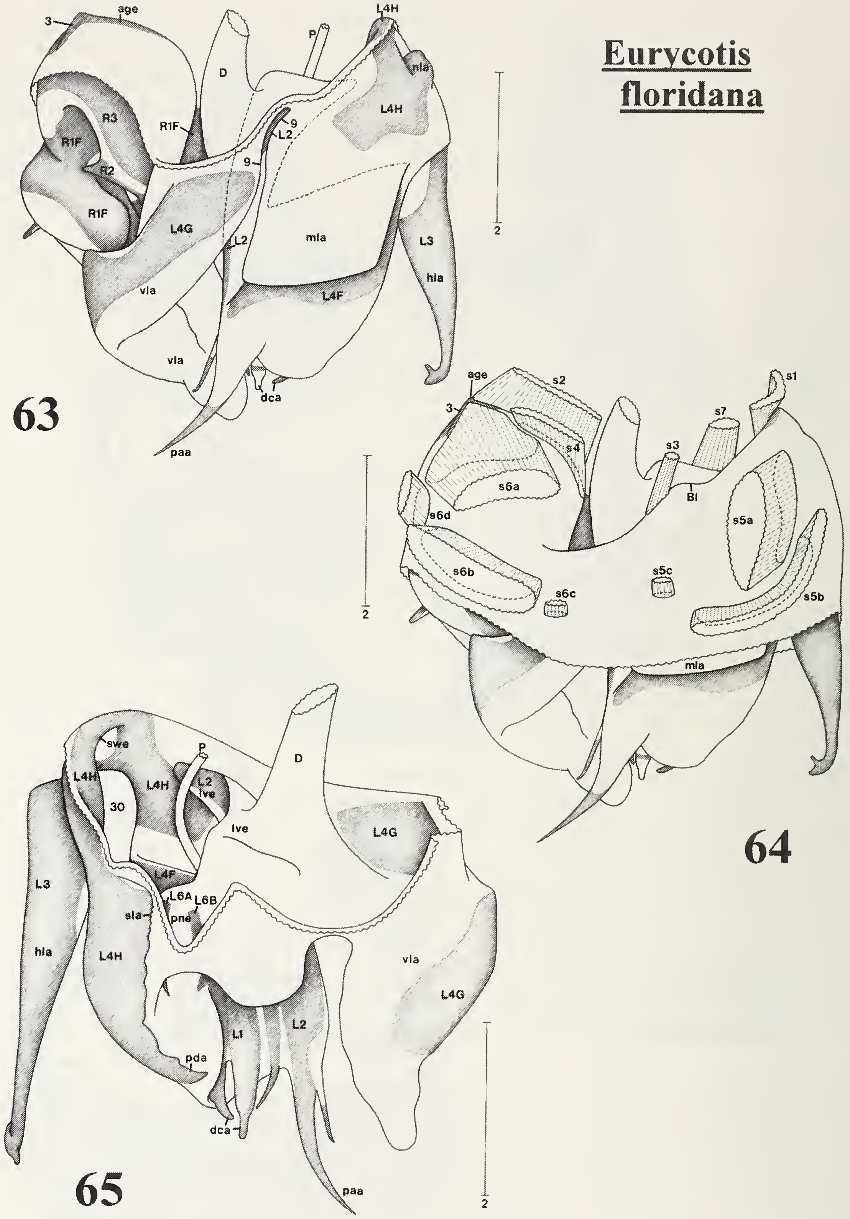
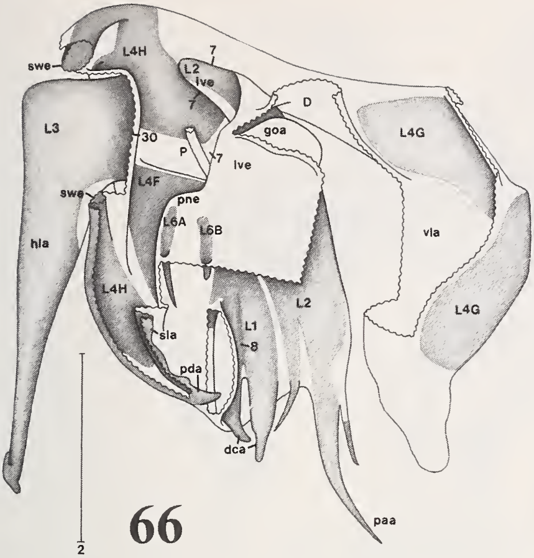
Eurycotis floridana



Figs.63-65: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – **63:** Phallomere complex in ventral view. – **64:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.63. – **65:** Left complex in dorsal view. – Scale: 2mm.

Eurycotis floridana



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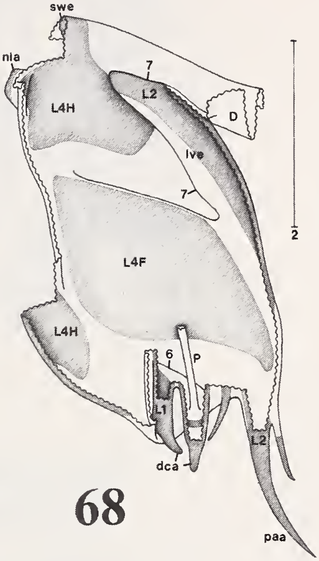

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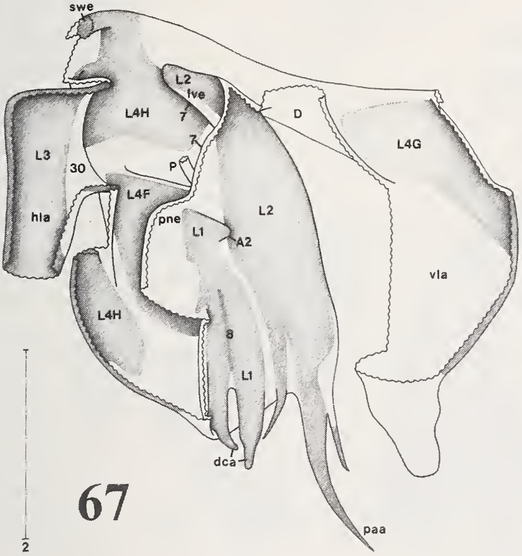

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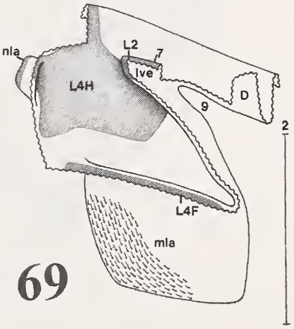

69

Figs.66-69: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 2mm.

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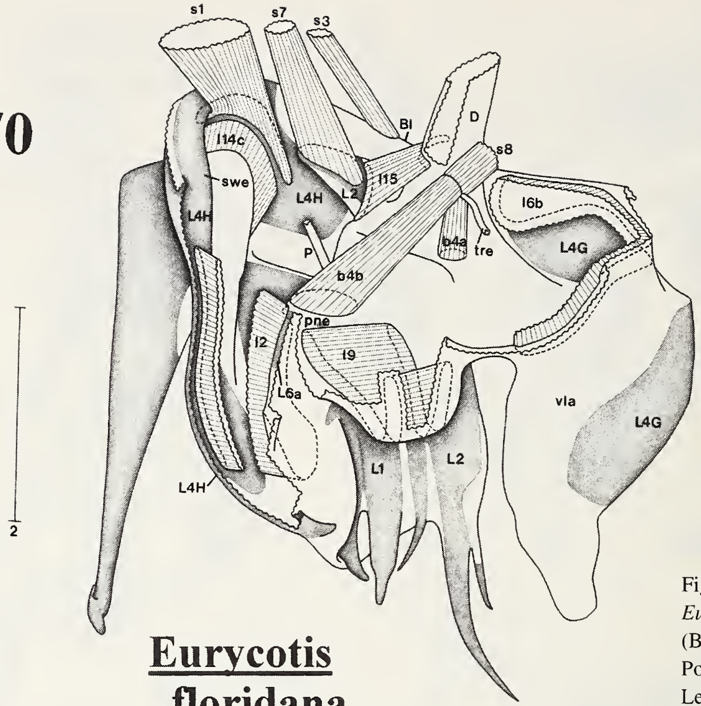

Eurycotis floridana

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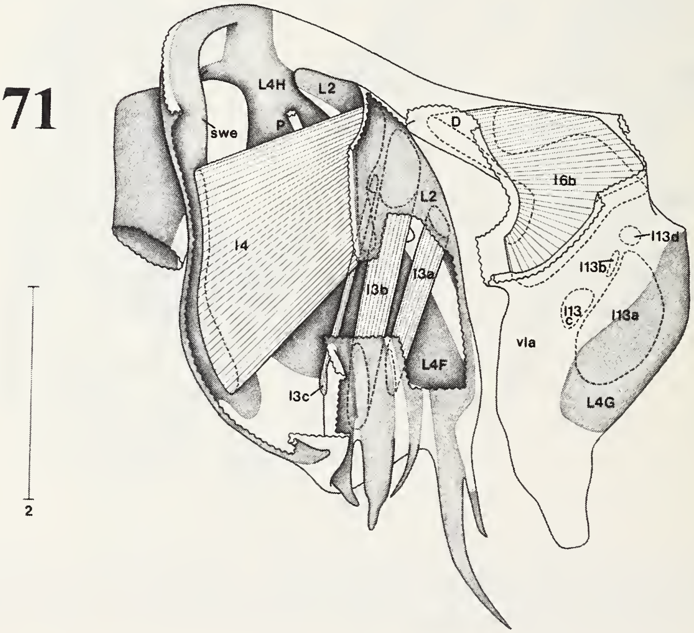

Figs.70,71: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 2mm.

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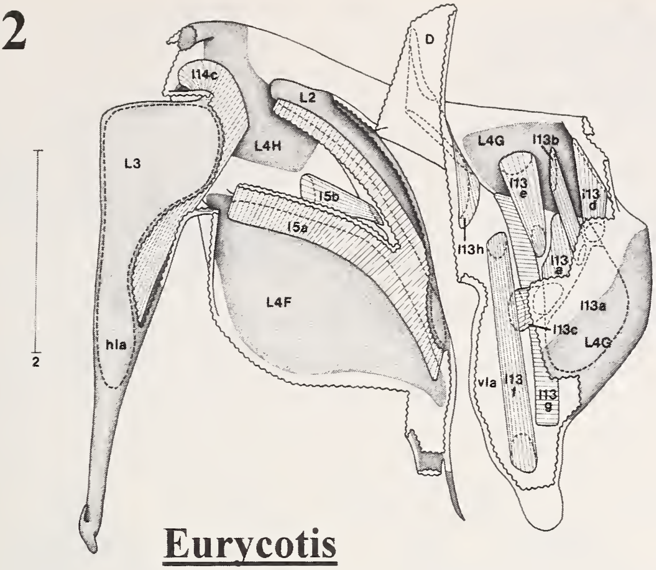
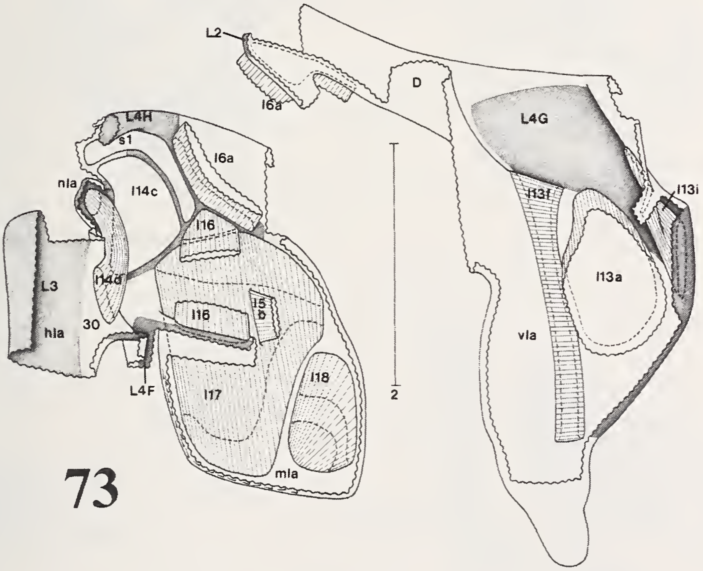


Eurycotis floridana



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Figs.72,73: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 2mm.

rotises the spine **sra**; the left end of **R1H** is somewhat spoon-shaped. The right end of **R1H** extends posteriorly onto the process **pra** (fig.74) and articulates anteriorly with the dorsal arm of **R1F** (**A8** in fig.74). The tendon **tre** (fig.74), a very long and narrow invagination of the cuticle, has its origin in the anteriormost dorsal wall of the **fda**-lobe. The ventral tooth **pia** is anteriorly sclerotised by the second arm of **R1F** (fig.77, 78); posteriorly **pia** is sclerotised by **R1G**, which articulates with **R1F** in the dorsal wall of **pia** (**A9** in fig.78). **R1G** has a narrow extension to the right, which reaches the **pra**-process and maintains a narrow connection with the dorsal **R1H** (fig.74, 77, 78). Anterior to this sclerite bridge there is a large membranous area (**17** in fig.74, 77).

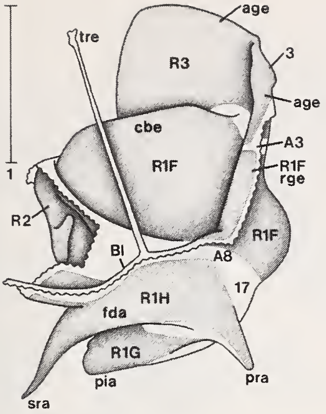
Subgenital plate and posterior abdominal segments

Fig.58, 59 (posterior segments); fig.62 (subgenital plate **S9**). The ventral part of tergite 10 **T10v** is very extensive. Strip-like **Pv**-sclerites are present; they are completely free from the paraprocts **Pp**. The **Ca**-sclerites lie on curved bulges immediately median to the cercal bases. The **Cc**-sclerites are dorsoventrally curved plates on paired shallow outfoldings beneath the anterior margin of **T10v** and above the subanal lobes **sbl**. **Cb**-sclerites are missing. The articulations **A98** and **A99** are well-developed.

Musculature

Muscles	Positions of insertions	in fig.
l2	Membranous left wall of **pne**-pouch – **L4H** (left part, on **swe**-apodeme)	70
l3a,b,c	**L1** and membrane to the left of **L1** (posteroventrally on **pne**-pouch) – **L2** (anterodorsal part)	71
l4	**L2** (anterodorsal part) – **L4H** (left part, on **swe**-apodeme)	71
l5a	**L4F** (anterior margin) – **L2** (ventral left margin)	72
l5b	Membranous ventral wall of left complex anterior to **L4F** – **L2** (ventral left margin)	72, 73
l6a	**L4H** (plate-like part in ventral wall of left complex) – anterior ventral wall of **lve**-pouch	73
l6b	**L4G** (anterior margin) and membrane anterior to **L4G** – dorsal wall of **vla**-lobe around genital opening	70, 71
l9	Transversely in central dorsal wall of left complex	59, 70
l13a-i	Muscles within **vla**-lobe; mainly diffuse	71, 72, 73
l14c	**L4H** (to the right of **nla**-process) – **hla**-hook (dorsally on **L3**)	70, 72, 73
l14d	**L4H** (on **nla**-process) – **hla**-hook (ventrally on membranous base **30**)	73
l15	Ejaculatory duct **D** next to its opening – **L2** (anterior margin)	70
l16	**L4H** (plate-like part in ventral wall of left complex) – **L4F** (anterior margin)	73
l17	**L4H** (plate-like part in ventral wall of left complex) and membrane posterior to it – ventral wall of **mla**-lobe	73

Figs.74-78: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – **74:** Right phallomere in dorsal view. – **75:** Right phallomere in left-dorsal (somewhat anterior) view. – **76:** Right phallomere in left-ventral view. – **77:** Right phallomere in right-ventral view; with transition to left complex. – **78:** Right phallomere in right-ventral view; most elements shown in fig.77 removed. – Scale: 1mm.



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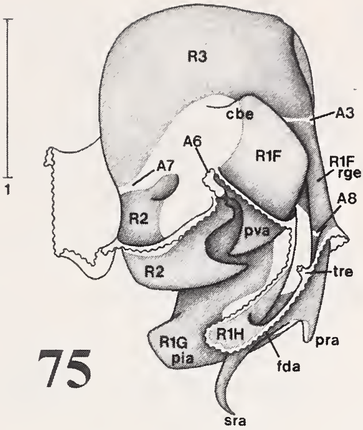

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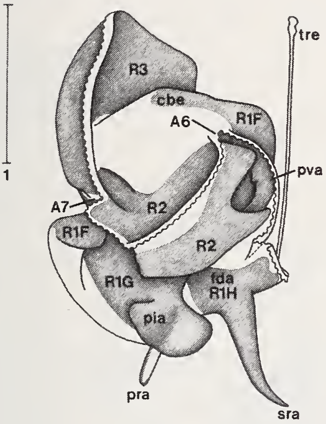

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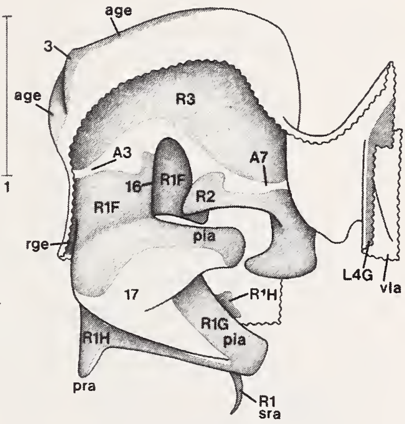

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Eurycotis
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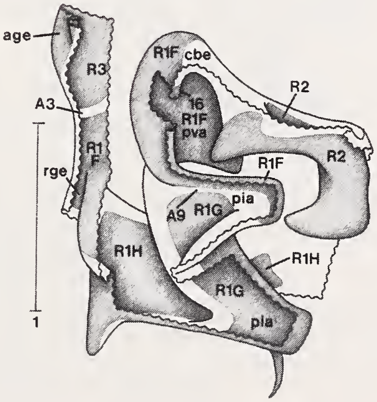
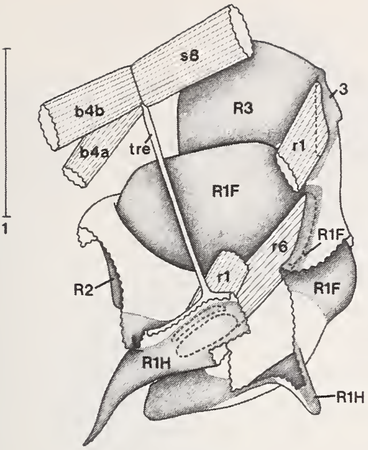


78

l18	Both insertions on ventral wall of **mla**-lobe	73
r1	**R3** (right margin) – **R1H** (anterior dorsal wall of **fda**-lobe)	58, 79
r2	**R3** – **cbe**-invagination: **R1F** (anterior margin), membrane, and **R2** (dorsal margin)	80, 81
r3	**R1F** (central part, posterior to articulation **A3**) – **R1G** (on **pia**-tooth)	80, 81, 82
r5	**R3** (right margin) – **R1F** (dorsal margin, on **rge**-apodeme)	58, 80
r6	**R1F** (dorsal margin, on **rge**-apodeme) – **R1H** (anterior dorsal wall of **fda**-lobe)	79
b4a	Outer wall of **lve**-pouch (anterior part next to genital opening) – **tre**-tendon	58, 70, 79
b4b	**pne**-pouch (anterodorsal wall) – **tre**-tendon	58, 70, 79
s1	**S9** left side (anteriorly on apophysis **S9a**) – **L4H** (anteriormost left ventral wall of left complex)	59, 62, 64 70
s2	**S9** right side (anteriorly on apophysis **S9a**) – **R3** (anterior margin)	59, 62, 64, 82
s3	**S9** left side (anteriorly on apophysis **S9a**) – anteriormost ventral wall of left complex	59, 62, 64, 70
s4	**S9** right side (anteriorly on apophysis **S9a**) – **R3** (left anterior margin)	59, 62, 64, 82
s5a	**S9** left side (posterior to apophysis **S9a**, medially) – anterior left ventral wall of genital pouch; diffuse	62, 64
s5b	**S9** left side (posteriorly and laterally) – posterior left ventral wall of genital pouch	59, 62, 64
s5c	**S9** left side (posteriorly and far medially) – median ventral wall of genital pouch; small, diffuse	62, 64
s6a	**S9** right side (posteriorly on apophysis **S9a**) – anteriormost right ventral wall of genital pouch	59, 62, 64, 82
s6b	**S9** right side (posteriorly and laterally) – posterior right ventral wall of genital pouch	59, 62, 64
s6c	**S9** right side (posterior to apophysis **S9a**) – median ventral wall of genital pouch; small, diffuse	62, 64
s6d	**S9** right side (posteriorly and far laterally) – right wall of genital pouch	59, 62, 64
s7	**S9** left side (anteriorly on apophysis **S9a**) – **L2** (anteriorly on **lve**-pouch)	58, 62, 64, 70
s8	**S9** right side (most anteriorly on apophysis **S9a**) – **tre**-tendon	58, 62, 70, 79
p1 (pair)	**S9** – **Pv**-sclerite (median part)	58, 62
p2 (pair)	**S9** – **T9** (lateral anterior margin); in most specimens the **p2** pass through eyelets of the vasa deferentia **Vd**. A pair of muscles having the same course is also present in segment 8: **p2(8)**.	58, 62
p3 (pair)	**S9** – rectum (ventral wall)	58, 62
p4 (pair)	**T9** (lateralmost anterior margin) – membrane far anterior to **Pv**-sclerite; ventral insertion of left **p4** far to the right	58
p5 (pair)	**T10** (lateralmost anterior margin) – **Pv**-sclerite	58
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin)	58, 61
p7 (pair)	Membrane anterior to **Pv**-sclerite – anterior margin of paratergite **T10p**	59
p9 (pair)	Membrane anterior to **Pv**-sclerite (next to **p7**) – membrane median to inner end of **Pv**-sclerite, beneath rectum	59

79



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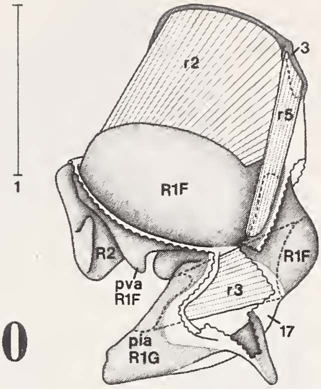

Eurycotis floridana

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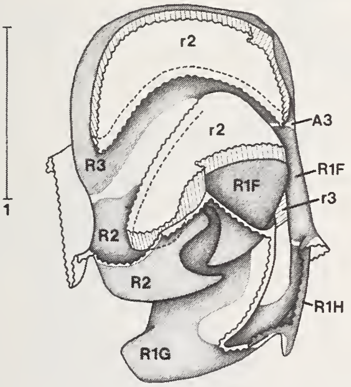

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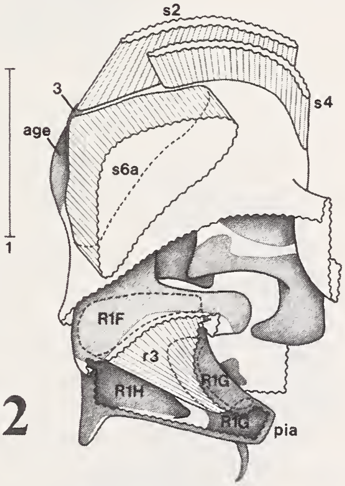


Figs.79-82: *Eurycotis floridana* (Blattaria, Blattidae, Polyzosteriinae) – **79:** Right phallomere in dorsal view; with some muscles; some dorsal elements removed. – **80:** Right phallomere in dorsal view; with some muscles; dorsal elements more extensively removed than in fig.79. – **81:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles; some dorsal elements removed. – **82:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.77; pia-tooth cut open to show muscle r3. – Scale: 1mm.

5.7. *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae)

Left complex

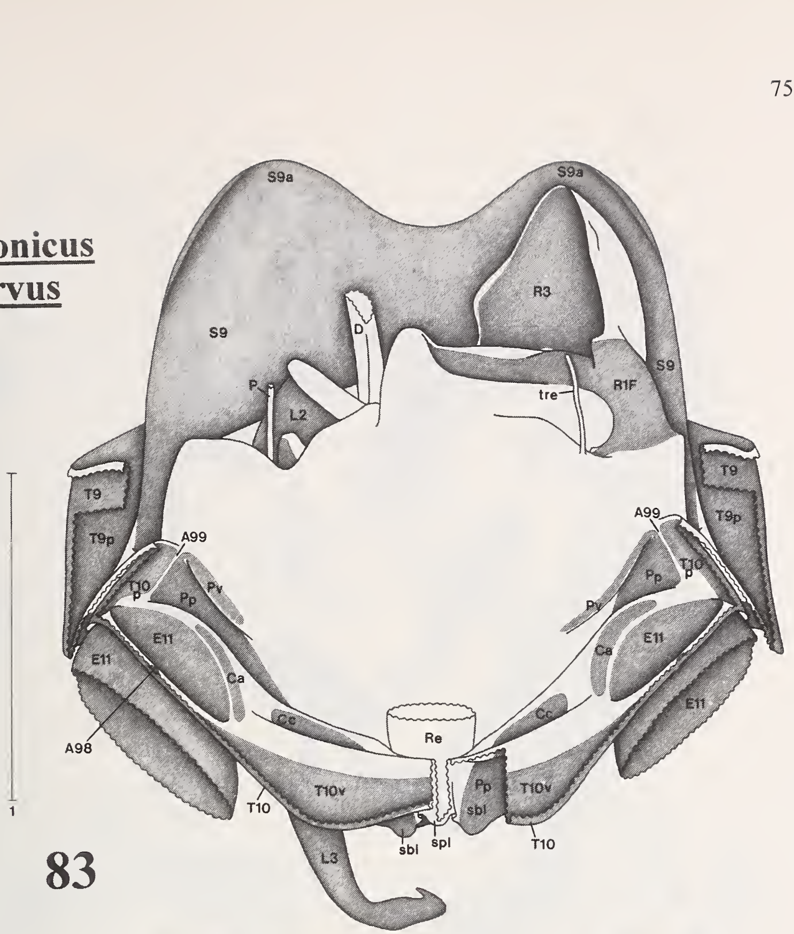
L4 is a group of three sclerites in the ventral wall and on the left edge of the left complex (fig.87, 88, 91): **L4G** occupies the ventral wall of a broad ventral lobe **vla** (= ventral phallomere; fig.87, 88, 98). **L4K** is a broadly horseshoe-shaped sclerite in the left anterior ventral wall and bears a bulge-like process (**nla** in fig.87-89, 97, 98). **L4N** occupies the posterior left edge of the left complex and has a hinge-like articulation with **L4K** (**A5** in fig.88, 97, 98). Anterodorsally **L4N** has a long ribbon-like extension to the anterior (**L4d** in fig.88-97). The posterior end of **L4N** is on a short bulge-like process **pda** (fig.91, 94, 96) and is to the right connected with the **L2**-sclerotisation of another process **paa** (fig.94).

The small sclerite **L11** lies in the anteriormost left dorsal wall (fig.88, 91). The right anterior part of the dorsal wall has some complicated membranous foldings (fig.91-93). Beneath and posterior to these foldings there are the somewhat cup-shaped **L1**-sclerite and, to the right of **L1**, the dorsoventrally curved **L2**-sclerite. The plate-like dorsal part of **L1** (fig.94) has a hinge-like articulation with **L2** (**A2** in fig.94). The posterior parts of **L1** occupy two bulge-like processes (**dca** in fig.94, 95; only the ventral wall of the right **dca**-process is membranous). The ventral part of **L1** sclerotises the dorsal wall of a broad pouch (**pne** in fig.95). This **pne**-pouch is strongly deepened in its rightmost part, where **L1** has a ribbon-like extension to the anterior. At the left end of the **pne**-pouch **L1** is in close contact with the anterior end of the **L4d**-ribbon (fig.94, 95). The ventral wall of the **pne**-pouch is membranous and contains the opening of the phallomere-gland (**P** in fig.96).

L2 occupies the dorsal wall right-anterior to **L1** (fig.94). From here it curves ventrad and back to the left (fig.95) into a position beneath the **pne**-pouch; then it extends, becoming narrower, to the posterior edge of the left complex (fig.97). The posterior end of **L2** occupies the **paa**-process, which is upcurved and somewhat hook-like. For most of its length **L2** extends broadly along the anterior edge of a pouch (**lve** in fig.94, 95, 97), which is dorsoventrally curved – in the same way as **L2** itself and as it has been described for **L2** and **lve** of *Archiblatta*. The edge along the bottom of the **lve**-pouch is labelled **7** in fig.92, 94, 96, 97. Ventrally the invagination of the **lve**-pouch begins at the posterior right margin of **L4K** (posterior end of edge **7** in fig.97). Immediately posterior to this point **L2** and **L4K** are in close contact. **L2** is restricted to the inner wall of the **lve**-pouch. The outer **lve**-wall is completely membranous and is at the same time the dorsal (or left) wall of the **vla**-lobe (fig.91, 92; in the figures **vla** is pulled to the right). The ejaculatory duct (**D** in fig.87, 91, 92) opens far anteriorly into this membrane. In the rightmost dorsal wall of the **vla**-lobe there lies a ribbon-like extension of the **R2**-sclerite of the right phallomere (**R2m** in fig.91, 101, 102).

Figs.83,84: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – **83:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, subanal lobes, paraprocts, Pv-sclerites, distal part of rectum, and basal parts of cerci. – **84:** Same as in fig.83, after removal of further parts of abdominal tergites 9 and 10 (especially T10v), parts of paraprocts, and supraanal lobe. Distal part of rectum, basal parts of cerci, and right subanal lobe cut open. Anterior to transverse line: like in fig.83. – Scale: 1mm.

Tryonicus parvus



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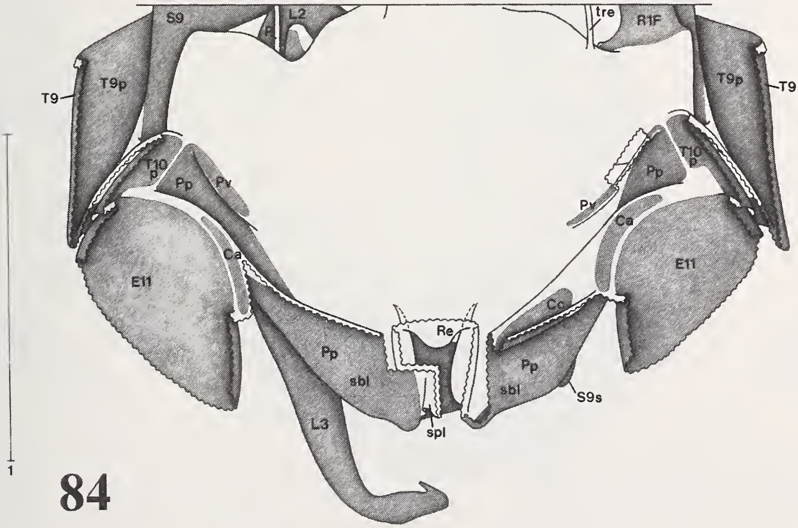

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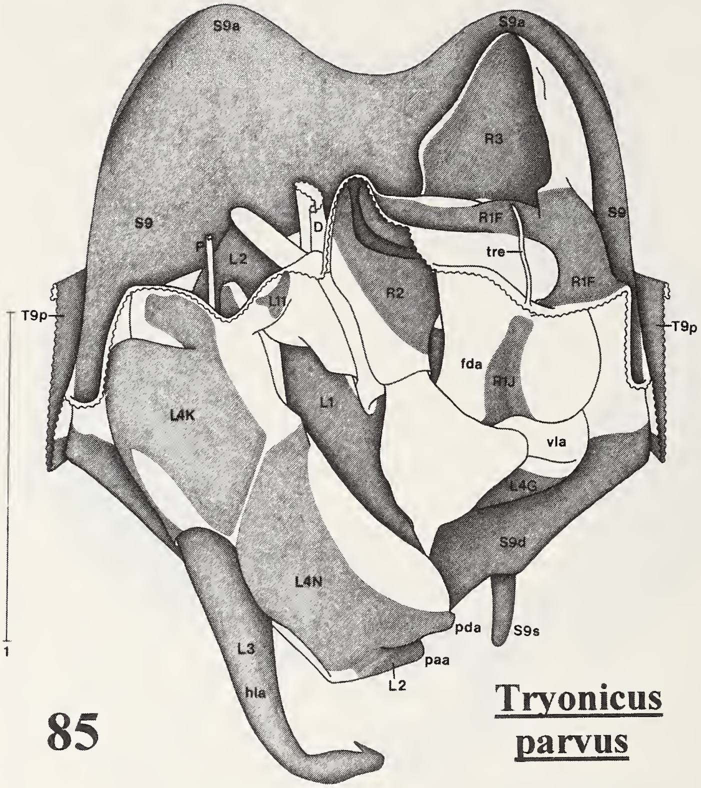

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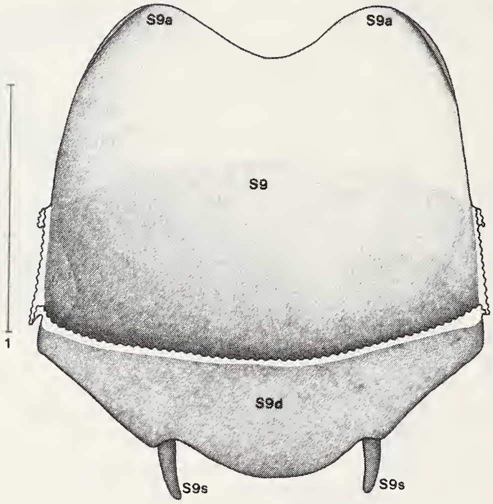

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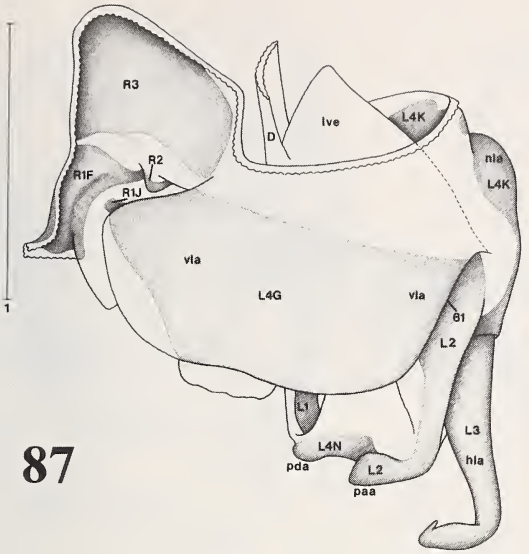
Figs.85,86: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – **85:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **86:** Subgenital plate in dorsal view. – Scale: 1mm.



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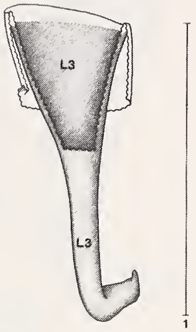

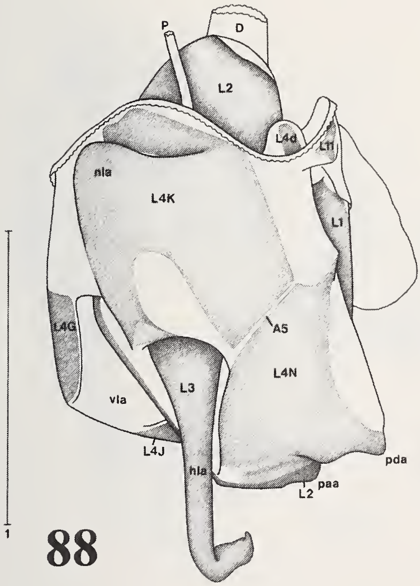

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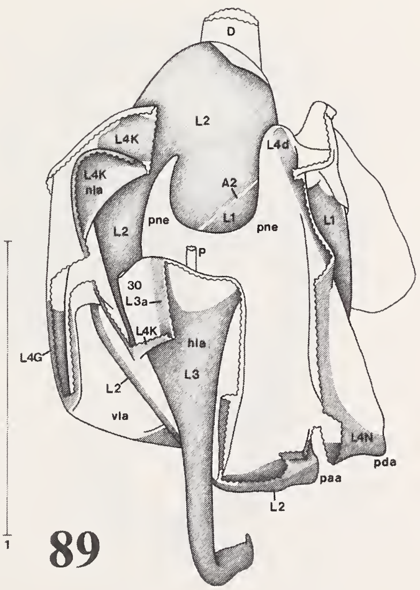

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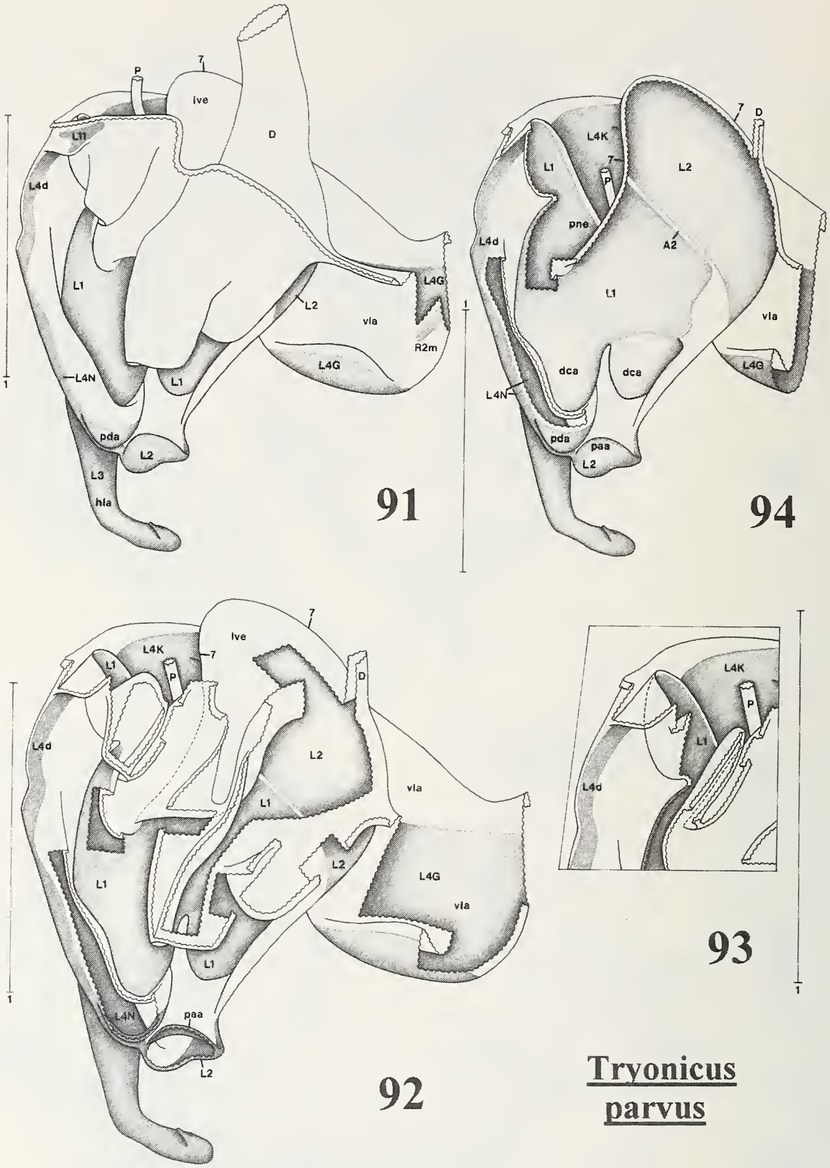
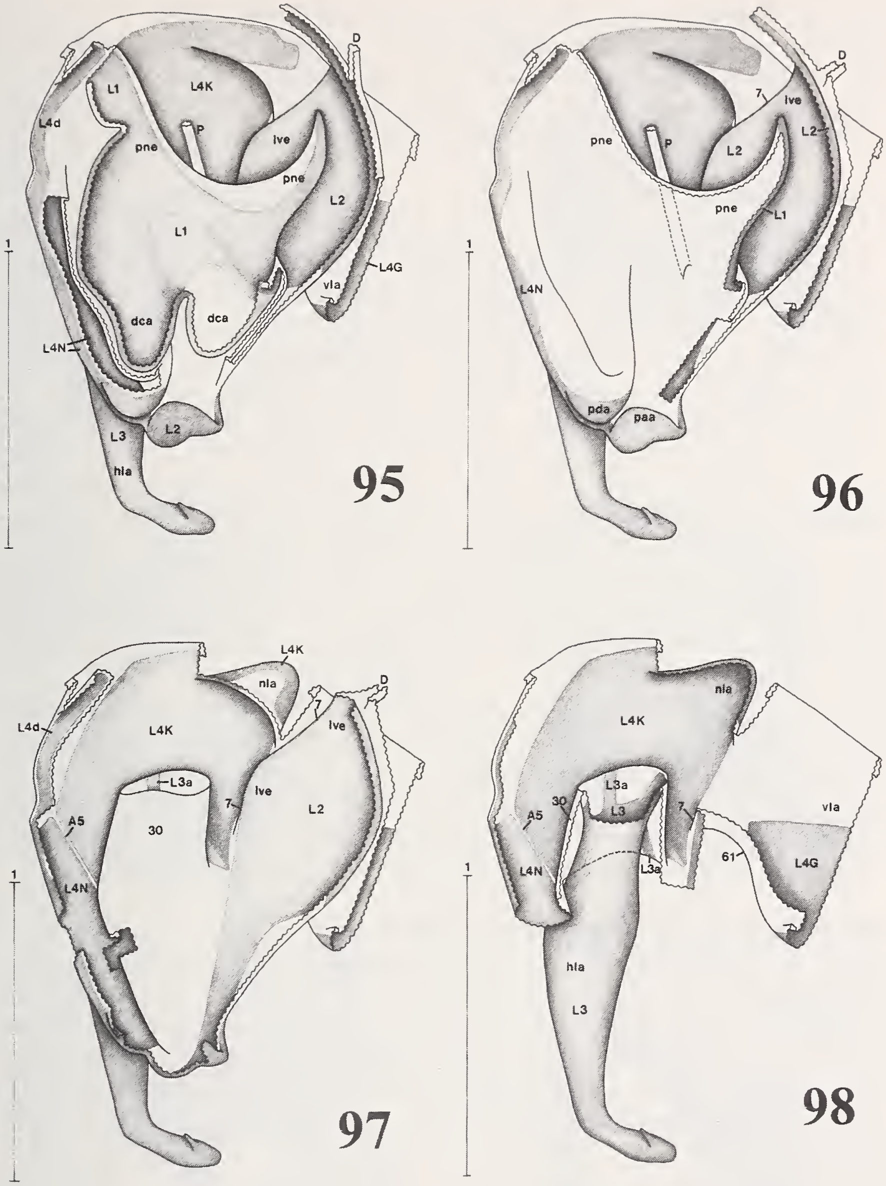
Tryonicus parvus

Figs.87-90: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – **87:** Phallomere complex in ventral view. – **88:** Left complex in left-dorsal view. – **89:** Left complex in left-dorsal view; some parts removed (compare fig.88). – **90:** hla-hook and sclerite L3 in left-dorsal view. – Scale: 1mm.



Figs.91-94: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – **91:** Left complex in right-dorsal view. (In the text this view is designated as dorsal). – **92-94:** Left complex in right-dorsal view; with successive removal of its parts (mainly of dorsal ones); figs.92,93: scale slightly larger; fig.93: detail from fig.92, some more parts removed. – Scale: 1mm.



Tryonicus parvus

Figs.95-98: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – Left complex in right-dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.

The large hook **hla** is evaginated from the left ventral wall of the left complex. The distal part of **hla** is sclerotised by **L3** (fig.87-90, 97, 98), a large basal part of **hla** is membranous (**30** in fig.97, 98). By introverting this membrane **30**, **hla** can be retracted rather far into the phallomere (the retracted state is shown in the figures). **L3** is connected with **L4K** by a ribbon of weak sclerotisation (**L3a** in fig.89, 98), which crosses the membrane **30**.

Right phallomere

Sclerite **R3** occupies the (right-)anterior ventral wall (fig.99-103). Sclerite **R2** articulates with the left posterior end of **R3** (**A7** in fig.100-102). **R2** is a plate of irregular shape, with a ridge-like elaboration in its left-dorsal part (fig.99, 100, 103). The right-ventral part of **R2** has the extension **R2m** (fig.101, 102) mentioned above. Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad and somewhat anteriad to form a central invagination (**cbe** in fig.99-101; compare fig.102 and 104).

Posterior to the right part of **R3** sclerite **R1F** adjoins, and the two sclerites articulate (**A3** in fig.99, 100, 102). **R1F** extends from its central part behind **A3** in two directions: The ventral arm bends left-dorsad (along edge **16**, fig.102, 104) and largely occupies the right-dorsal wall of the **cbe**-invagination (fig.99, 104). The posterior margin of this arm forms a ridge (**pva** in fig.99, 103). The median end of this arm articulates with the left-dorsal end of **R2** (**A6** in fig.99, 100, 101). The dorsal arm of **R1F** extends posterodorsad (fig.99, 100, 102); its dorsal margin folds back to the right and ventrad to form a sclerotised groove **rge** (fig.99, 102). Behind **A3** and on the ventral arm the sclerotised cuticle is considerably thickened (cross-sections in fig.104).

The posterior part of the right phallomere is a large dorsal lobe **fda** (fig.99, 103), whose dorsal and ventral walls are partly occupied by sclerite **R1J**. The dorsal anterior end of **R1J** articulates with the dorsal arm of **R1F** (**A8** in fig.99), its ventral anterior end is in close contact with the base of the ventral arm of **R1F** (**A9** in fig.102, 103). The tendon **tre** (fig.99) originates from the anteriormost dorsal wall of the **fda**-lobe. In its right wall the **fda**-lobe has a large membranous area (**17** in fig.99, 103).

Subgenital plate and posterior abdominal segments

Fig.83, 84 (posterior segments); fig.86 (subgenital plate **S9**). The ventral part of tergite 10 **T10v** is moderately extensive. Strip-like **Pv**-sclerites are present; they are laterally connected with the paraprocts **Pp**. The **Ca**-sclerites are curved ribbons immediately median to the cercal bases (no distinct bulges present). The **Cc**-sclerites are dorsoventrally curved plates on paired shallow outfoldings beneath the anterior margin of **T10v** and above the subanal lobes **sbl**. **Cb**-sclerites are missing. The articulations **A98** and **A99** are well-developed.

Figs.99-104: *Tryonicus parvus* (Blattaria, Blattidae, Tryonicinae) – **99:** Right phallomere in dorsal view. – **100:** Right phallomere in left-dorsal (somewhat anterior) view. – **101:** Right phallomere in left-ventral view. – **102:** Right phallomere in right-ventral view. – **103:** Right phallomere in dorsal view; some dorsal elements removed. – **104:** Right phallomere in right-ventral view; most elements shown in fig.102 removed. – Scale: 1mm.

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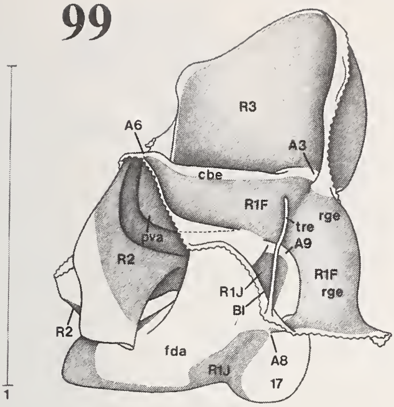

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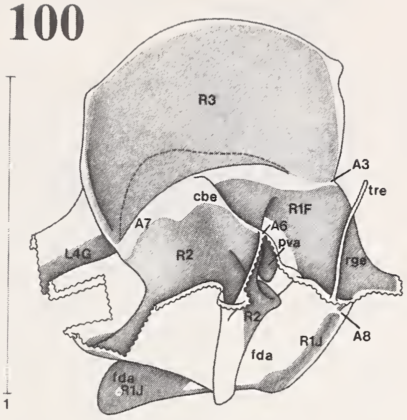

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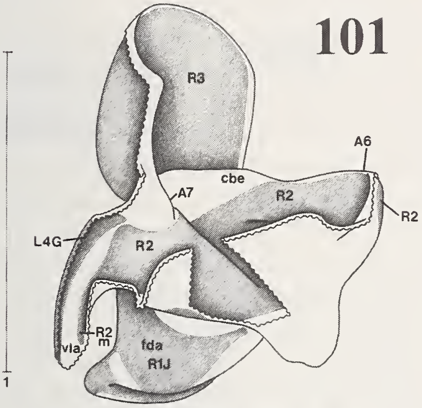

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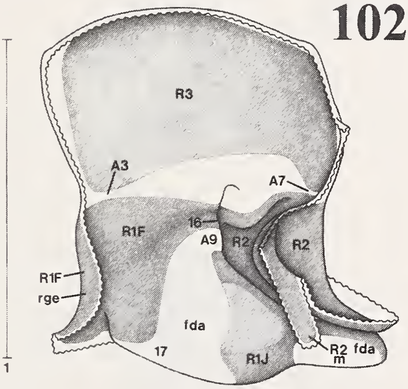

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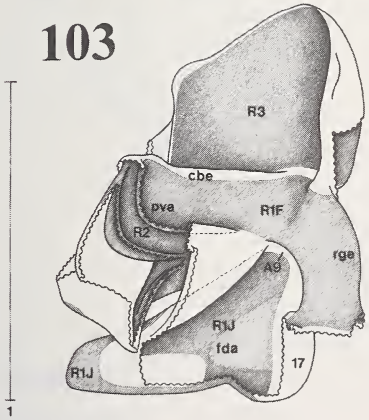
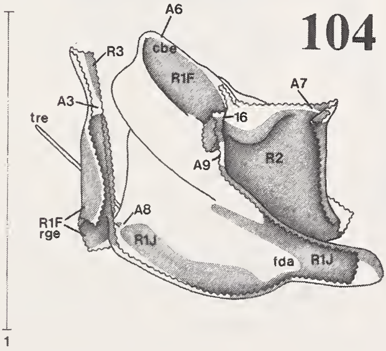
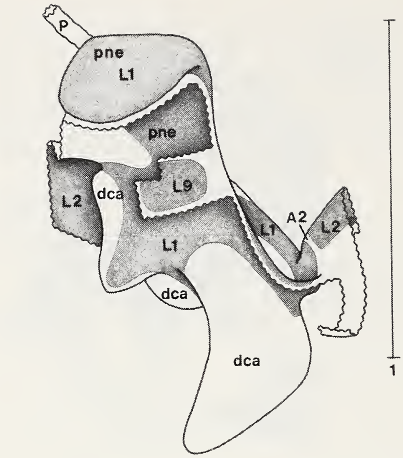


Tryonicus parvus

104





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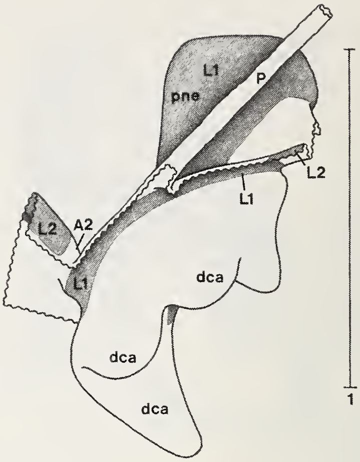

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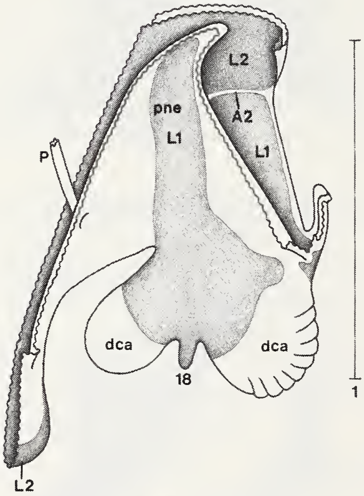
Ergaula capensis



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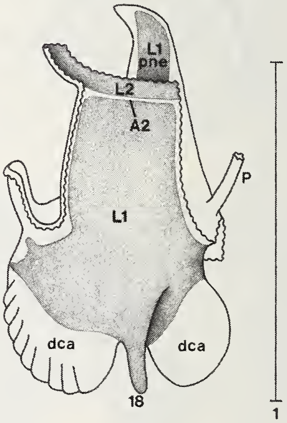


108

Tryonicus angustus

5.8. *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae)

Left complex

Sclerite **L1** is situated in the central dorsal wall; its anterior part lies within a deep pouch (**pne** in fig.117). Beneath the **pne**-pouch there is another very deep and broad pouch (**lve** in fig.118, 122), with the arch-shaped **L2**-sclerite extending along its edges. The left posterior dorsal wall contains the sclerotisation of two processes (**pda** and **paa** in fig.117, 118) and of an intervening invagination (**dte** in fig.117, 118), which is firmly connected with the **L2**-sclerotisation in the **lve**-pouch around the posterior edge of the left complex (**10** in fig.118, 122). This dorsal sclerotisation is composed of parts of **L2** (right part) and of **L4** (left part: **L4N**). Sclerite **L8** lies in the right dorsal wall of the left complex (fig.117). From the left wall of the left complex there protrudes a large hook-process (**hla** in fig.117) with its **L3**-sclerite. The large **L4M**-sclerite occupies the ventral wall (fig.115, 117, 126). Another **L4**-sclerite lies within the ventral base of the **hla**-hook (**L4K** in fig.122-124).

The anterior hood-shaped part of **L1** largely occupies the walls of the **pne**-pouch (fig.111, 118, 119, 120). In the left-dorsal half of the **pne**-pouch the walls are membranous – especially in the posterior part, where the phallomere-gland (**P** in fig.118, 120, 121) opens from ventrally. The anterior end of **L1** is flat and plateau-like. Posteriorly **L1** leaves the pouch and has an arm-like extension on each side (fig.118, 120, 121). The extensions curve ventrad and approach each other again (fig.121). The membranous cuticle enclosed by this (open) sclerite-ring forms two cushion-like evaginations (**dca** in fig.117, 120, 121).

The **lve**-pouch (fig.118, 122) spans almost the whole breadth of the left complex. (The edge along the bottom of the **lve**-pouch is labelled **7** in fig.122, 123). **L2** occupies the margins of the dorsal (fig.122) and ventral (fig.123) walls of the **lve**-pouch. The left part of **L2** in the dorsal **lve**-wall broadens posteriorly and bends around the posterior edge of the left complex (along **10** in fig.118, 119a, 122) into the dorsal wall. Here it continues into the sclerotisation of the **paa**- and **pda**-processes and of the **dte**-invagination (fig.117-119b; **L2** and **L4N**, with the border between them somewhere within **dte**). The **pda**-process is finger-like; the **paa**-process is saucer-shaped and partially encloses the **dca**-processes from left-ventrally. The **pda**-sclerotisation has a tongue-like extension to the left (**L4d** in fig.118, 123, 124). The **paa**-sclerotisation has an arm-like extension to the right (**12** in fig.118, 119a). The right parts of **L2** and of the **lve**-pouch curve dorsad and back to the left (fig.118, 122, 123), and along this curvature the **lve**-pouch becomes rapidly less deep.

Figs.105-108: **105,106**: *Ergaula capensis* (Blattaria, Polyphagidae, Polyphaginae) – **105:** Sclerite L1 in dorsal pouch pne in dorsal view; with some surrounding elements and phallomere-gland P. – **106:** Sclerite L1 in dorsal pouch pne in ventral view; with some surrounding elements and phallomere-gland P. – **107,108**: *Tryonicus angustus* (Blattaria, Blattidae, Tryonicinae) – **107:** Sclerite L1 in dorsal pouch pne in left-dorsal view; with some surrounding elements and phallomere-gland P. – **108:** Sclerite L1 in dorsal pouch pne in right-ventral view; with some surrounding elements and phallomere-gland P. – Scale: 1mm.

This recurved dorsal part of the **lve**-pouch, with its dorsal and ventral walls sclerotised by **L2**, approaches **L1** and articulates with it (**A2** in fig.118, 120, 121). The ventral wall of the **lve**-pouch also shows this dorsoventral curvature, but it is in its posterior part additionally invaginated to the right, and the invagination is strengthened by an arm-like extension of **L2** (**11** in fig.118, 122, 123). The posterior end of this **L2**-extension is, around an edge, in close contact with the posterior margin of sclerite **L8** (fig.117, 118).

The ventral wall of the **lve**-pouch is, except for the **L2**-sclerotisations along its margins, membranous; it is at the same time the anterior dorsal wall of the very broad ventral lobe **vla** (fig.123). The ejaculatory duct (**D** in fig.123, 124) opens into the right part of this membrane. Dorsal to the genital opening there are some membranous outfoldings (**goa** in fig.122-124). Sclerite **L5** lies in the left dorsal wall of the **vla**-lobe and is in close contact with the posterior margin of **L2** (fig.123, 124).

The **hla**-hook (with **L3**) is evaginated from the left wall of the left complex (fig.117). The base of **hla** is rather complicated (fig.122-125a) and contains sclerite **L4K** in its posteroventral part. **L4K** shows a horseshoe-like dorsoventral curvature, with a broad ventral and a pointed dorsal part. The rightmost part of the left complex is the lobe **lba** with sclerite **L7** in its ventral wall (fig.115, 117, 118). The **lba**-lobe is distinctly separated from the **vla**-lobe.

Right phallomere

Sclerite **R3** occupies the anterior (right-)ventral wall (fig.134-137). The right margin of **R3** forms a groove-like apodeme **age** (fig.134, 137). Posterior to the left part of **R3** sclerite **R2** adjoins (fig.135-137), and the two sclerites are fused; a strip of weaker sclerotisation is probably the suture (**A7*** in fig.135-137). Along its ventral margin **R2** forms a ridge bearing several processes (fig.136, 137, 141), the largest of which is behind **A7***. Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad and somewhat anteriad to form a sclerotised central invagination (**cbe** in fig.134-136; compare fig.137 and 138).

⟶ p.85

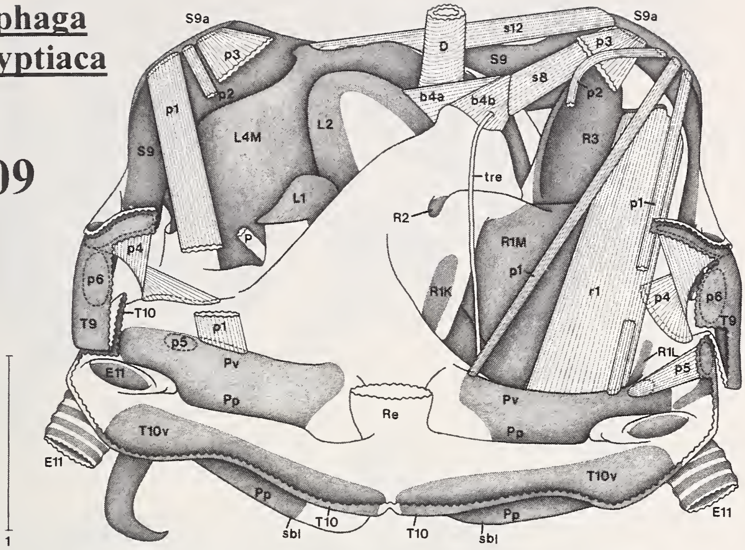
Figs.109,110: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **109:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, subanal lobes, paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. – **110:** Same as in fig.109, after removal of further parts of abdominal tergites 9 and 10 (especially T10v). Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Scale: 1mm.

⟶ p.86

Figs.111-114: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **111:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **112a,b:** Left (a) and right (b) margins of subgenital plate (compare fig.111); with insertions of muscles p6. – **113:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6); most of dorsal sclerotisation S9d of subgenital plate removed. – **114:** Subgenital plate in dorsal view; anterior part of ventral sclerotisation removed, dorsal sclerotisation S9d complete. – Scale: 1mm.

Polyphaga aegyptiaca

109



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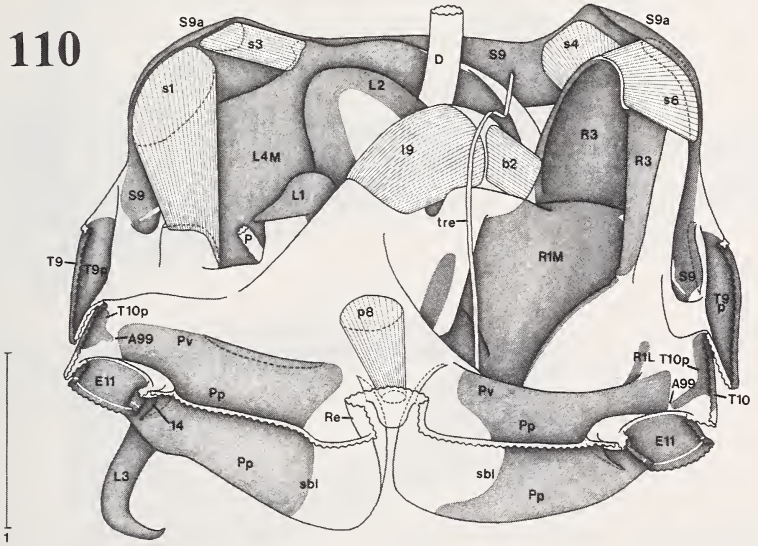

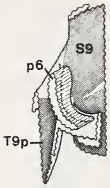

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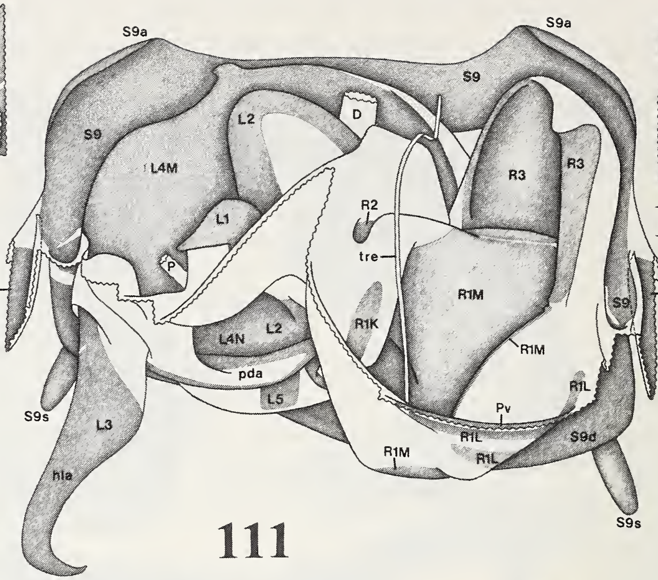

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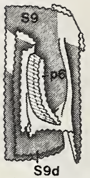

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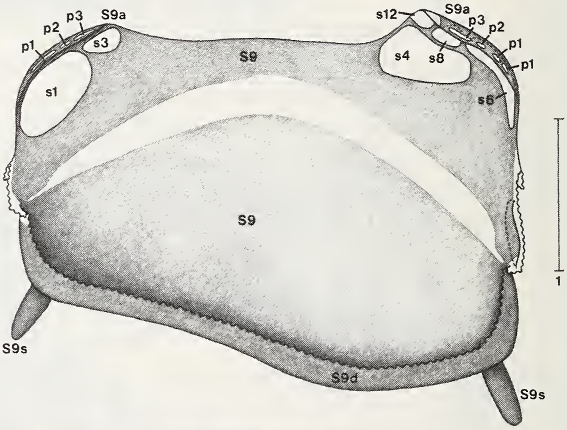

Polyphaga aegyptiaca

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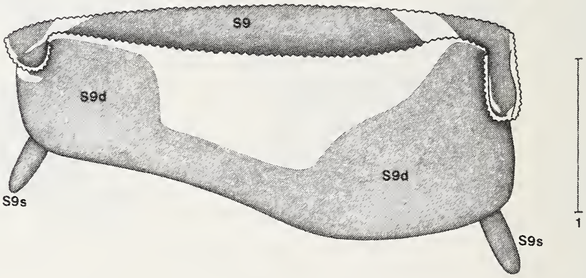

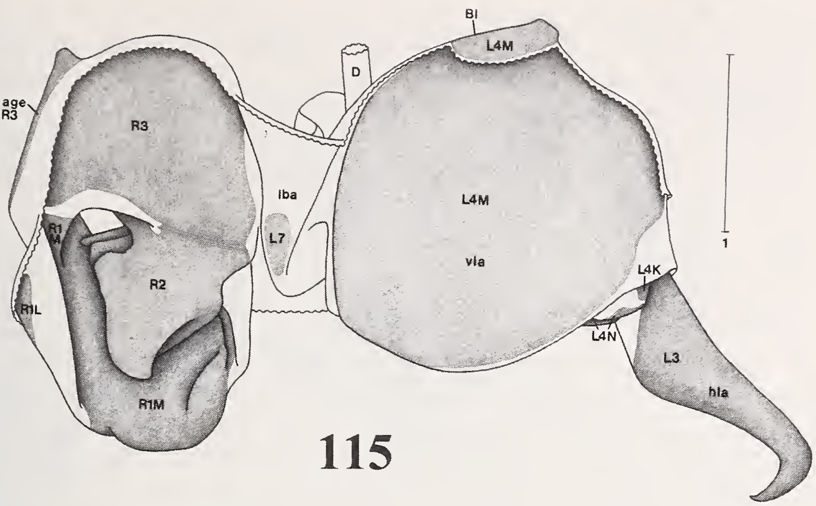

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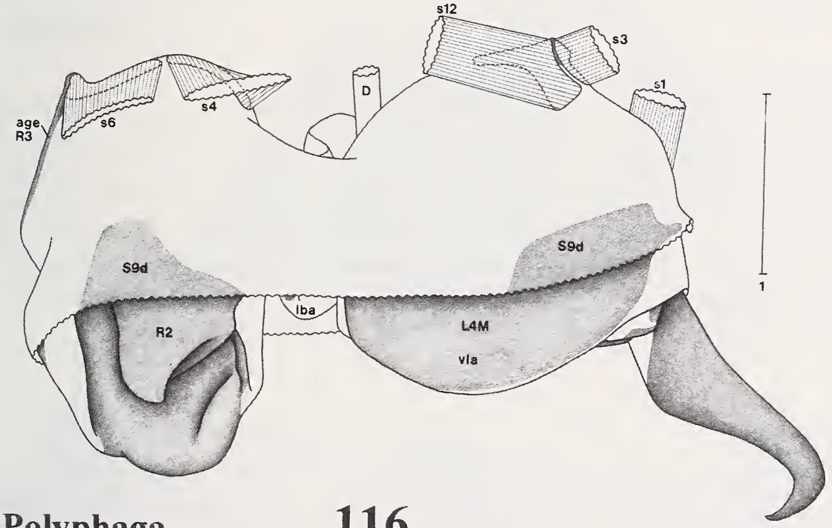

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Polyphaga
aegyptiaca

Figs.115,116: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **115:** Phallomere complex in ventral view. – **116:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.115, with parts of dorsal sclerotisation S9d of subgenital plate in its posterior part (compare fig.114). – Scale: 1mm.

Posterior to the right part of **R3** the large **R1M**-sclerite adjoins, and the two sclerites articulate (**A3** in fig.134, 135, 137). From its central part behind **A3** sclerite **R1M** extends to the left, where it bends left-dorsad (along edge **16**; fig.137, 138) and then occupies the right-dorsal wall of the **cbe**-invagination (fig.134). The left-ventral wall and the top of **cbe** are sclerotised by a plate-like part of **R2** (fig.134-137); the dorsal margin of this **R2**-part is fused to the anterior margin of **R1M**. A line of weaker sclerotisation (**13** in fig.134, 138) is probably the boundary between **R2** and **R1M**.

From its fusion line **13** with **R2** and from articulation **A3**, **R1M** extends far posteriad as a dorsoventrally curved plate of irregular shape (fig.134, 137). It largely occupies the ventral and right walls of the posterior part of the right phallomere (labelled **fda** and **pva** in fig.134-138). The dorsal margin of **R1M** folds back to the right to form a sclerotised groove (**rge** in fig.134, 138, 140); **rge** is a posterior continuation of the **age**-groove on **R3** and extends to the posterior edge of the **fda**-lobe. Dorsal to **rge** there is an outfolding to the right, which contains the very weak ribbon-like sclerites **R1L** (fig.134). At the left end of the **fda**-lobe there is a dorsal outfolding to the left, which contains sclerite **R1K** in its ventral wall (fig.134). Beneath **R1K** the left marginal part of **R1M** forms a longitudinal ridge projecting to the left (**pva**, compare fig.134 and 139). The dorsal wall of the **fda**-lobe is mostly membranous (fig.134), and most anteriorly the tendon **tre** has its origin (fig.134, 135, 139).

Subgenital plate and posterior abdominal segments

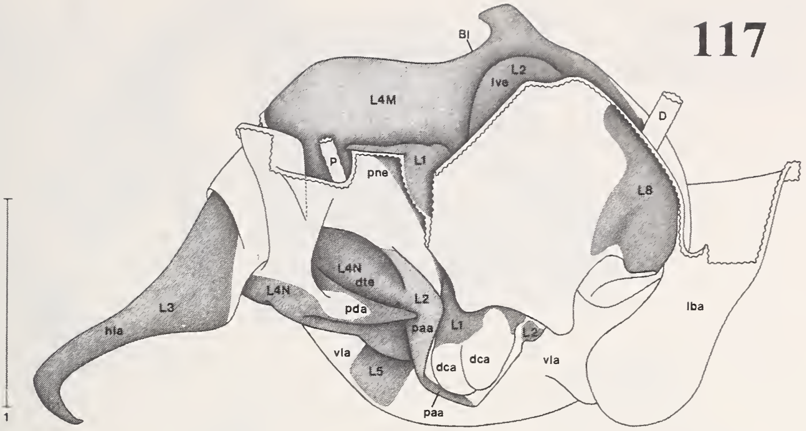
Fig.109, 110 (posterior segments); fig.113, 114 (subgenital plate **S9**). The entire tergite 10 **T10**, including its ventral part **T10v**, is divided along its midline. **T10v** is moderately extensive. Separate **Pv**-sclerites are missing; they are assumed to have been incorporated into the anterior margins of the paraprocts **Pp**. The sclerites **Ca, Cb,** and **Cc** are missing. The bulges next to the cercal bases the **Ca**-sclerites lie upon in other species, however, are present (compare fig.59). The articulations **A99** are well-developed. The articulations **A98** are missing: the sclerotisations **E11** and **T10** are far away from each other. Each subanal lobe **sbl** has a small groove (**14** in fig.110) beneath the cercal base.

——→ p.89

Figs.117-121: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **117:** Left complex in dorsal view. – **118:** Left complex in dorsal view; some parts removed (mainly dorsal ones). – **119a,b:** Dorsal parts of sclerites L4 and L2, separated from remainder of left complex, in dorsal view. – **120:** Sclerite L1 in dorsal pouch pne, separated from remainder of left complex, in dorsal view; with some surrounding elements and phallomere- gland P. – **121:** Sclerite L1 in dorsal pouch pne, separated from remainder of left complex, in ventral view; with some surrounding elements and phallomere-gland P. – Scale: 1mm.

——→ p.90

Figs.122-124: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – Left complex in dorsal view; with further successive removal of its parts (mainly of dorsal ones); fig.122: left complex after removal of the parts shown in fig.119-121. – Scale: 1mm.



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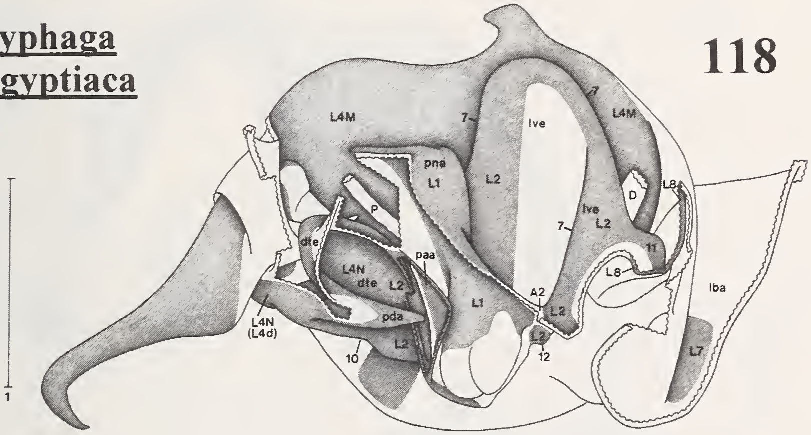
Polyphaga
aegyptiaca



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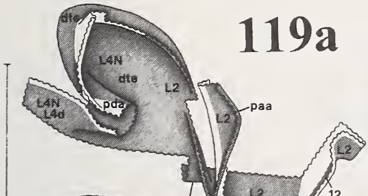

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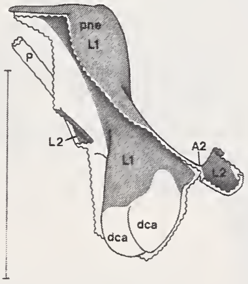

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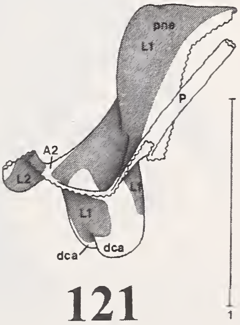

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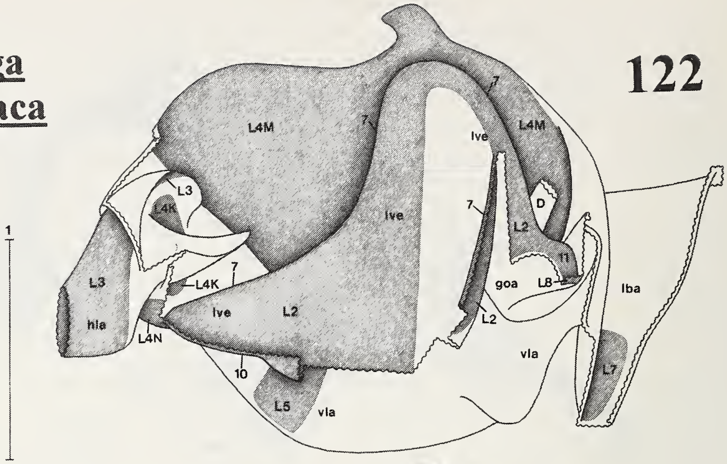
Polyphaga aegyptiaca



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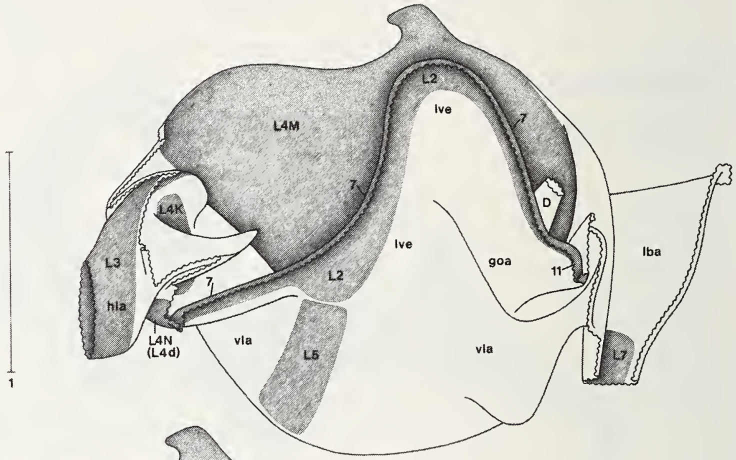

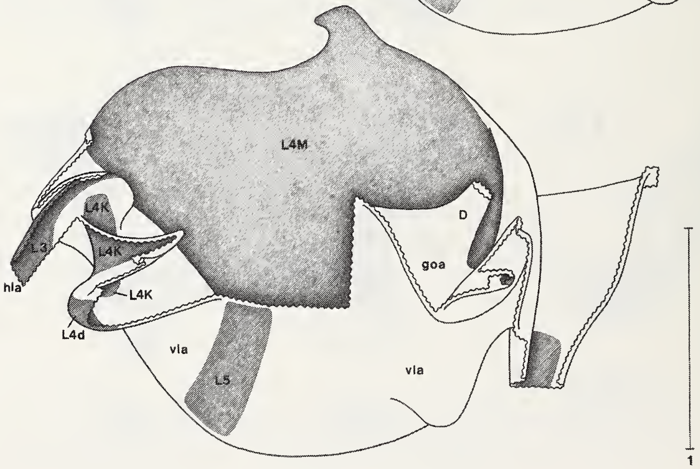

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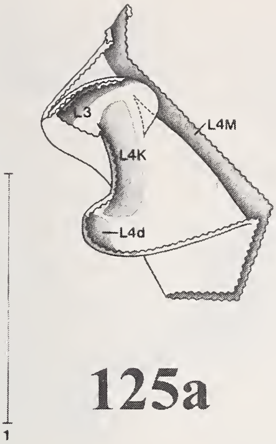

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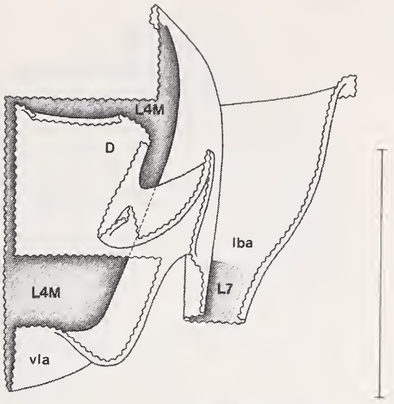

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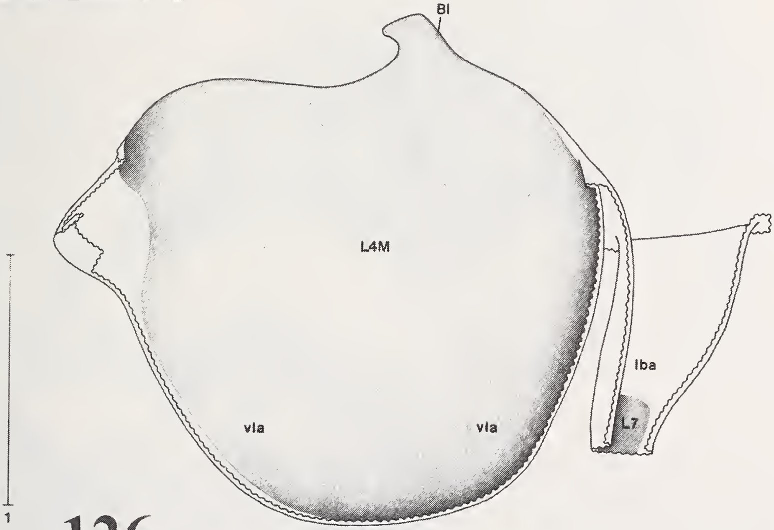
Polyphaga aegyptiaca



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Figs.125,126: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **125a,b:** Left (a) and right (b) part of left complex, separated from remainder of left complex, in dorsal view; further parts removed (mainly dorsal ones; compare fig.124). – **126:** Ventral wall of left complex in dorsal view. – Scale: 1mm.

Musculature

Muscles	Positions of insertions	in fig.
l2	**L1** (plateau-like anterior end of **pne**-pouch) – **L4M** (left anterior part)	127, 128, 129, 131
l3	**L1** (right-ventrally on **pne**-pouch) – **L2** (right anterior part)	128, 130, 131
l4	**L2** (left anterior part) – **L4K** (dorsal right end, within base of **hla**-hook)	129, 130, 132
l5	**L4M** (anterior part) – **L2** (left part) and membrane to the left of it	130, 133
l6a	**L4M** (anterior part) – **L2** (right anterior part)	130, 133
l6b	**L4M** (posterior to **l6a**) – ejaculatory duct **D** next to its opening	132
l9	Transversely within right dorsal wall of left complex; ventral parts: **L1** – **L2** (areas next to articulation **A2**)	110, 127, 129, 130
l10	**L2** (left posterior part) – **L4N** and **L2** on invagination **dte**	129, 130
l11	**L4K** (anteroventral part) – **L4d** (= left part of **L4N**)	128, 132
l12	**L2** (rightmost part) – **L8**; very short and stout	128, 129, 130
l13	Ejaculatory duct **D** next to its opening (ventral wall) – dorsal wall of **vla**-lobe (rightmost part)	132
r1	**R3** (right margin) – **R1M** (dorsal margin, on posterior part of **rge**-groove), **R1L**, and membrane in between these sclerotisations	109, 139
r2	**R3** – **cbe**-invagination: **R1M** (anterior margin) and **R2** (right-dorsal part)	140, 141
r6	**R1M** (dorsal margin, on **rge**-groove) – **R1K** and surrounding membranes	140
r9	**R3** (left-posterior part) – **R2** (left-ventral part)	141
b2	Right dorsal wall of left complex (next to **L8**) – **R3** (left-posterior part)	110, 127, 141
b4a	**L2** (right anterior edge of **lve**-pouch) – **tre**-tendon	109, 127, 129, 130, 139
b4b	**L8** (anterior margin) – **tre**-tendon	109, 127, 139
s1	**S9** left side (laterally and anteriorly) – membrane anterior to **hla**-hook	110, 113, 116, 127

⟶ p.93

Figs.127-129: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 1mm.

⟶ p.94

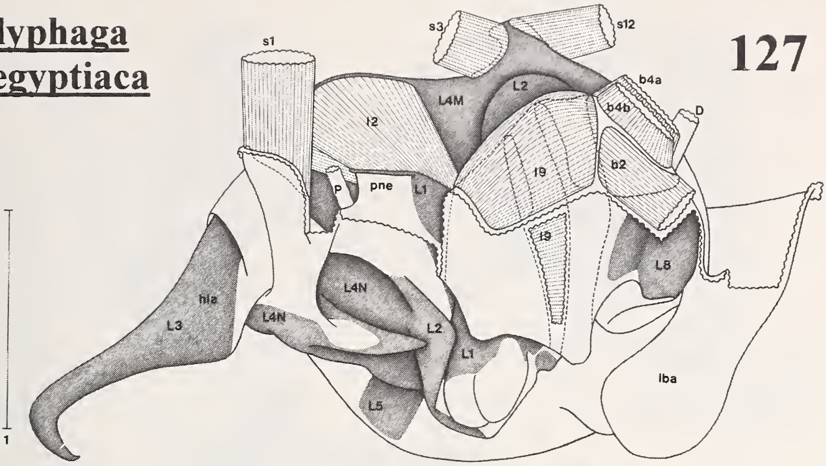
Figs.130-133: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **130:** Sclerite L2 in ventral pouch lve in dorsal view; with insertion areas (white) of muscles (compare fig.122). – **131:** Sclerite L1 in dorsal pouch pne in ventral view; with muscles l2 and l3 (compare fig.121). – **132,133:** Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 1mm.

⟶ p.95

Figs.134-138: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **134:** Right phallomere in dorsal view. – **135:** Right phallomere in left-dorsal (somewhat anterior) view. – **136:** Right phallomere in left-ventral view. – **137:** Right phallomere in right-ventral view. – **138:** Right phallomere in right-ventral view; most elements shown in fig.137 removed. – Scale: 1mm.

Polyphaga aegyptiaca

127



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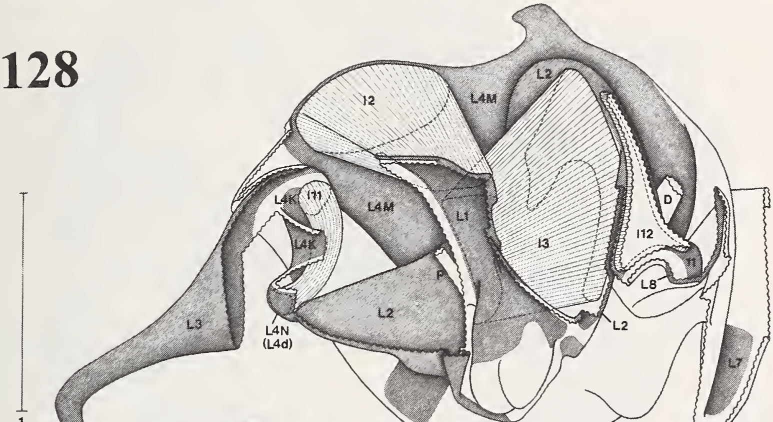

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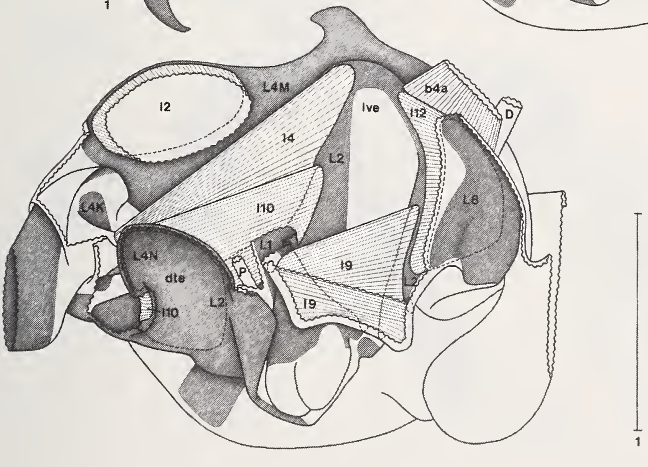

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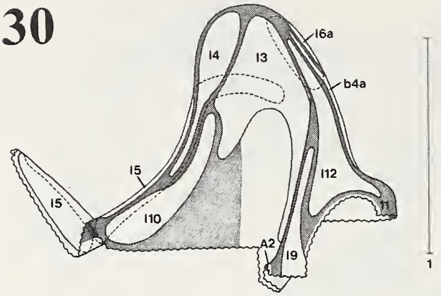

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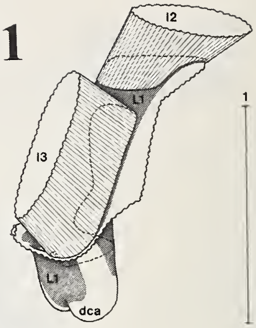

Polyphaga aegyptiaca

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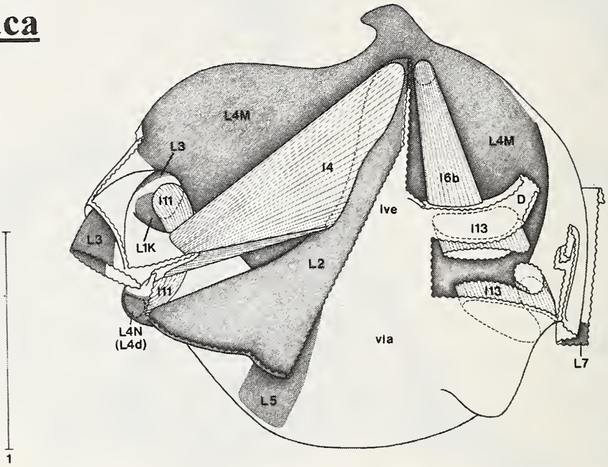

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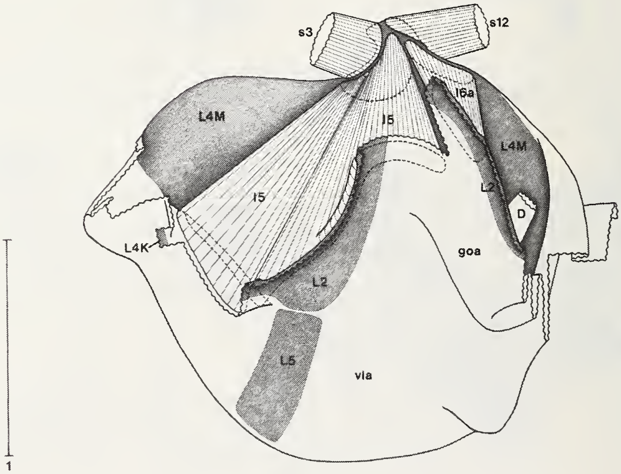

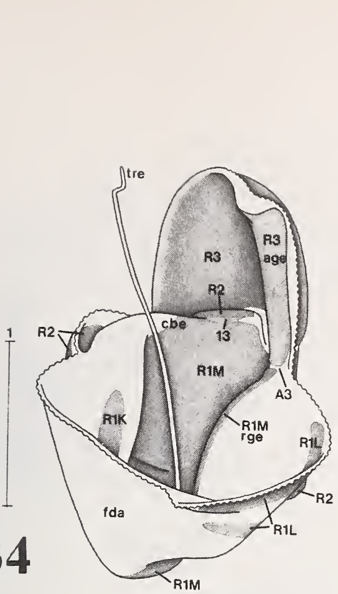

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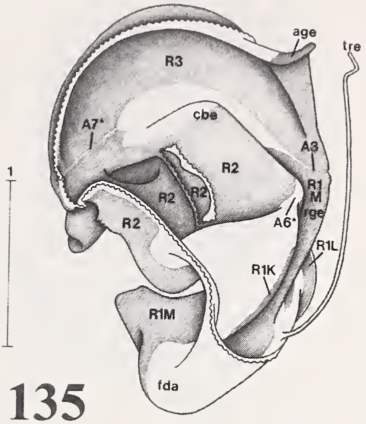

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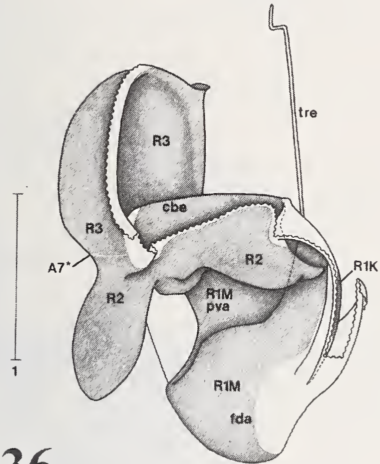

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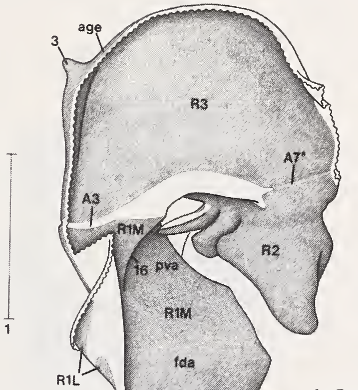
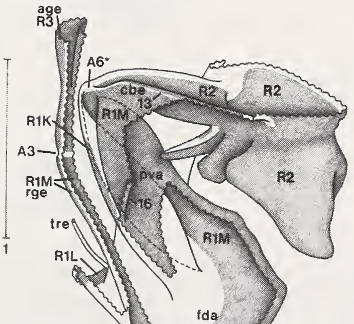


137

Polyphaga aegyptiaca



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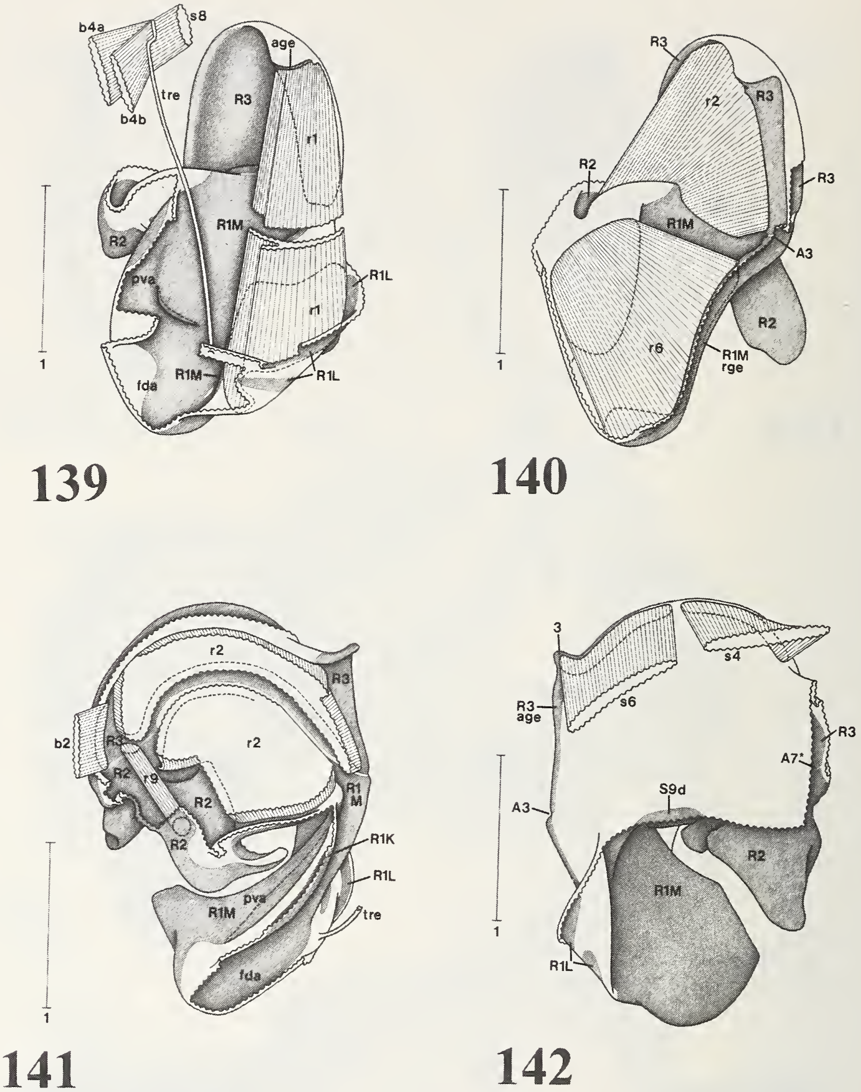


Polyphaga aegyptiaca

Figs.139-142: *Polyphaga aegyptiaca* (Blattaria, Polyphagidae, Polyphaginae) – **139,140:** Right phallomere in dorsal view; each figure with some muscles; dorsal elements removed to various extents. – **141:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles; some left-dorsal elements removed. – **142:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.137. – Scale: 1mm.

s3	**S9** left side (most anteriorly, median to **s1**) – **L4M** (anterior margin)	110, 113, 116, 127, 133
s4	**S9** right side (anteriorly) – **R3** (left anterior margin)	110, 113, 116, 142
s6	**S9** right side (laterally and anteriorly) – **R3** (right anterior margin)	110, 113, 116, 142
s8	**S9** right side (anteriorly) – **tre**-tendon	109, 113, 139
s12	**S9** right side (most anteriorly, median to **s8**) – **L4M** (anterior margin)	109, 113, 116, 127, 133
p1 (pair)	**S9** – paraproct **Pp** (anterior margin, corresponding to **Pv**-sclerotisation); right muscle divided into two bundles	109, 113
p2 (pair)	**S9** – **T9** (lateral anterior margin)	109, 113
p3 (pair)	**S9** – rectum (ventral wall)	109, 113
p4 (pair)	**T9** (lateralmost anterior margin) – membrane anterior to paraproct **Pp** (far laterally); right muscle inserting on lateral wall of genital pouch, next to right phallomere; both muscles twisted	109
p5 (pair)	**T10** (lateralmost anterior margin) – paraproct **Pp** (lateral anterior margin, corresponding to the **Pv**-sclerotisation)	109
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin) (left muscle only) and adjacent membranes; ventral insertion of right muscle extending far anteriad into right wall of genital pouch, lying immediately anterior to insertion of **p4**	109, 112a,b
p8	Longitudinally within membrane between **Pv**-sclerotisations	110

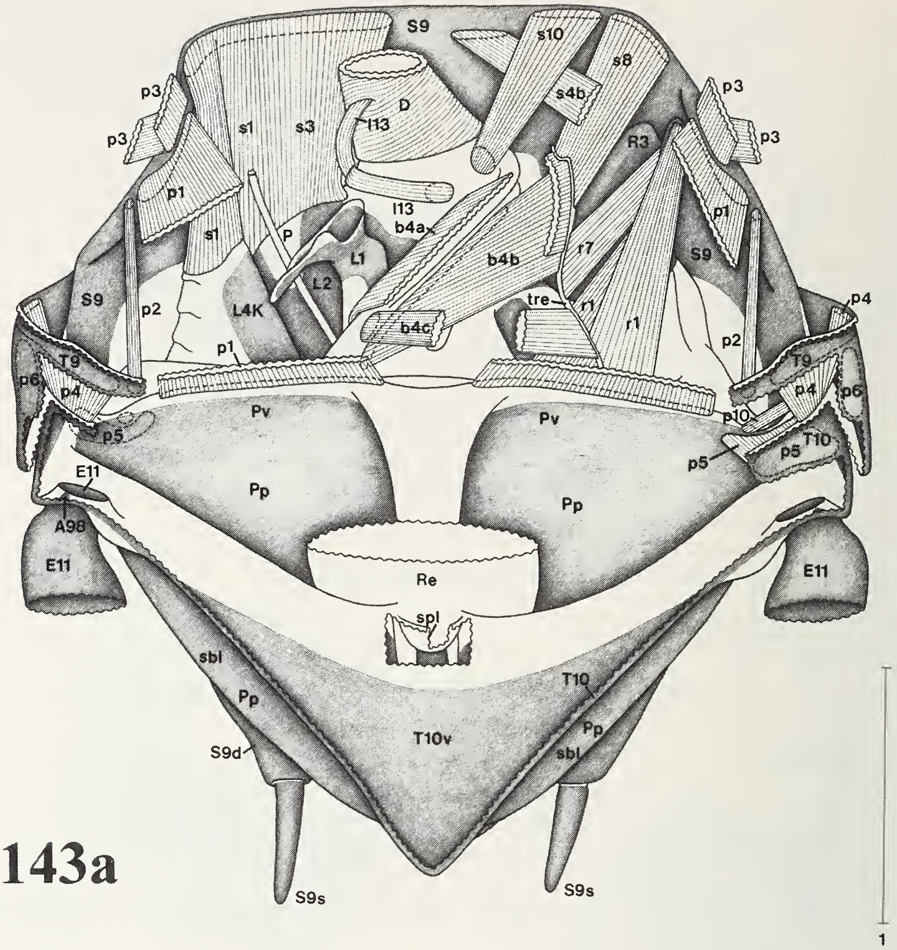
5.9. *Cryptocercus punctulatus* (Blattaria, Cryptocercidae)

Left complex

L4 is a group of four sclerites: The ribbon-shaped **L4N** (fig.150; **L4d** is part of **L4N**) lies on a transverse outfolding of the dorsal wall, whose right end is somewhat lobe-like (**paa** in fig.150). The ventral wall of this outfolding extends far anteriad, where **L4K** takes its position. The small **L4P**, not present in all specimens, lies at the anteriormost left edge of the left complex. **L4G** is a plate in the posterior ventral wall of the ventral lobe **vla** (= ventral phallomere; fig.148, 152).

Sclerite **L1** lies in the central dorsal wall. Its hood-shaped anterior part occupies most of the walls of a deep pouch (**pne** in fig.150-154). The anterior summits of **L1** and **pne** are expanded and plateau-like, with upcurved margins. The posterior part of **L1** leaves the **pne**-pouch and has an arm-like extension on each side. These extensions curve ventrad and join each other again to form a complete sclerite ring (fig.153, 154). The membranous cuticle enclosed by this ring forms two cushion-like bulges **dca**, with a small sclerotised peak between them (**18** in fig.153). The phallomere-gland (**P** in fig.152, 153) opens into the membrane to the left of **L1**.

The large sclerite **L2** lies ventral to **L1** (fig.152). To the posterior **L2** becomes narrower, and then it curves around the posterior edge of the left complex into the dorsal wall (fig.151, 152). The area of this curvature forms a large bulge (**paa** in fig.150-152). In the dorsal wall **L2** extends anteriad as far as to the opening of the phallomere-gland. The right anterior part of **L2** lies in the dorsal wall of a pouch (**lve** in fig.150-152; the edge along



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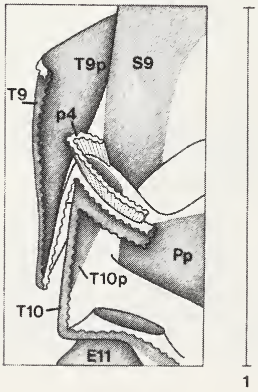


143b

Cryptocercus punctulatus

the bottom of the pouch is labelled **7**). The broad ejaculatory duct (**D** in fig.150, 151) opens most anteriorly into this **lve**-pouch.

The ventral wall of the **lve**-pouch is at the same time an anterior part of the dorsal wall of the **vla**-lobe. The ribbon-shaped sclerite **L5** (fig.151, 152) lies more posteriorly in the dorsal **vla**-wall. The ventral **vla**-wall is membranous anteriorly and sclerotised by **L4G** posteriorly.

The large hook **hla** (fig.150, 151), whose distal part is sclerotised by **L3**, is evaginated from the left wall of the left complex – beneath and somewhat posterior to **L4K**.

Right phallomere

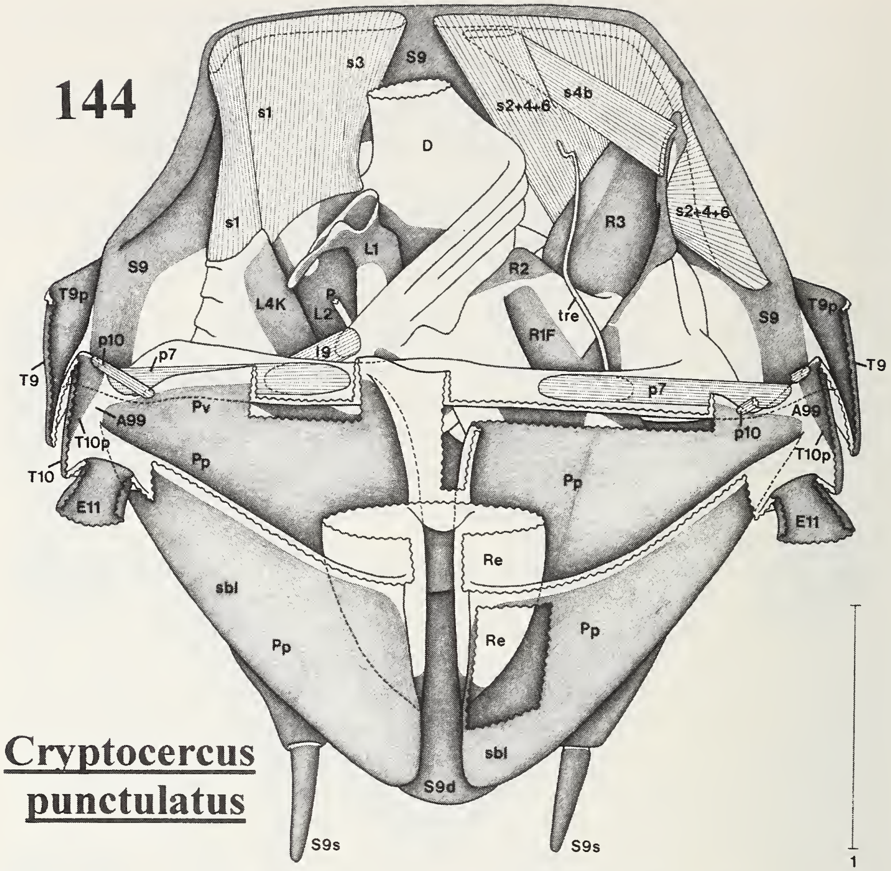
Sclerite **R3** occupies the anterior (right-)ventral wall (fig.160-163). The lateral and anterior margins of **R3** form a weakly sclerotised groove-like apodeme **age** (fig.160, 163). Along the right margin of **R3** the ventral sclerotisation of **age** folds to the left (**19** in fig.163, 164). Sclerite **R2** articulates with the left part of **R3** (**A7** in fig.161-163). **R2** has the shape of a ridge (fig.161, 162). Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad and somewhat anteriad to form a central invagination (**cbe** in fig.160-162; compare fig.163 and 164).

Posterior to the right part of **R3** sclerite **R1F** adjoins, and the two sclerites articulate (**A3** in fig.160, 161, 163). From its central part behind the **A3**-articulation **R1F** extends in two directions: The ventral arm bends left-dorsad (behind the edge **16** in fig.163, 164) and extends into the right-dorsal wall of the **cbe**-invagination (fig.160, 164). This part of **R1F** bulges outwards (**pva** in fig.163, 164) by the cuticle being extensively thickened (cross-section in fig.164). The median end of this arm articulates with the left-dorsal end of **R2** (**A6** in fig.160, 164). The dorsal arm of **R1F** extends posterodorsad (fig.160, 163); anteriorly its dorsal margin folds back to the right to form a sclerotised groove (**rge** in fig.160, 163), which is a posterior continuation of the **age**-groove on **R3**.

The posterior part of the right phallomere is a large dorsal lobe **fda** (fig.160-163, 166), whose dorsal and ventral walls are partly occupied by sclerite **R1J**. The dorsal anterior tip of **R1J** approaches the dorsal arm of **R1F** (**A8** in fig.160), its ventral anterior tip approaches the base of the ventral arm of **R1F** (**A9** in fig.163, 166). The tendon **tre** has its origin in the anteriormost dorsal wall of **fda** (fig.160). In its right wall **fda** has a large membranous area (**17** in fig.160, 166). At the left end of **fda** there is another small sclerite **R1K** (fig.160).

Figs.143a,b: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **a:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, subanal lobes, paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. Supraanal lobe shown through a window cut into the membrane anterior to ventral sclerotisation of abdominal tergite 10 T10v. – **b:** Posterior insertion of muscle p4 at anterior margin of abdominal tergite 10 T10. Enlarged detail from left part of fig.143a, further parts of abdominal tergite 9 T9 and anterior part of p4 removed. – Scale: 1mm.

144



Cryptocercus punctulatus

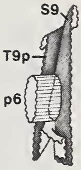
Fig.144: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – Male postabdomen as in fig.143a, after removal of further parts of abdominal tergites 9 and 10 (especially T10v) and supraanal lobe. Distal part of rectum, basal parts of cerci, dorsal wall of right subanal lobe, and anterior margins of paraprocts cut open. – Scale: 1mm.

⟶ p.101

Figs.145-147: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **145:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **146:** Left margin of subgenital plate (compare fig.145); with insertion of muscle p6. – **147:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6); dorsal sclerotisation S9d of subgenital plate complete in the right part but largely removed in the left part. – Scale: 1mm.

⟶ p.102

Figs.148,149: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **148:** Phallomere complex in ventral view. – **149:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.148. – Scale: 1mm.



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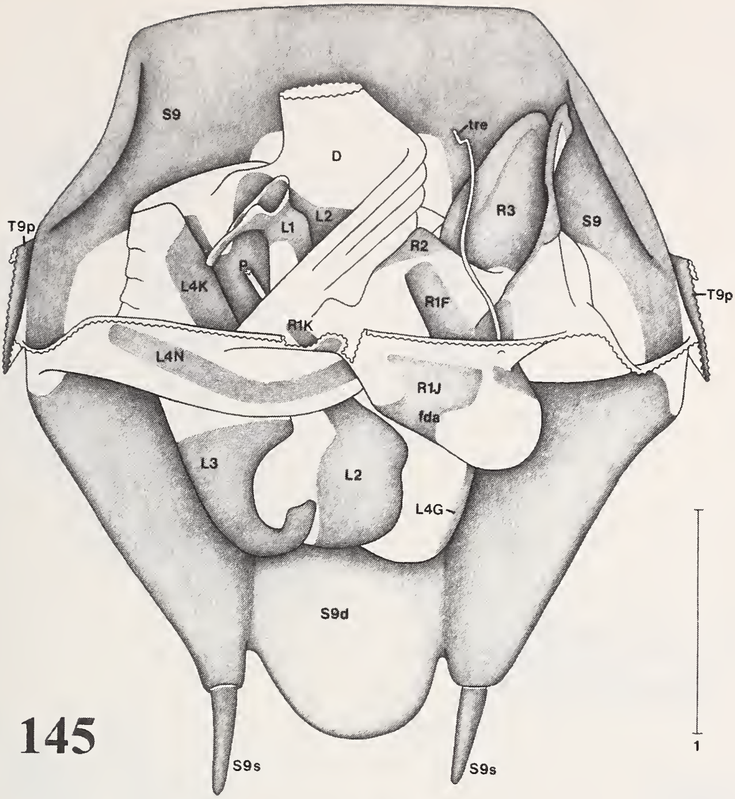

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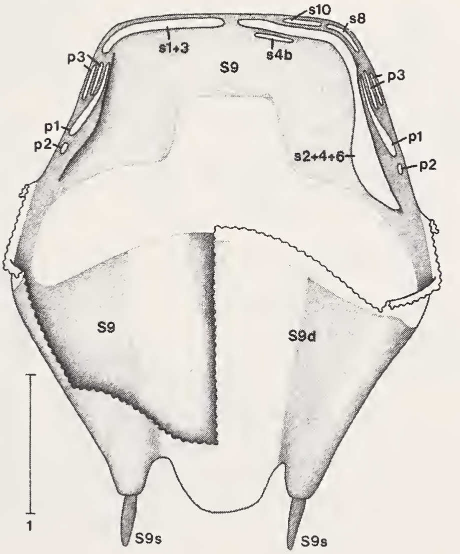
Cryptocercus punctulatus



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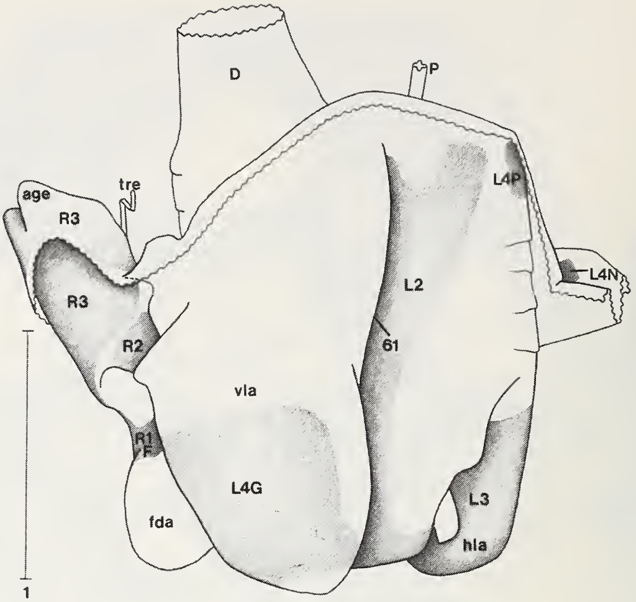
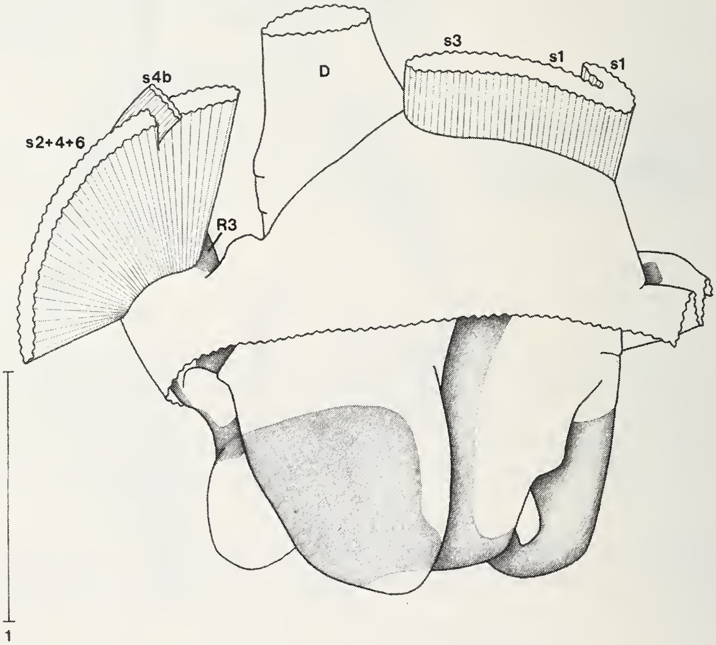
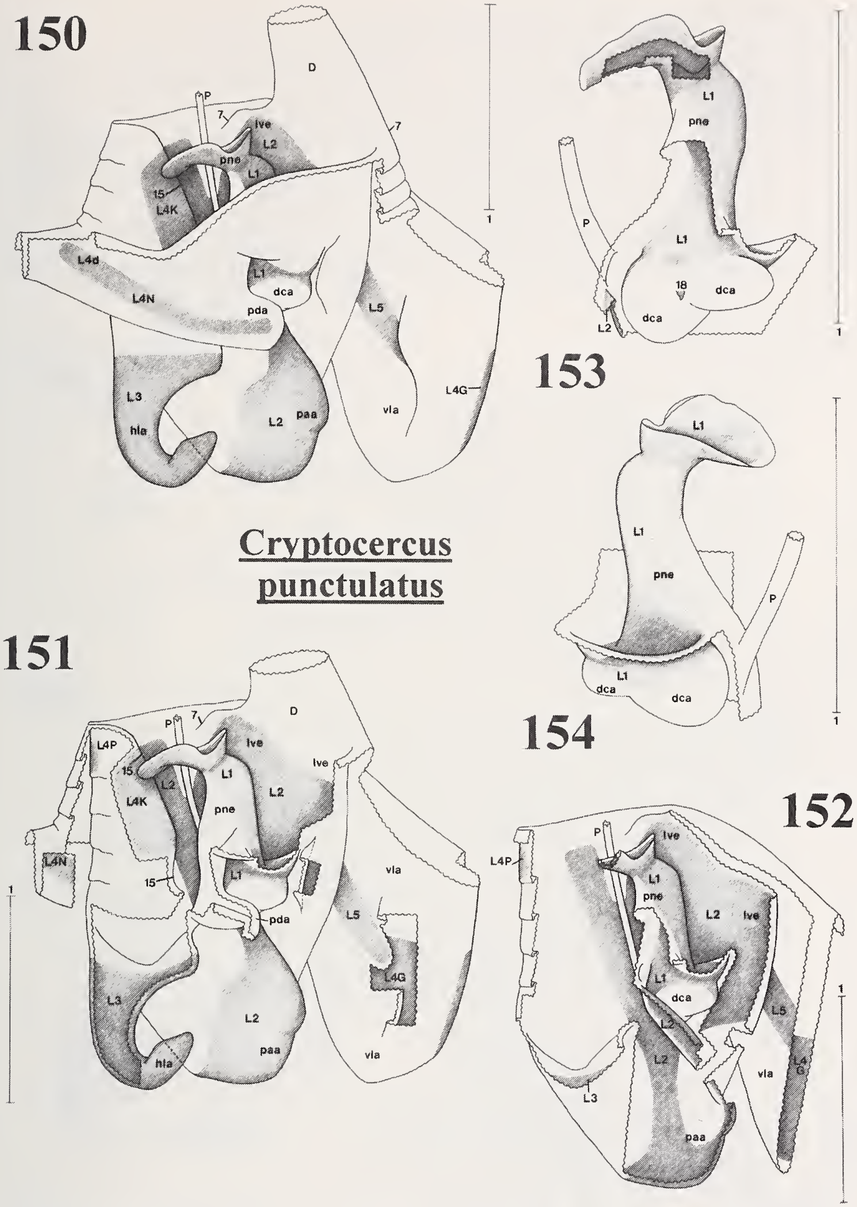


Cryptocercus punctulatus

149





Figs.150-154: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **150:** Left complex in dorsal view. – **151, 152:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.152: pne-pouch with some adjacent parts completely cut off from the other elements. – **153:** Sclerite L1 in dorsal pouch pne in dorsal view; with some surrounding membranes, part of sclerite L2, and phallomere-gland P. – **154:** Sclerite L1 in dorsal pouch pne in ventral view; with some surrounding membranes and phallomere-gland P. – Scale: 1mm.

Subgenital plate and posterior abdominal segments

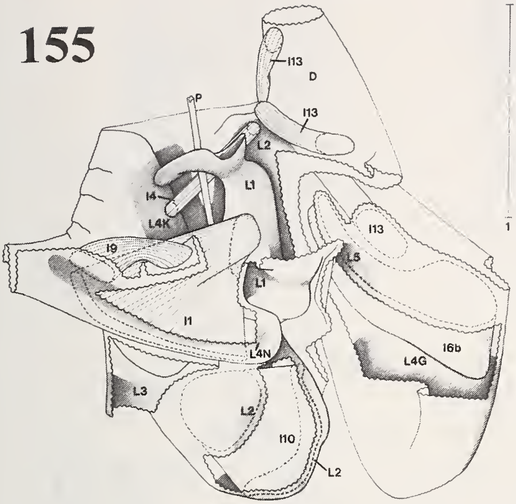
Fig.143a,b, 144 (posterior segments); fig.147 (subgenital plate **S9**). The whole postabdomen is retracted anteriad and completely covered by the heavily sclerotised tergite and sternite of abdominal segment 7. The tergal and sternal sclerotisations of the postabdomen are rather weak. The ventral part of tergite 10 **T10v** is rather extensive. Separate **Pv**-sclerites are missing; they are assumed to have been incorporated into the anterior margins of the paraprocts **Pp**. The sclerites **Ca**, **Cb**, and **Cc** are missing, and there are no **Ca**-bulges (compare fig.59). The articulations **A98** are well-developed. **A99** are not true articulations since the contact between paratergite **T10p** and paraproct **Pp** is not very close.

Musculature

Muscles	Positions of insertions	in fig.
l1	Membranous posterior dorsal wall of **pne**-pouch – **L4N** (including **L4d**) and adjacent membranes	155, 159
l2	**L1** (plateau-like anterior end of **pne**-pouch) – **L4K**	156
l3	**L1** (right-ventrally on **pne**- pouch) – **L2** (most of anterior half)	158, 159
l4	**L2** (right anterior part) – **L4K**; very delicate	155, 158
l6b	**L4G** (anterior margin) and membrane anterior to **L4G** – dorsal wall of **vla**-lobe posterior to genital opening (in part on **L5**)	155, 157
l7	Left ventral wall of left complex – left posterior edge of left complex	158
l9	Transversely within anterior left dorsal wall of left complex	144, 155
l10	**L2** (posteriormost part, on **paa**-process) – membrane left-dorsal to **paa**-process	155
l13	Ejaculatory duct **D** next to its opening (dorsal wall) – anterior dorsal wall of **vla**-lobe; anterior part of muscle divided into two bundles.	143a, 155
l14	**L4K** and membrane anterior to base of **hla**-hook – **hla**-hook (dorsal anterior margin of **L3** and membrane anterior to it)	157
l19	Left posterior ventral wall of left complex – **hla**-hook (ventral anterior margin of **L3** and membrane anterior to it)	156, 158
r1	**R3** (right margin) – anterior dorsal wall of **fda**-lobe, in part on anterior margin of **R1J** and on base of **tre**-tendon	143a, 164, 165
r2	**R3** – **cbe**-invagination: **R1F** (anterior margin and left part), membrane, and **R2** (dorsal margin)	166, 167
r3	**R1F** (dorsal and central parts, posterior to articulation **A3**) – **R1J** (right margin)	166, 167, 168
r7	**R3** (right anterior part) – **tre**-tendon	143a, 165
r8	Both insertions on central part of **R3**	167
b4a	Right dorsal wall of left complex – **tre**-tendon	143a, 156, 165
b4b	Right dorsal wall of left complex – **tre**-tendon	143a, 165
b4c	Central dorsal wall of left complex – **tre**-tendon	143a, 165

Figs.155-159: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **155-158:** Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – **159:** Sclerite L1 in dorsal pouch pne in ventral view; with muscles l1 and l3 (compare fig.154). – Scale: 1mm.

155



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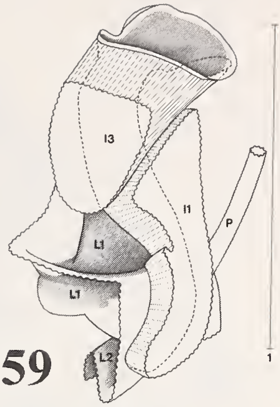

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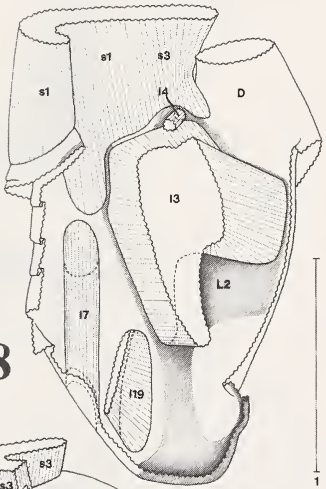

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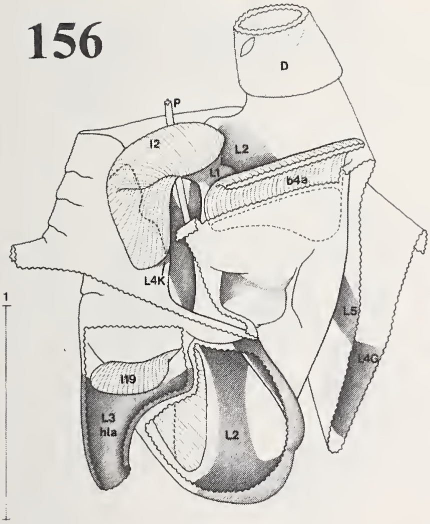

Cryptocercus punctulatus

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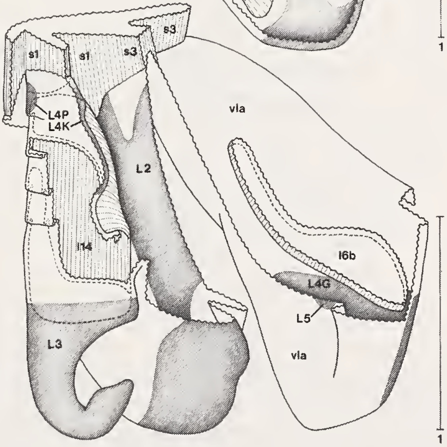
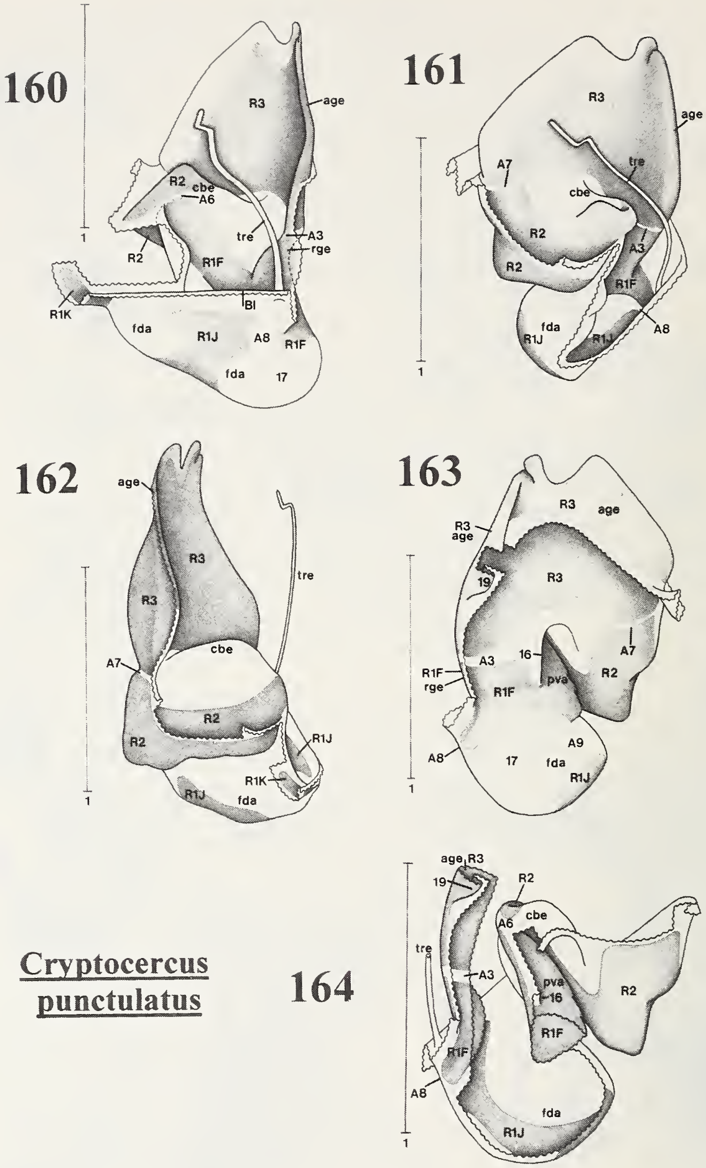
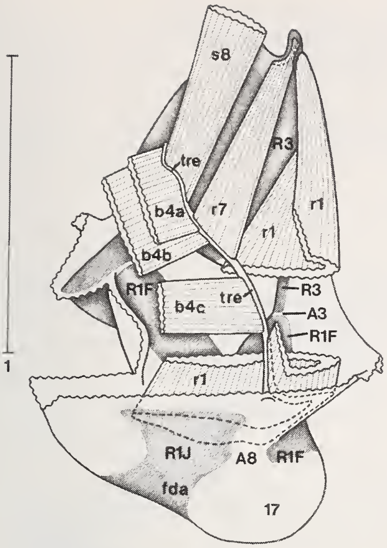




Figs.160-164: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **160:** Right phallomere in dorsal view. – **161:** Right phallomere in left-dorsal (somewhat anterior) view. – **162:** Right phallomere in left-ventral view. – **163:** Right phallomere in right-ventral view. – **164:** Right phallomere in right-ventral view; most elements shown in fig.163 removed. – Scale: 1mm.



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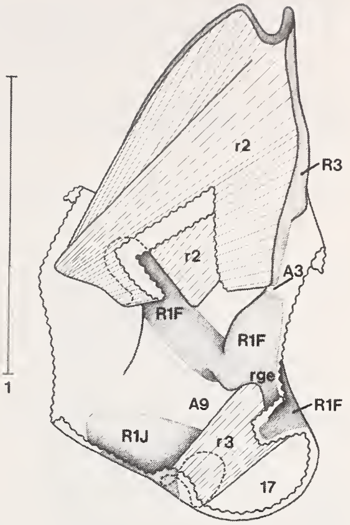

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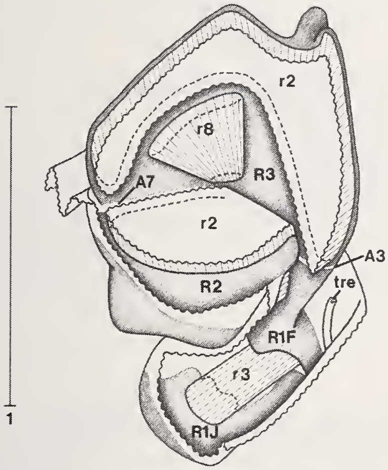
Cryptocercus punctulatus



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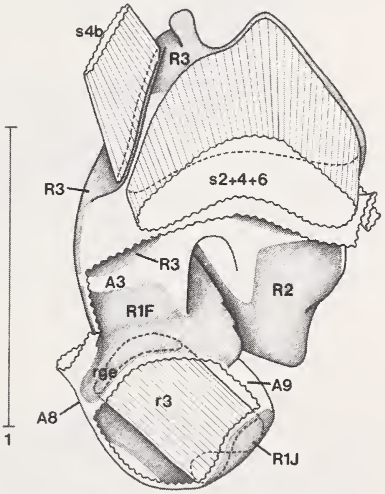

168

s1+3(+7?)	**S9** left side (most anteriorly; only medially) – ventral basal line **Bl** of left complex and membrane anterior to base of **hla**-hook; right part of muscle inserting also on anterior margin of **L2** (= **s7**?)	143a, 144, 147, 149, 157, 158
s2+4+6	**S9** right side (anteriorly; medially and laterally) – **R3** (anterior margin) and anterior ventral wall of genital pouch	144, 147, 149, 168
s4b	**S9** right side (medially and anteriorly) – **R3** (right anterior margin); present in some specimens only	143a, 144, 147, 149, 168
s8	**S9** right side (most anteriorly) – **tre**-tendon	143a, 147, 165
s10	**S9** right side (medially and most anteriorly) – ejaculatory duct **D** next to its opening (right wall)	143a, 147
p1 (pair)	**S9** – membrane anterior to paraproct **Pp** or **Pv**-sclerotisation; very broad	143a, 147
p2 (pair)	**S9** – **T9** (lateral anterior margin)	143a, 147
p3 (pair)	**S9** – rectum (ventral wall); divided into two groups of fibers on both sides	143a, 147
p4 (pair)	**T9** (lateralmost anterior margin, also extending onto paratergite **T9p**) – **T10** (lateralmost anterior margin, also extending onto paratergite **T10p**)	143a,b
p5 (pair)	**T10** (lateral anterior margin) – paraproct **Pp** (lateral anterior margin, corresponding to **Pv**-sclerotisation)	143a
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin)	143a, 146
p7 (pair)	Posteriad-directed outfolding anterior to paraproct **Pp** – membrane anterior to "articulation" **A99** (between paratergite **T10p** and paraproct **Pp**)	144
p10 (pair)	Paratergite **T10p** (anterior margin) – paraproct **Pp** (lateral anterior margin, corresponding to **Pv**-sclerotisation)	143a, 144

5.10. *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae)

Left complex

Sclerite **L1** is situated in the right anterior dorsal wall; its anterior part lies within a large pouch **pne** (fig.177, 178). Posterior to **L1** there is a complicated sclerotisation (**L4T** and **L2C**: fig.177-179, 182) bearing two processes **pda** and **paa**. Beneath these elements there is a large pouch **lve** (fig.180) containing the sclerites **L2A** and **L2B** in its dorsal wall. The

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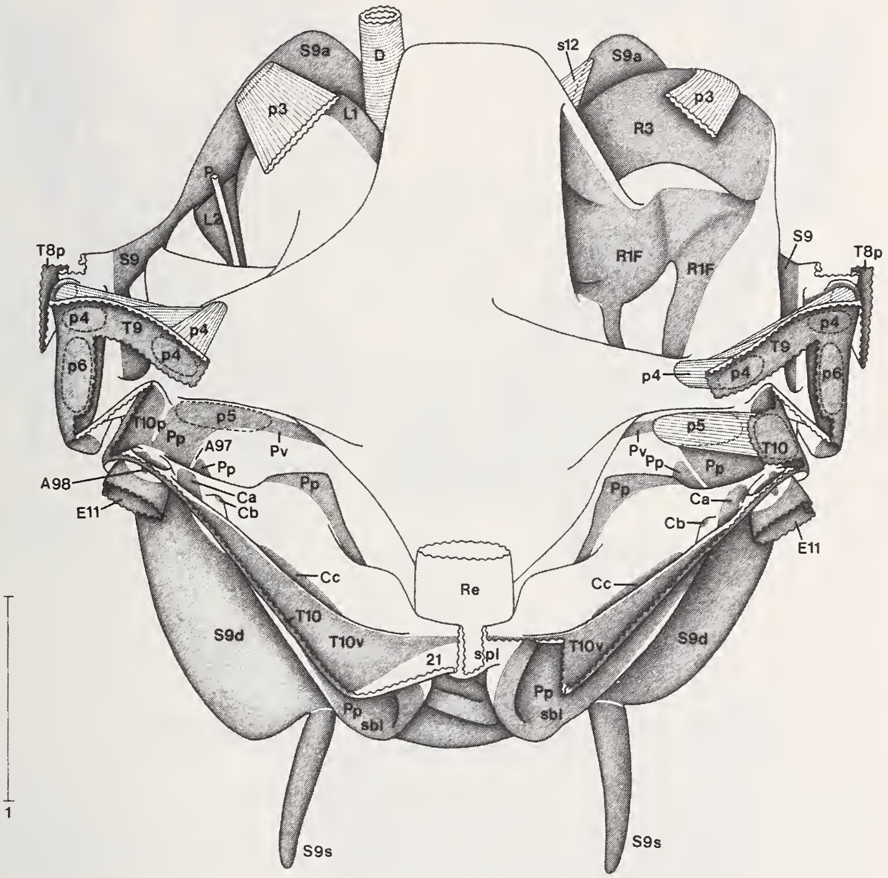
Figs.165-168: *Cryptocercus punctulatus* (Blattaria, Cryptocercidae) – **165:** Right phallomere in dorsal view; with some muscles. – **166:** Right phallomere in dorsal view; with some muscles; some dorsal elements removed. – **167:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles; some left-dorsal elements removed. – **168:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.163; fda-lobe cut open to show muscle r3. – Scale: 1mm.

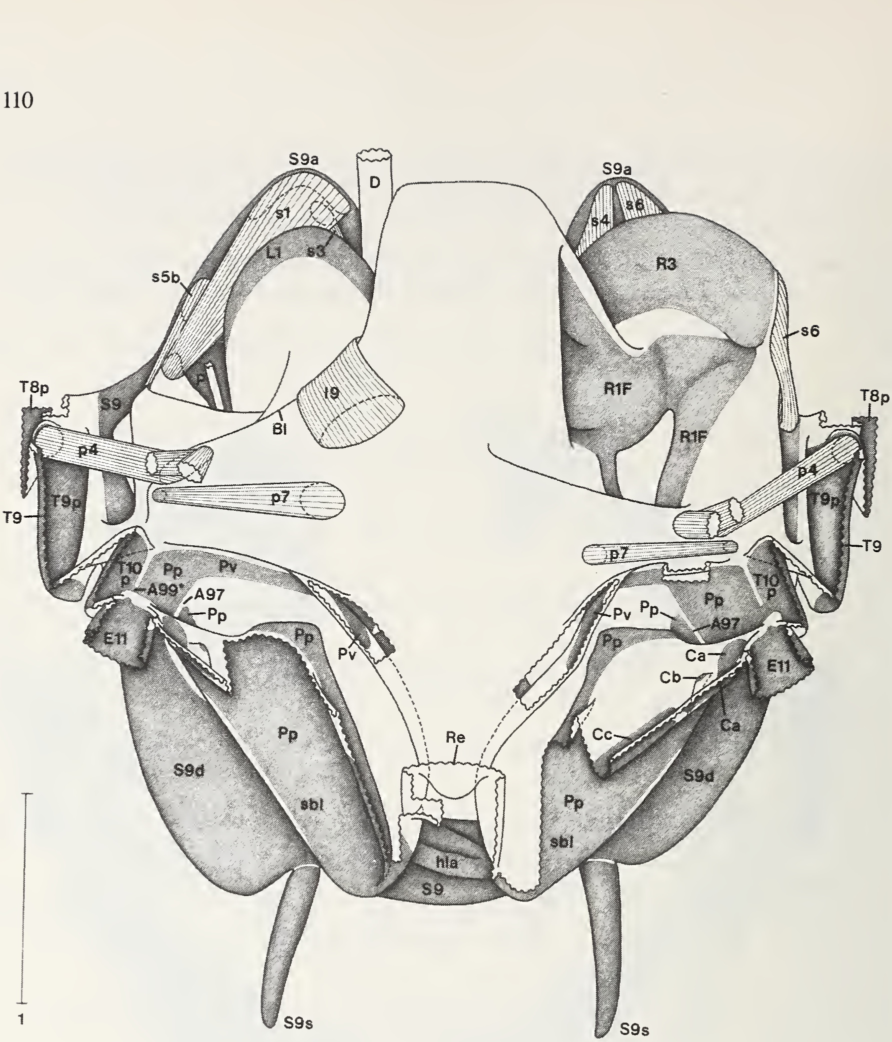
large hook-process **hla** (fig.177) with its sclerite **L3** protrudes from the left wall. Sclerite **L4K** takes a position dorsal to the base of **hla** (fig.177). **L4R** is the sclerotisation of the ventral wall of a broad ventral lobe **vla** (= ventral phallomere; fig.174, 181).

The **pne**-pouch (fig.177, 178) is deep but rather flat. The anterior part of **L1** occupies the ventral wall of the **pne**-pouch and its anterior dorsal wall. The posterior part of **L1**



169 **Lamproblatta albipalpus**

Fig.169: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 8, 9, and 10, supraanal lobe, subanal lobes, paraprocts, Pv-sclerites, distal part of rectum, basal parts of cerci, and part of musculature. – Scale: 1mm.

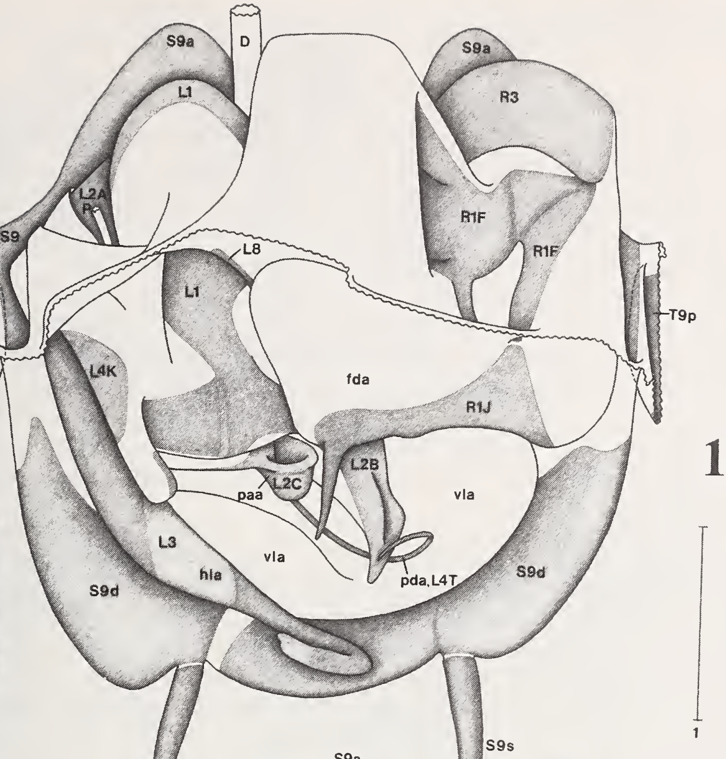


170 Lamproblatta albipalpus

Fig.170: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – Male postabdomen as in fig.169, after removal of further parts of abdominal tergites 9 and 10 (especially T10v), parts of right paraproct, and supraanal lobe. Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Scale: 1mm.

⟶ p.111

Figs.171-173: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **171:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **172:** Left margin of subgenital plate (compare fig.171); with insertion of muscle p6. – **173:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6). – Scale: 1mm.



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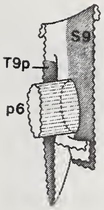

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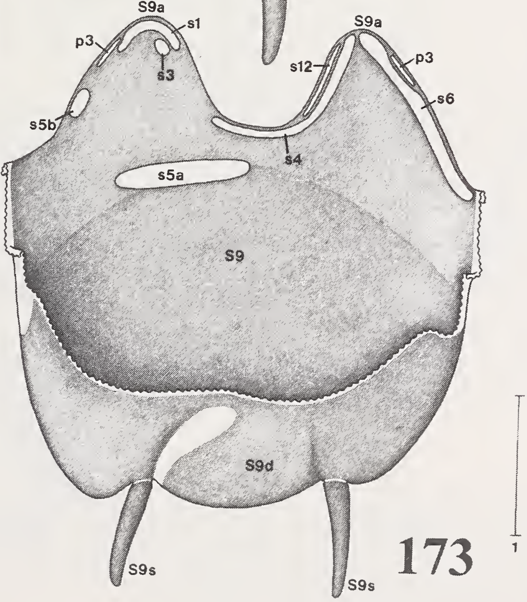


173

Lamproblatta albipalpus

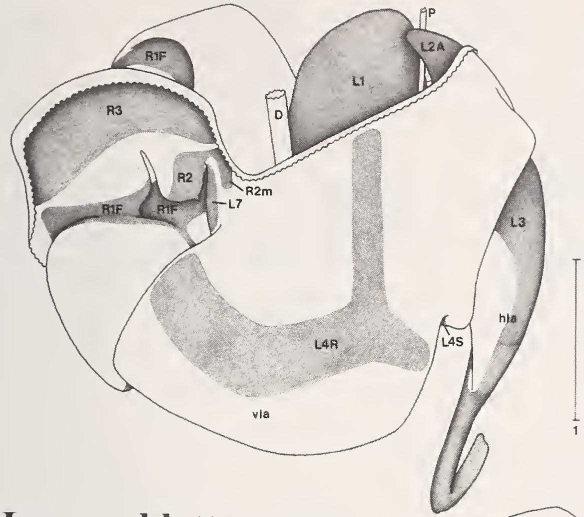
sclerotises a process (**dca** in fig.177, 178) and has a plate-like extension to the left, which is separated from the main part of **L1** by a strip of weaker sclerotisation (**22** in fig.176, 177).

The complex sclerite posterior to **L1** is composed of **L4T** – the sclerotisation of the spine-shaped **pda** – and **L2C** – the sclerotisation of the cup-shaped **paa** (fig.176-179). **pda** is almost completely sclerotised in its dorsal wall but only basally in its ventral wall (fig.179, 182), and it resembles a hypodermic needle: At its pointed end (**26** in fig.182) the cuticle is invaginated to form a very narrow channel (**sbe** in fig.182) which runs back through the whole spine and whose end is expanded and bulb-like (**sbe** in fig.182, 183; possibly the reservoir of a gland). The **paa**-process is completely sclerotised. At its right base the cuticle is deeply invaginated to form a heavily sclerotised hood-shaped apodeme (**boe** in fig.179, 182, 183) which caps the right end of the **sbe**-bulb (fig.182). The membrane (**25** in fig.178, 179, 182) that adjoins this **L4T+L2C**-sclerite ventrally is somewhat invaginated anteriad, and here the phallomere-gland opens (**P** in fig.178, 179). Ventral to and to the left of this invagination the membrane extends posteriad towards the transverse edge **23**, along which the cuticle bends ventrad and anteriad to continue into the dorsal wall of the **lve**-pouch (fig.180).

The **lve**-pouch spans almost the whole breadth of the left complex. (The edge along the bottom of the pouch is labelled **7** in fig.180). Its dorsal wall is largely occupied by the sclerites **L2A** (left part) and **L2B** (right part), which articulate with each other (**A4** in fig.180). In the area around **A4** the **lve**-pouch has a very deep recess from anteriorly. The right part of **L2B** bends dorsad and back to the left along the longitudinal part of edge **23** (compare fig.178 and 180). This dorsal part of **L2B** articulates with **L1** anteriorly (**A2** in fig.176, 178, 180); posteriorly it has an extension to the left (**24** in fig.176, 178). **L2A** extends like an arch along the margins of the left dorsal **lve**-wall. Only in the anteriormost part of the **lve**-pouch **L2A** enters the ventral wall (fig.181). At the left posterior end of the **lve**-pouch the sclerite abruptly narrows, leaves the pouch (sclerotisation now designated **L4S**, fig.178, 180, with **L4d** as its distalmost part), and curves into the dorsal wall of the left complex (fig.177, 178).

The membranous ventral wall of the **lve**-pouch is at the same time the anterior dorsal wall of the **vla**-lobe (fig.174, 180, 181). The ejaculatory duct (**D** in fig.178-181) opens far on the right into this membrane. Dorsal to the genital opening there is a small membranous outfolding (**goa** in fig.177, 179-181). **L4R** in the ventral wall of the **vla**-lobe is a transverse plate with a ribbon-like anterior extension (fig.174, 181). The small sclerite **L7** lies in the anterior right edge of the **vla**-lobe and is in close contact with a ribbon-like extension of the **R2**-sclerite of the right phallomere (**R2m** in fig.174, 191-193). Another small sclerite **L8** lies in the right dorsal wall of the left complex (fig.176, 177).

Figs.174-176: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **174:** Phallomere complex in ventral view. – **175:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.174. – **176:** Left complex in right-dorsal view; dorsal wall of pne-pouch largely removed. – Scale: 1mm.



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Lamproblatta albipalpus

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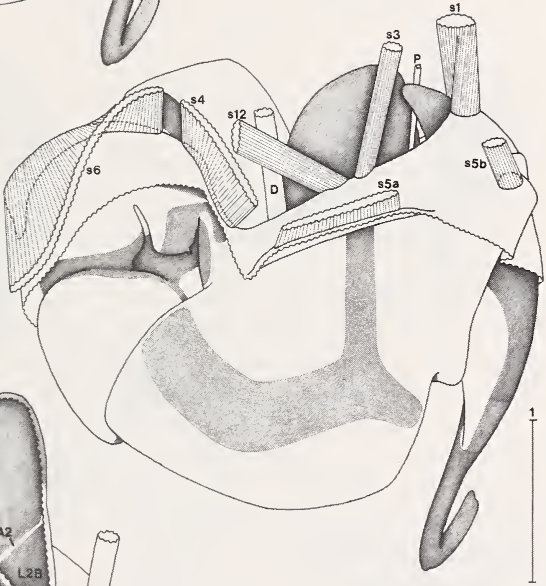

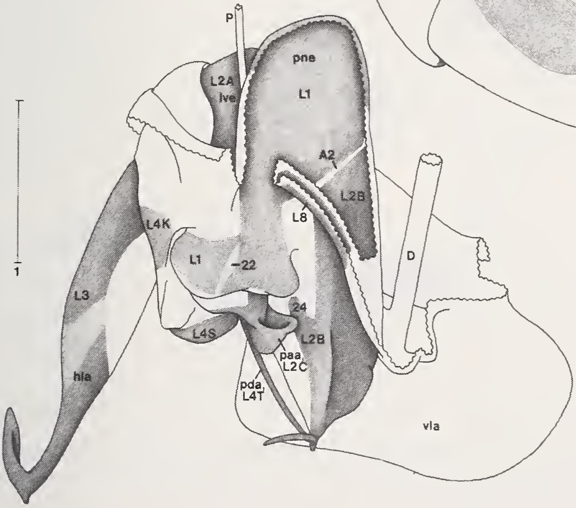

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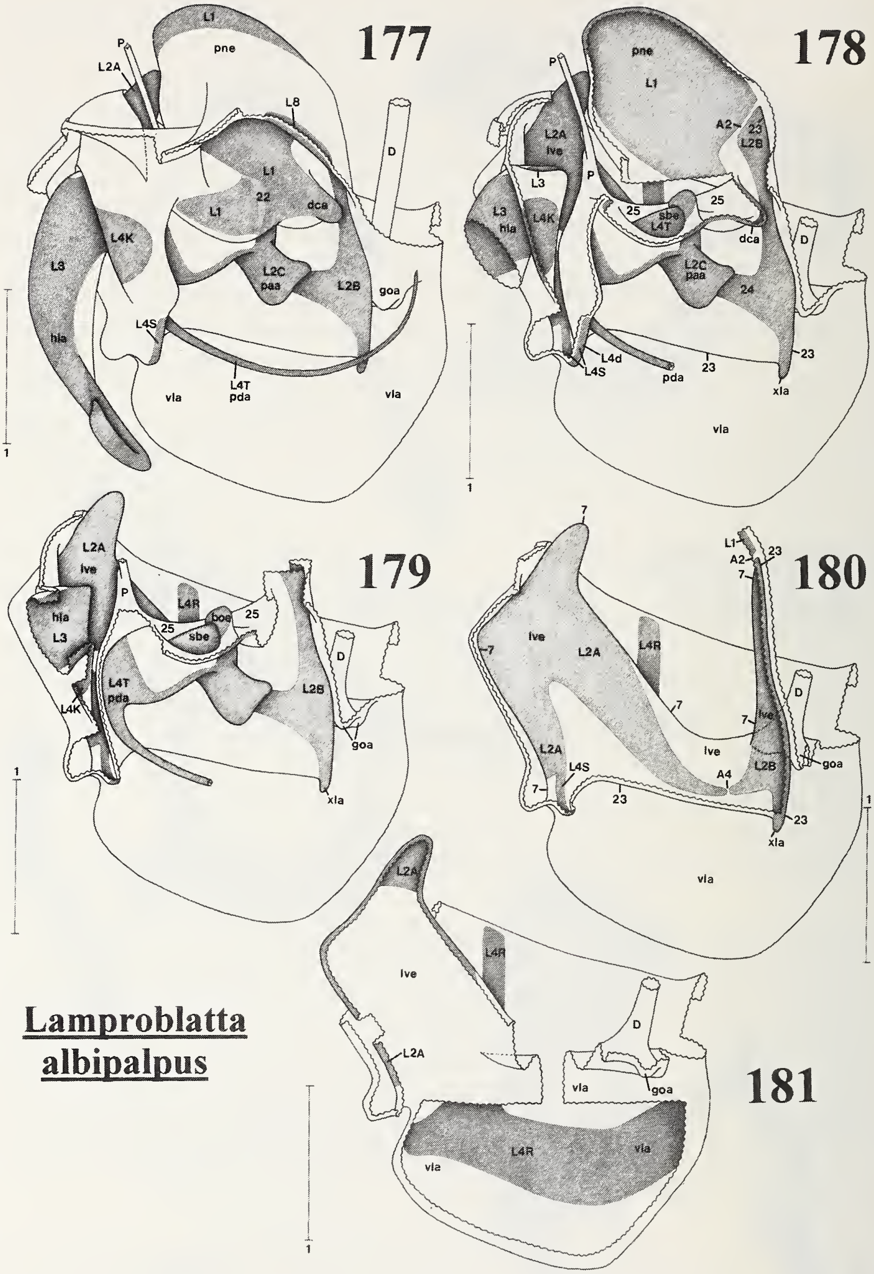


Figs.177-181: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **177:** Left complex in dorsal view. – **178-181:** Left complex in dorsal view; with successive removal of parts of left complex (mainly of dorsal ones). – Scale: 1mm.

The **hla**-hook (fig.174, 177) is evaginated from the left wall of the left complex and is largely sclerotised by **L3**. Around the base of **hla** the cuticle is circularly invaginated (fig.178, 179). Sclerite **L4K** shows a dorsoventral curvature: it lies mainly in the left dorsal wall of the left complex, above the base of **hla** (fig.177), but its left part bends like a horseshoe ventrad into the invagination around the **hla**-base (fig.178).

Right phallomere

Sclerite **R3** occupies the anterior ventral wall (fig.190-194). In the posterior part of **R3** the cuticle is considerably thickened (cross-section in fig.193). Sclerite **R2** articulates with the left posterior margin of **R3** (**A7** in fig.190-194). **R2** forms a large ridge (fig.191, 192, 194), whose left-dorsal part curves dorsad and slightly back to the right (fig.190). The right-ventral end of **R2** has the extension **R2m** (fig.191-195). Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad to form a narrow, groove-like central invagination (**cbe** in fig.190, 191; compare fig.193 and 195).

Posterior to the right part of **R3** sclerite **R1F** adjoins, and the two sclerites articulate (**A3** in fig.190-194). From its central part behind the **A3**-articulation **R1F** extends in two directions: The ventral arm bends left-dorsad (at and behind edge **16** in fig.193, 195) and largely occupies the right-dorsal wall of the **cbe**-invagination (fig.190). The distal part of this arm forms a somewhat spoon-shaped process **pva** (fig.190-195). At its distal anterior margin this arm articulates with **R2** (**A6** in fig.190, 195); at its basal posterior margin it has a distinct extension (**20** in fig.190, 192-195). The dorsal arm of **R1F** extends posterodorsad (fig.190, 191) and forms a sclerotised groove (**rge** in fig.190, 195). The part of **R1F** posterior to **A3**, the extension **20**, and the dorsal arm show an extensive thickening of the cuticle directed to the interior of the phallomere (cross-sections in fig.195).

The posterior part of the right phallomere is a large dorsal lobe **fda** (fig.190, 194; in the figures **fda** is pulled to the right and to the posterior), whose dorsal and ventral walls are partly occupied by sclerite **R1J**. The dorsal anterior tip of **R1J** articulates with the dorsal arm of **R1F** (**A8** in fig.190), its ventral anterior margin articulates with the extension **20** of **R1F** (**A9** in fig.192-195, 197). Near the **A9**-articulation the cuticle of **R1J** is, like that of extension **20**, thickened to the interior, and the articulation is thus very stout and deeply immersed in the phallomere (fig.193, 195). The right wall of **fda** has a large membranous area (**17** in fig.190, 193, 194). The posterior edge of **fda** bears a sclerotised spine (**sra** in fig.190).

Subgenital plate and posterior abdominal segments

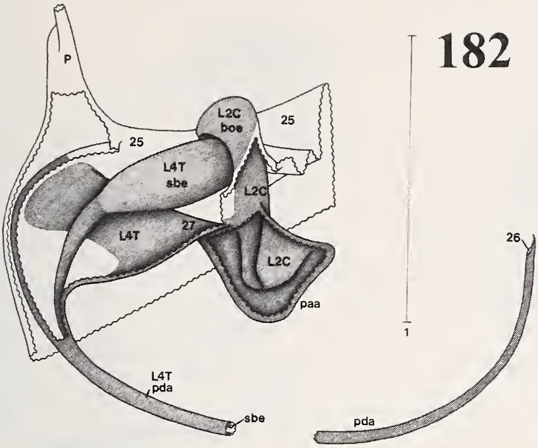
Fig.169, 170 (posterior segments); fig.173 (subgenital plate **S9**). Tergite 10 **T10** is not completely divided longitudinally, but around its posterior edge there is a median membranous field (**21** in fig.169). The ventral part of tergite 10 **T10v** is moderately extensive and is, except for an anterior transverse bridge, also divided by membrane **21**. The paraprocts **Pp** are divided (by the articulations **A97**) into a large median part sclerotising the dorsal wall of the subanal lobe **sbl** and a small lateral plate-like part. Along the anteriormost and medianmost dorsal wall of the subanal lobe **sbl** each paraproct forms a heavy groove-like apodeme (fig.170; cut through on the right side). The lateral plate of

Pp is narrowly connected with the paratergite **T10p** laterally, and **A99*** is hence no longer a true articulation. Strip-like and twisted **Pv**-sclerites are present; they are laterally connected with the lateral plates of the paraprocts **Pp**. The **Ca**-sclerites are curved ribbons on rather indistinct bulges immediately median to the cercal bases. The very small **Cb**-sclerites lie at the bottom of a small funnel-like invagination. The **Cc**-sclerites are dorsoventrally curved plates on a paired shallow outfolding beneath the anterior margin of **T10v** and above the subanal lobes **sbl**. The articulations **A98** are well-developed.

Musculature

Muscles	Positions of insertions	in fig.
l2	**L1** (left-anteriorly on **pne**-pouch) – membrane anterior to **L4K** and to **hla**-base	184
l3	**L1** (ventrally on **pne**-pouch) – **L2A** and **L2B** (area of articulation **A4**)	187
l5	**L4R** (anteriormost part) – **L2A** (anteriormost part)	188
l6a	**L4R** (anteriormost part) – **L2B** (left posterior part)	188
l6b	Left bundle: **L4R** (left-posterior part) – dorsal wall of **vla**-lobe, far left-posterior to genital opening	188, 189
	Right bundle: **L4R** (right-posterior part) – dorsal wall of **vla**-lobe, posterior to genital opening	188, 189
l9	Anterior dorsal wall of genital pouch – **L8**	170, 184, 185
l10	**L2A** (anteriormost part) – **L4T** and **L2C** between processes **paa** and **pda**, membranous area **25** (compare fig.182)	186
l11	**L4K** (posterodorsal part) – **L4d** (= dorsal part of **L4S**) and membrane to the left of it	184, 188
l12	Membrane next to **L2B** (right ventral wall of **lve**-pouch) – **L8** and membrane in dorsal wall of **pne**-pouch	184, 185, 186, 188
l13a	Ejaculatory duct **D** next to its opening – dorsal wall of **goa**-lobe	188
l13b	Ejaculatory duct **D** next to its opening – dorsal wall of **vla**-lobe immediately to the right of genital opening	188
l14	Membrane anterior to **L4K** and to **hla**-base – **hla**-hook (on **L3**); muscle divided into an anterior and a posterior bundle inside **hla**.	184, 185
l20	**L2A** (leftmost part) – membrane left-posterior to opening of phallomere-gland **P**	188
l21	Membrane anterior to **L4K** – membrane left-posterior to opening of phallomere-gland **P**; very delicate	184
l22	Membrane anterior to **L4K** – **hla**-hook (basally and dorsally on **L3**)	184, 185
l23	**L4K** – **hla**-hook (basally and ventrally on **L3**)	184, 186
l24	Membrane posterior to **L4K** – membrane left-posterior to opening of phallomere-gland **P**; very few diffuse fibers	185

Figs.182-185: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **182:** Sclerites L2C and L4T, processes paa and pda, and phallomere-gland P in dorsal view. – **183:** Sclerites L2C and L4T and process paa in dorsal view; some further parts removed (compare fig.182). – **184,185:** Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 1mm.



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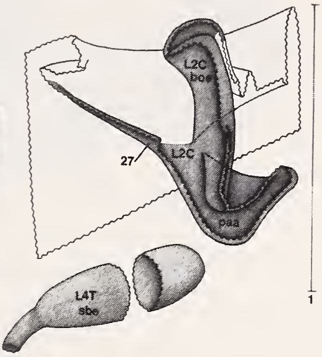

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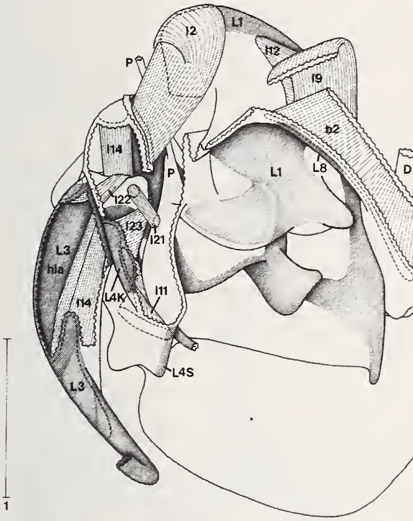

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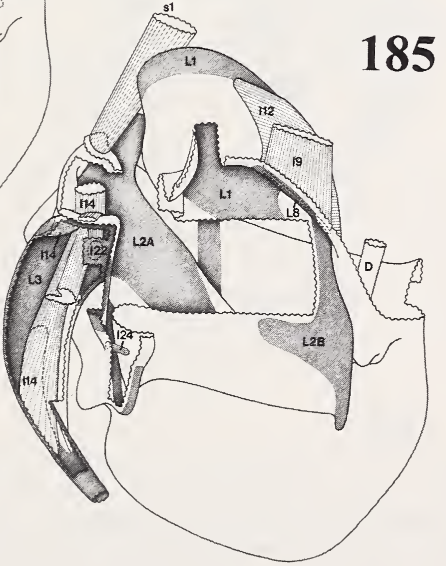

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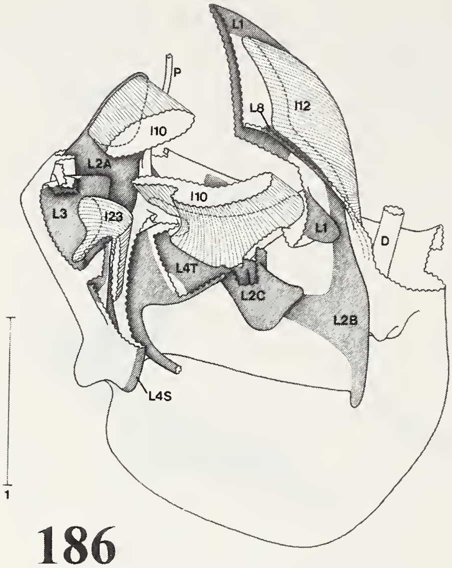
Lamproblatta albipalpus



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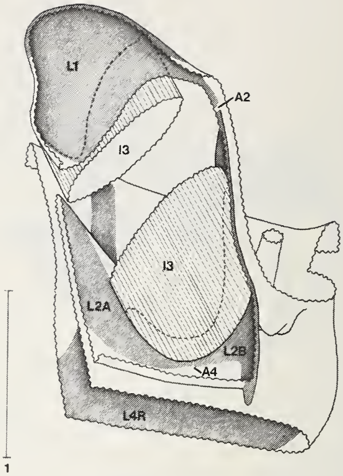

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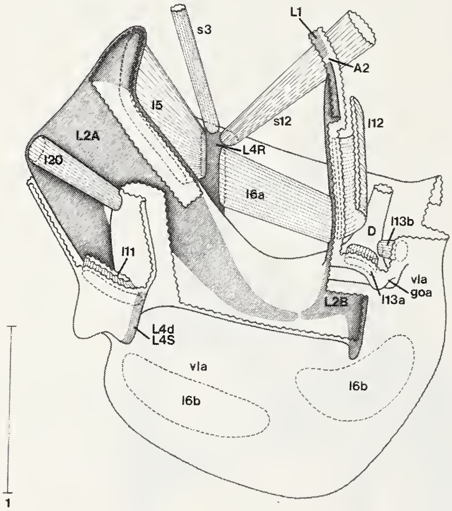
Lamproblatta albipalpus



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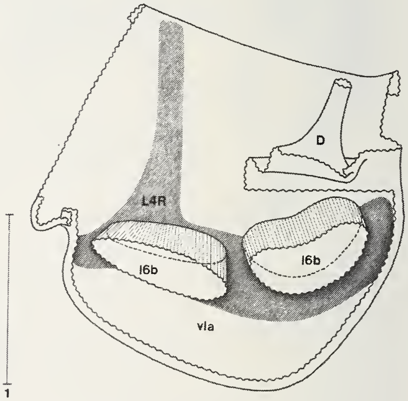

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Figs.186-189: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 1mm.

r2	**R3** – **cbe**-invagination: **R1F** (anterior margin), membrane, and **R2** (dorsal margin)	197, 198
r3	**R1F** (dorsal and central parts, posterior to articulation **A3**) – **R1J** (right margin)	197, 198, 199
r6	**R1F** (dorsal margin, on **rge**-groove) – dorsal wall of **fda**-lobe (in part on **R1J**)	196
b2	**L8** and membrane to the right of it (= right dorsal wall of **vla**-lobe) – membrane ventral to **R2**	184, 198
s1	**S9** left side (most anteriorly on apophysis **S9a**) – membrane anterior to **hla**-base	170, 173, 175, 185
s3	**S9** left side (anteriorly on apophysis **S9a**) – **L4R** (anteriormost part)	170, 173, 175, 188
s4	**S9** right side (anteriorly on and median to apophysis **S9a**) – **R3** (left anterior margin)	170, 173, 175, 199
s5a	**S9** left side (posteriorly and medially) – left ventral wall of genital pouch	173, 175
s5b	**S9** left side (posteriorly and quite laterally) – left wall of genital pouch	170, 173, 175
s6	**S9** right side (anteriorly on apophysis **S9a** and laterally) – **R3** (right anterior margin)	170, 173, 175, 199
s12	**S9** right side (anteriorly on apophysis **S9a**) – **L4R** (anteriormost part)	169, 173, 175, 188
p3 (pair)	**S9** – rectum (ventral wall)	169, 173
p4 (pair)	**T9** (lateral anterior margin, also extending onto paratergite **T9p**) – membrane far anterior to **Pv**-sclerite; muscles on both sides divided into three bundles (except for their ventralmost parts)	169, 170
p5 (pair)	**T10** (lateralmost anterior margin) – **Pv**-sclerite	169
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin)	169, 172
p7 (pair)	Membrane anterior to **Pv**-sclerite – membrane (far) anterior to contact **A99*** between paratergite **T10p** and paraproct **Pp**	170

5.11. *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae)

Left complex

Sclerite **L4K** (fig.205, 208-210) lies in the left wall. Its posterior part partly encloses the (retracted) hook **hla** (fig.209, 210) and its sclerite **L3**. The highly complicated **L2**-sclerite is in the center of the left complex (fig.210-215). Its anterior part forms a tube-like apodeme (**lve**-apodeme = anterior part of **lve**-pouch), on which the **nla**-bulge rests. At the left base of the **lve**-apodeme **L2** forms, together with parts of **L4** (**L4N**), a stout sclerite ring (fig.211, 212) bearing two processes: **pda** and **paa** (fig.209, 211, 214). From the right

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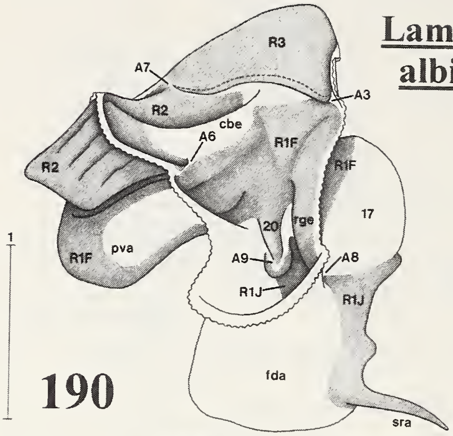
⟶ p.120

Figs.190-195: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **190:** Right phallomere in dorsal view. – **191:** Right phallomere in left-dorsal (somewhat anterior) view. – **192:** Right phallomere in left-ventral view. – **193:** Right phallomere in right-ventral view; membrane 17 largely removed. – **194:** Right phallomere in ventral (somewhat posterior) view. – **195:** Right phallomere in right-ventral view; most elements shown in fig.193 removed. – Scale: 1mm.

Lamproblatta albipalpus



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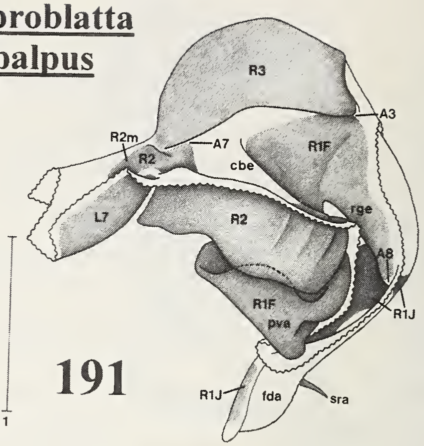

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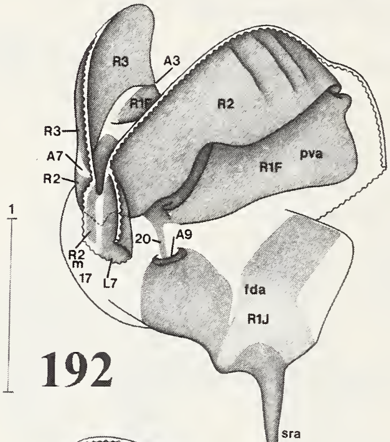

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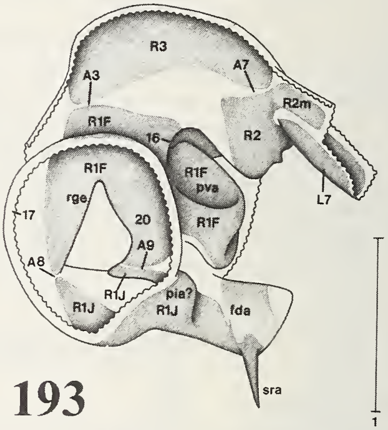

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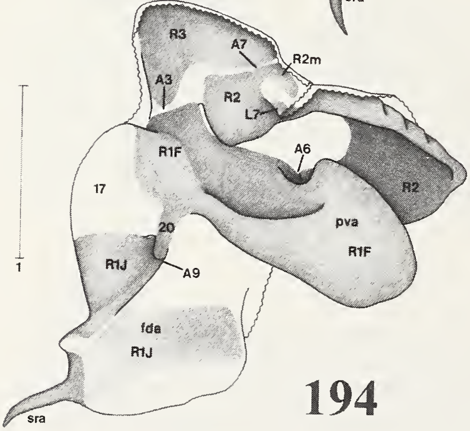

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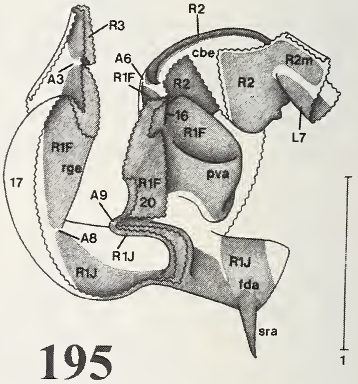

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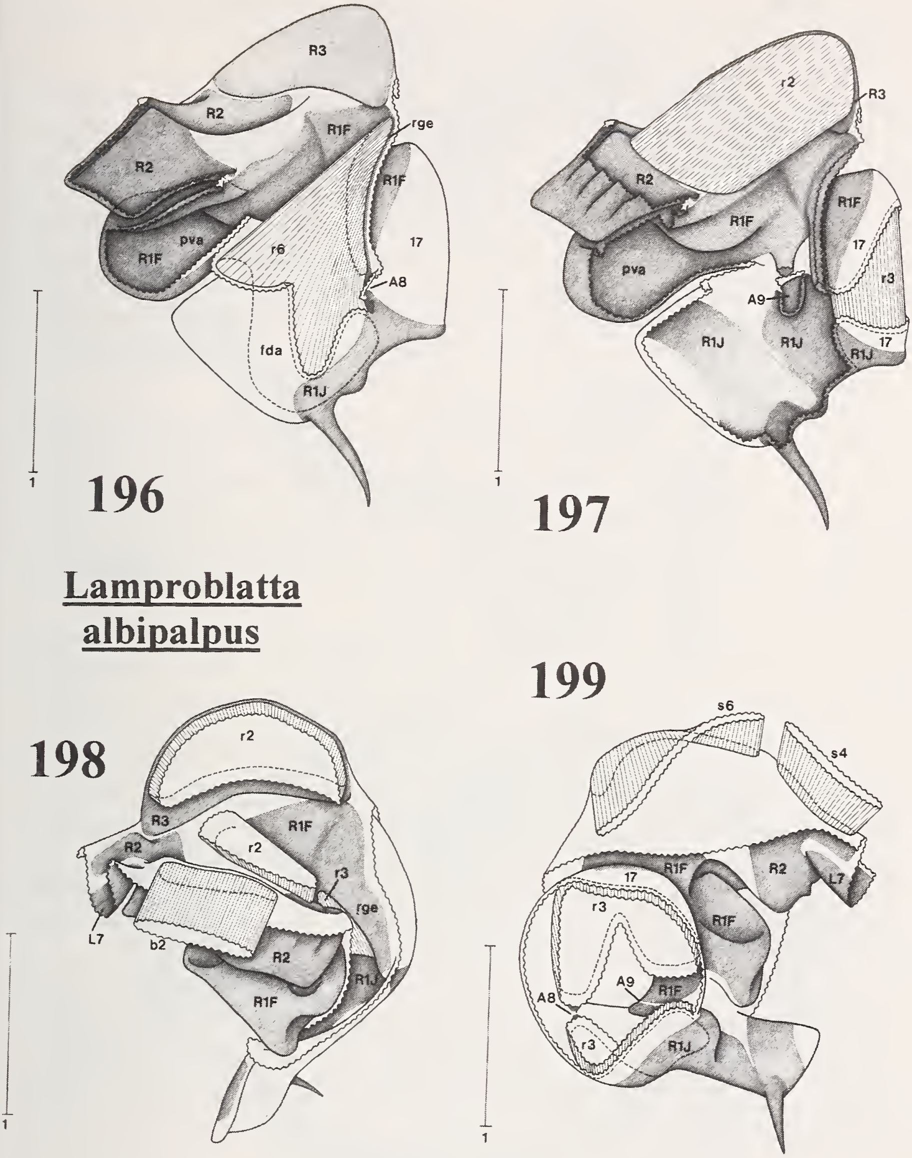


Figs.196-199: *Lamproblatta albipalpus* (Blattaria, Blattidae, Lamproblattinae) – **196:** Right phallomere in dorsal view; with muscle r6; some dorsal elements removed. – **197:** Right phallomere in dorsal view; with some muscles; dorsal elements more extensively removed than in fig.196. – **198:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles. – **199:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.193; membrane 17 cut open to show muscle r3 (cut through). – Scale: 1mm.

base of the **lve**-apodeme **L2** extends to the right to form a curved plate-like sclerotisation (fig.212-214). The large lobe **vla**, with sclerite **L4G** in its ventral wall (fig.205), is the ventralmost part of the left complex.

L4K consists of a plate-like, dorsoventrally curved posterior and a bulge-like (**nla** in fig.206, 209; veiled by membrane in fig.208) anterior part (fig.209, 210), which are only narrowly connected (fig.205). The dorsal wall to the right of **L4K** is membranous; its central part is depressed ventrad and anteriad (**pne** in fig.208, 209). The **hla**-hook is evaginated from the left posterior wall of the left complex (fig.210, 212). The distal half of **hla** is sclerotised by **L3**, which is rather weak except for its distalmost part. The basal membranous half of the **hla**-hook (**30** in fig.210-212) can be introverted and **hla** can thus be deeply retracted into the left complex (this state is shown in the figures). To the right of the **hla**-base the posterior wall of the left complex folds inwards (**fpe** in fig.210-213) – separating the area of **hla** from the area dominated by **L2** (fig.211).

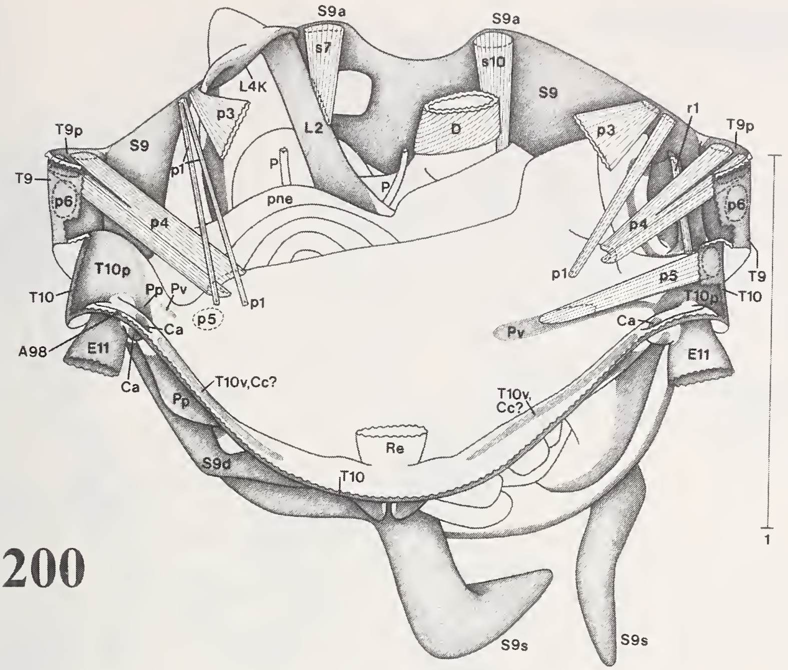
The **lve**-apodeme has its entire dorsal wall (fig.210, 211) and the margins of its ventral wall (fig.211, 225) sclerotised by **L2**. The sclerotised cuticle is considerably thickened (cross-sections in fig.211-215). The top of the **lve**-apodeme and the **nla**-process are firmly connected (two areas of the internal surface of the cuticle adhere to each other). The **lve**-apodeme is the narrow anterior part of a **lve**-pouch, which posteriorly expands to the right. At the base of the **lve**-apodeme, **L2** forks into a left and a right branch (immediately posterior to the cross-section through **lve** in fig.213).

The left branch bears a node-like apodeme (**29** in fig.212, with a tuft of fine cuticular threads) and forms the sclerite-ring mentioned above (fig.211-213). This ring is slightly sunken anteriad into the left complex; the cuticle within the ring is evaginated to form the processes **paa** and **pda**, which are both sclerotised in their ventral walls only (fig.209, 214; the sclerotisations of both are connected with the basal ring). The membrane **31** in fig.211-214 is the area of contact between the bases of **paa** and **pda** (cut through in fig.214). Apart from **L2** (dorsal part of the ring, **paa**-sclerotisation), **L4** also contributes to this structure (**L4N**: ventral part of the ring, **pda**-sclerotisation). The left branch of **L2** has another posteriad-directed extension on its ventral side (**28** in fig.214, 215) which lies in the dorsal wall of another process (**gta** in fig.215, 216). The sclerotised cuticle of the left **L2**-branch is thickened in most of its parts (cross-sections in fig.212-215).

The right branch of **L2** broadens and extends far to the right, where it curves dorsad (fig.212-214). Posteriorly this upcurved part extends somewhat back to the left and is involved in some complicated cuticular foldings (near **32** in fig.211, compare fig.209-213). Posterodorsal to the right **L2**-branch there are some additional membranous in- and outfoldings (fig.210-213).

⟶ p.123

Figs.200,201: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **200:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, subanal lobes, paraprocts, Pv-sclerites, distal part of rectum, basal parts of cerci, and part of musculature. – **201:** Same as in fig.200, after removal of further parts of abdominal tergites 9 and 10 (especially T10v). Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Scale: 1mm.



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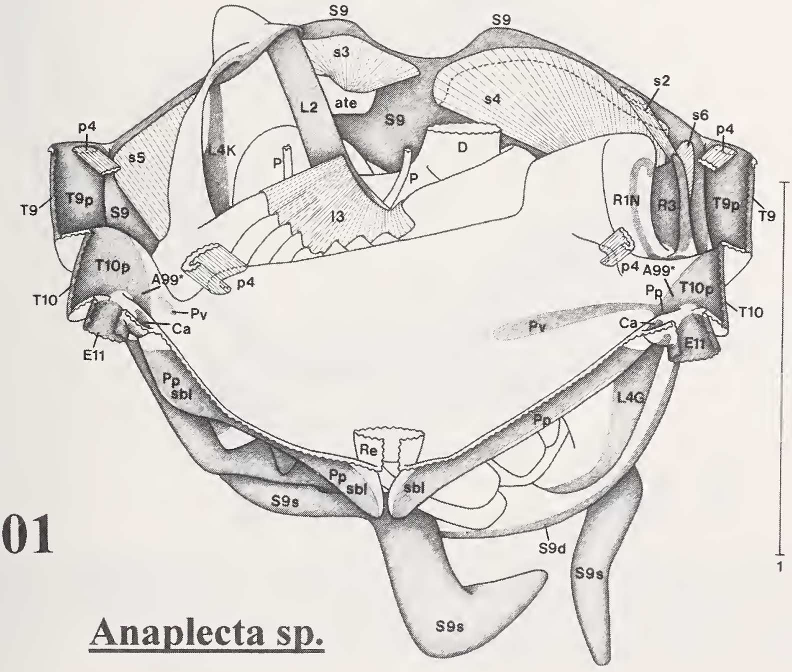
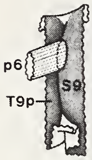


201

Anaplecta sp.

Anaplecta sp.



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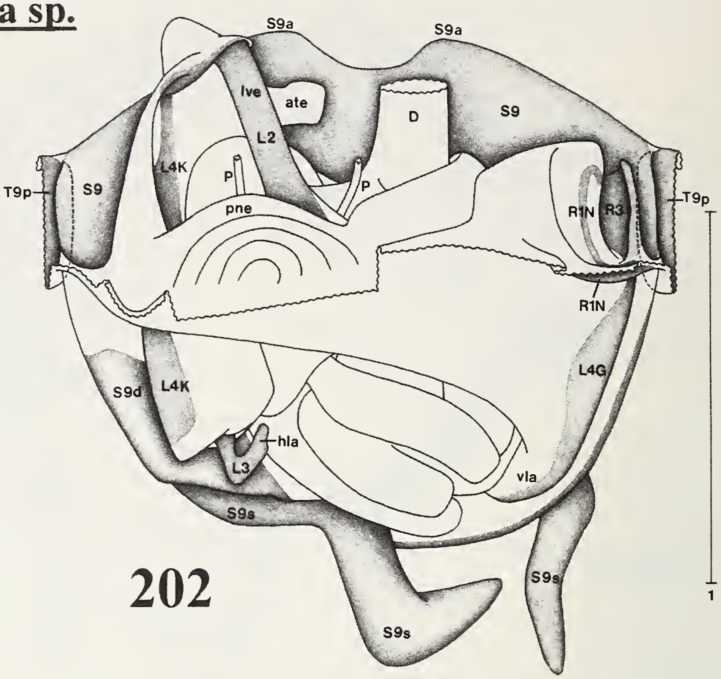

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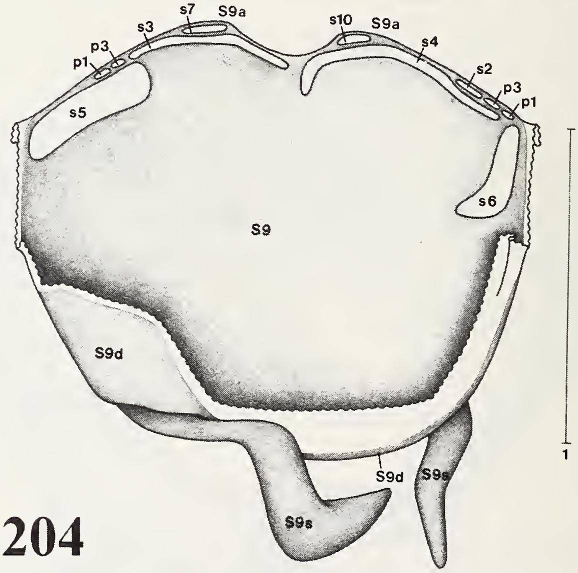

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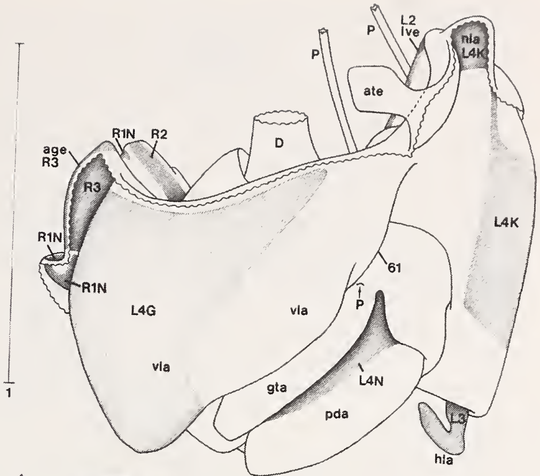
Figs.202-204: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **202:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **203:** Left margin of subgenital plate (compare fig.202); with insertion of muscle p6. – **204:** Subgenital plate in dorsal view; with insertion areas of muscles (except p6). – Scale: 1mm.

Anaplecta sp.

205



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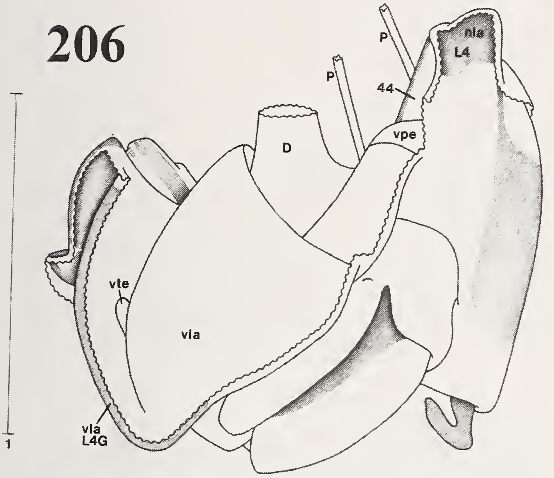

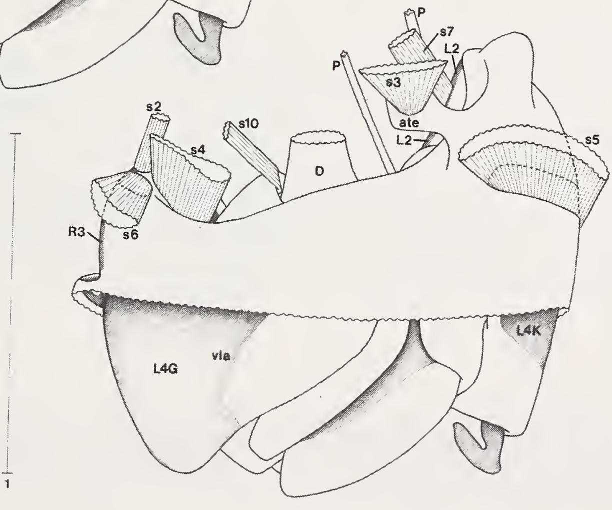

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The ejaculatory duct **D** opens anterior to the right **L2**-branch (fig.210, 211). In its dorsal wall there is a small outfolding (**goa** in fig.212). The ventral wall of the duct continues posteriad into the dorsal wall of a broad membranous outfolding **vfa** (fig.211, 215). The **vla**-lobe, with sclerite **L4G** in its ventral wall (fig.205; cut open in fig.206; fig.214-220) is another broad outfolding ventral to **vfa**. The right part of the **vla**-lobe curves dorsad (fig.208). The right dorsal wall of the **vla**-lobe has a broad and flat invagination **vte** (fig.206, 208, 209, 219) functioning as a tendon (muscle **l6b** in fig.221).

Two phallomere-gland ducts (**P** in fig.215, 216) open anterior to the ventral wall of the **gta**-process. Between the orifices there is a small infolding (**ipe** in fig.215-217). Anterior to the orifices the ventral wall has a broad membranous pouch (**vpe** in fig.209-214, 216-218). Anterior to **vpe** the **nla**-bulge with its **L4K**-sclerotisation adjoins (fig.218, 219). Posterior to **nla** the anteriormost ventral wall of the genital pouch forms a membranous pouch **ate** (fig.205, 208), which functions as a tendon (muscles **s3** and **l6a** in fig.222).

Right phallomere

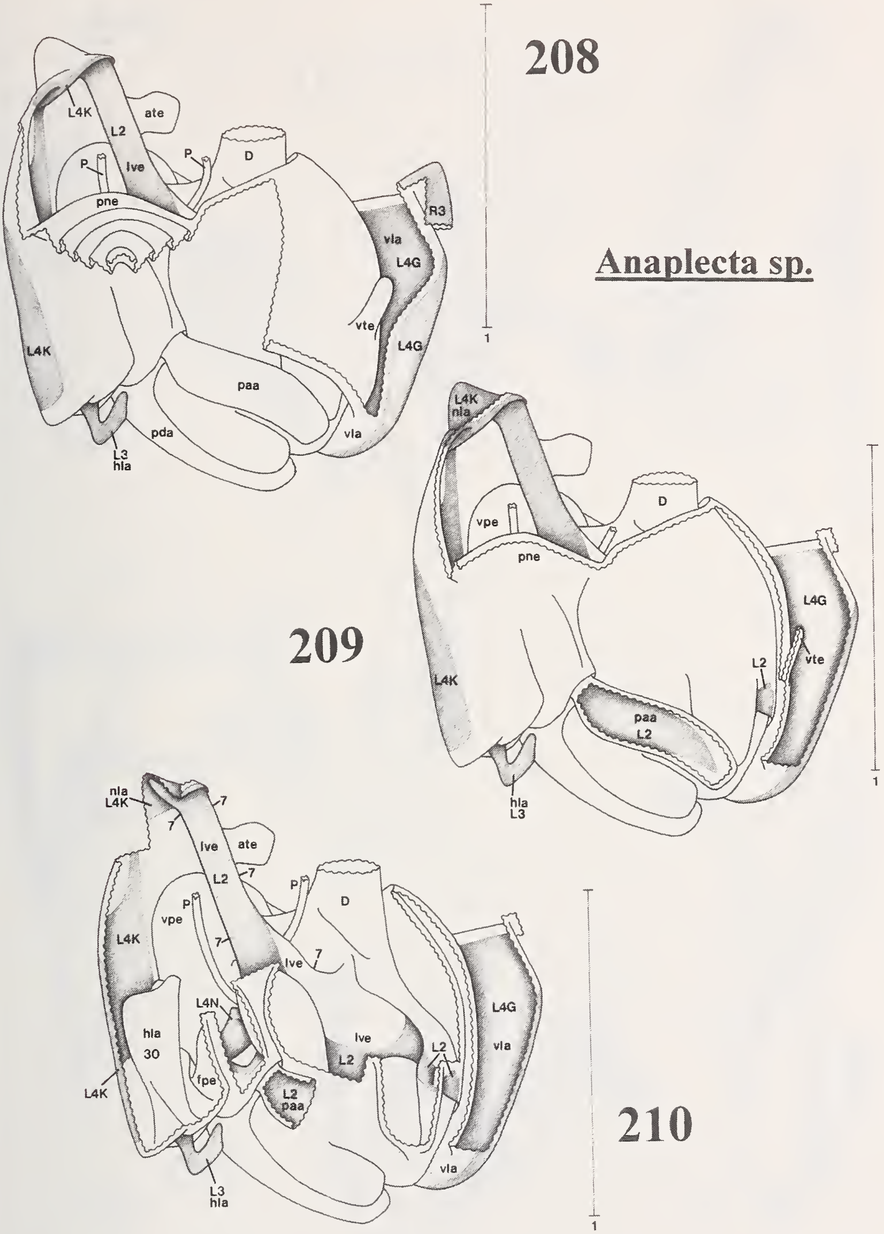
The triangular **R3**-sclerite occupies the anterior (right-)ventral wall (fig.226-229). The right and anterior margins of **R3** form a groove-like apodeme (**age** in fig.226, 229). Sclerite **R2** articulates with the left posterior margin of **R3** in two points (**A7** in fig.227-229). **R2** forms a ridge (fig.227, 228) with three bulges. Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad and anteriad to form a central invagination (**cbe** in fig.226-228; compare fig.229 and 230). Posterior to the right part of **R3** there adjoins the large sclerite **R1N**, and the two sclerites articulate (**A3** in fig.226, 227, 229). **R1N** occupies most of the posterior part of the right phallomere, the broad dorsal lobe **fda** (fig.226, 231). From behind the **A3**-articulation **R1N** has a long extension to the left (**34** in fig.226), which lies in the dorsal wall of the **cbe**-invagination. The left end of extension **34** turns back to the right like a hook, and it articulates with the left-dorsal end of **R2** (**A6** in fig.226, 227, 230). The **fda**-lobe bears a sclerotised bulge in its ventral wall (**33** in fig.227, 228, 231).

Subgenital plate and posterior abdominal segments

Fig.200, 201 (posterior segments); fig.204 (subgenital plate **S9**). Within the membrane extending anteroventrad from the posterior edge of tergite 10 **T10** there is a pair of ribbon-like sclerites (**T10v** or **Cc**?). Strip-like **Pv**-sclerites are present: The right one is well developed and connected with the paraproct **Pp** (or with paratergite 10 **T10p**?) laterally. The left one is very small and isolated. The articulations **A99** are missing (**A99*** in fig.201: paratergites **T10p** and paraprocts **Pp** have fused). The **Ca**-sclerites lie on curved bulges immediately median to the cercal bases. **Cb**- and **Cc**-sclerites are missing. The articulations **A98** are well-developed.

⟵ p.125

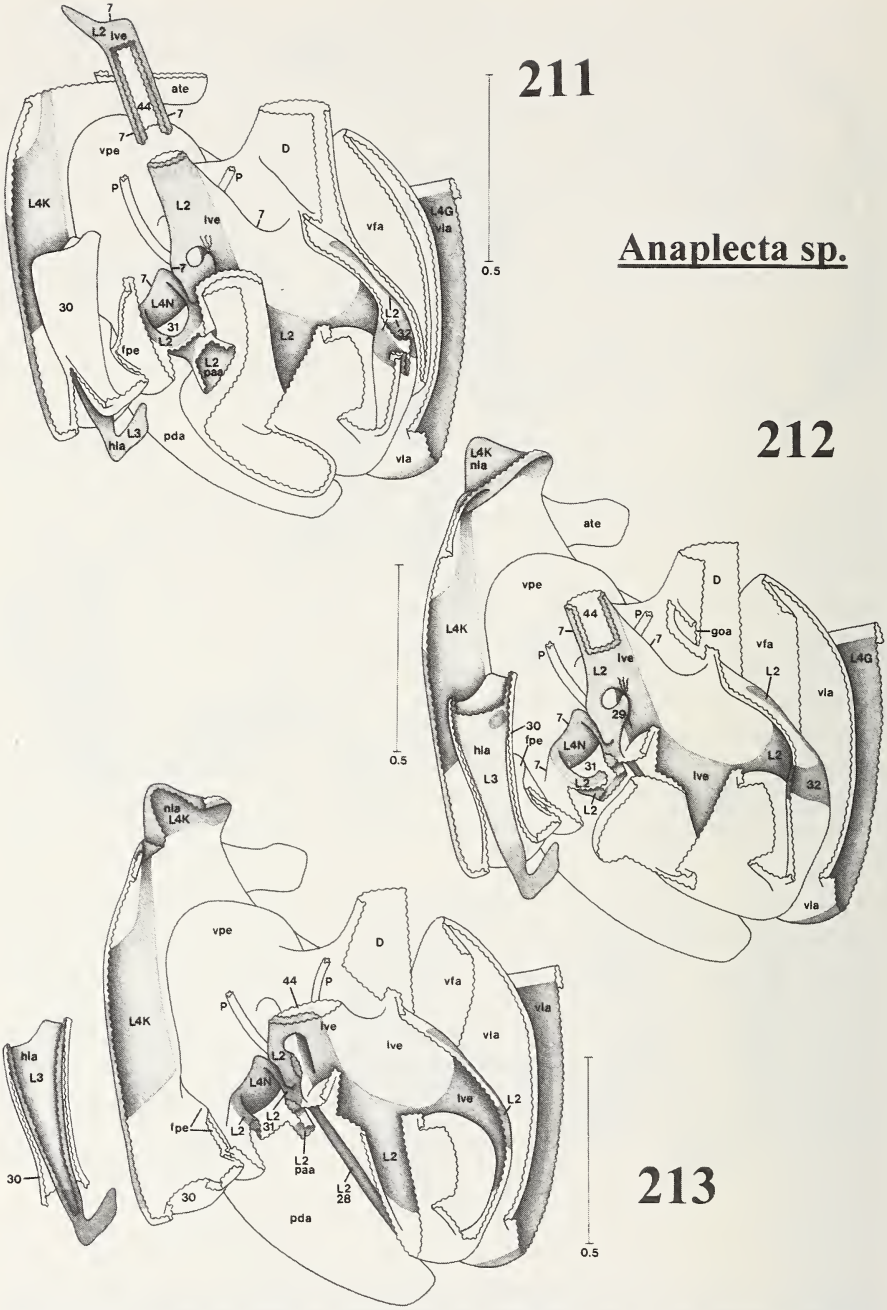
Figs.205-207: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **205:** Phallomere complex in ventral view. – **206:** Phallomere complex in· ventral view; some ventral parts removed (compare fig.205). – **207:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.205. – Scale: 1mm.



Anaplecta sp.

Figs.208-210: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **208:** Left complex in dorsal view. – **209,210:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.

Anaplecta sp.



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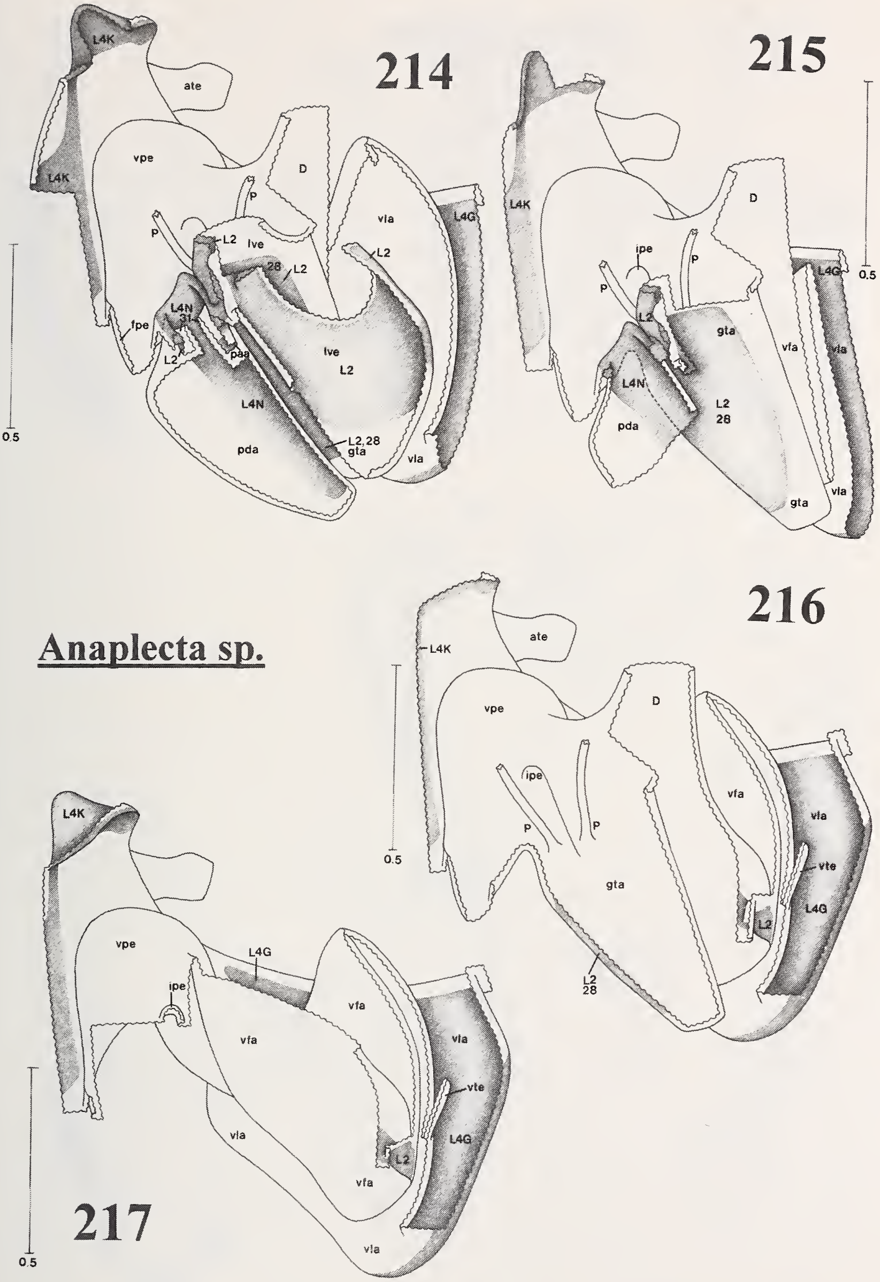
Figs.211-213: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.213: hla-hook separated from remainder of left complex. – Scale: 0.5mm.

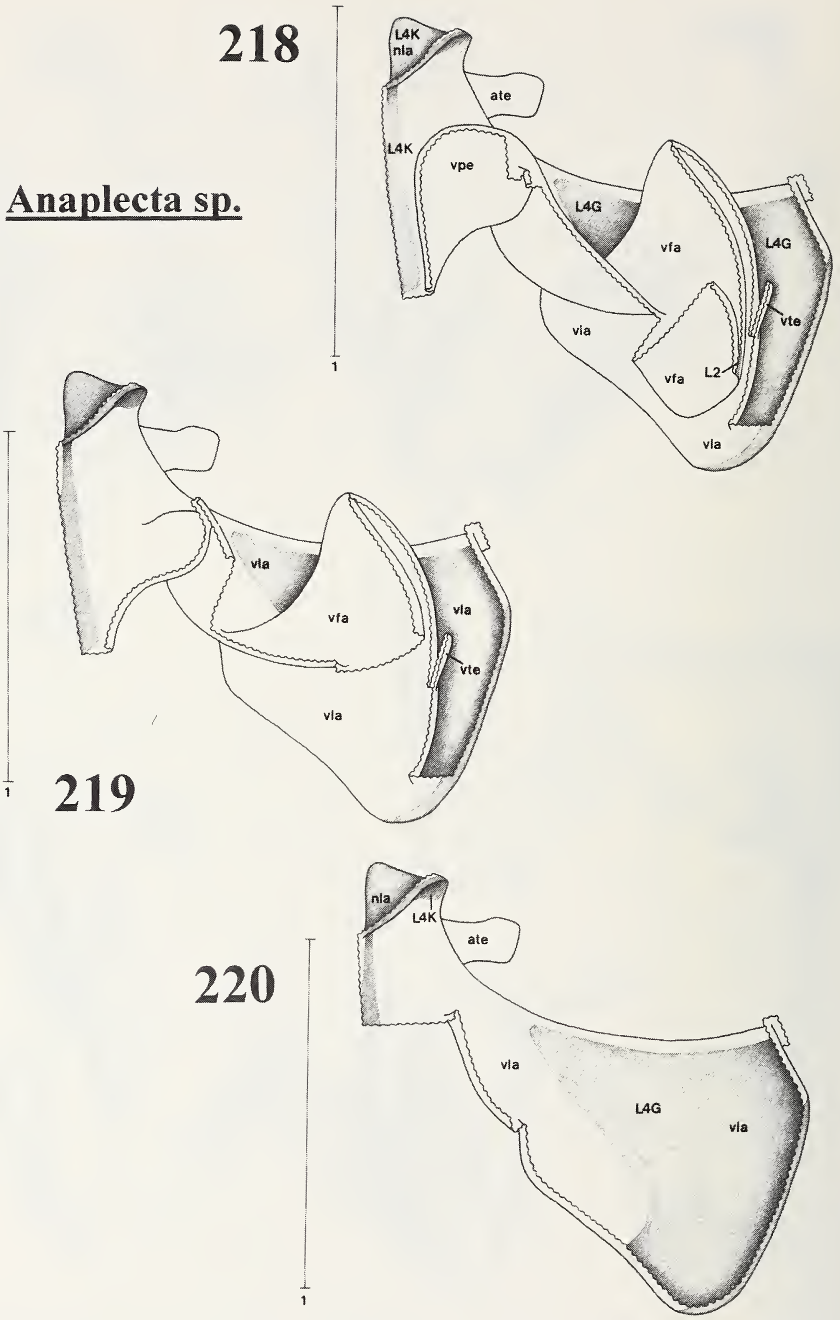
Anaplecta sp.



Figs.214-217: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 0.5mm.

Anaplecta sp.

218



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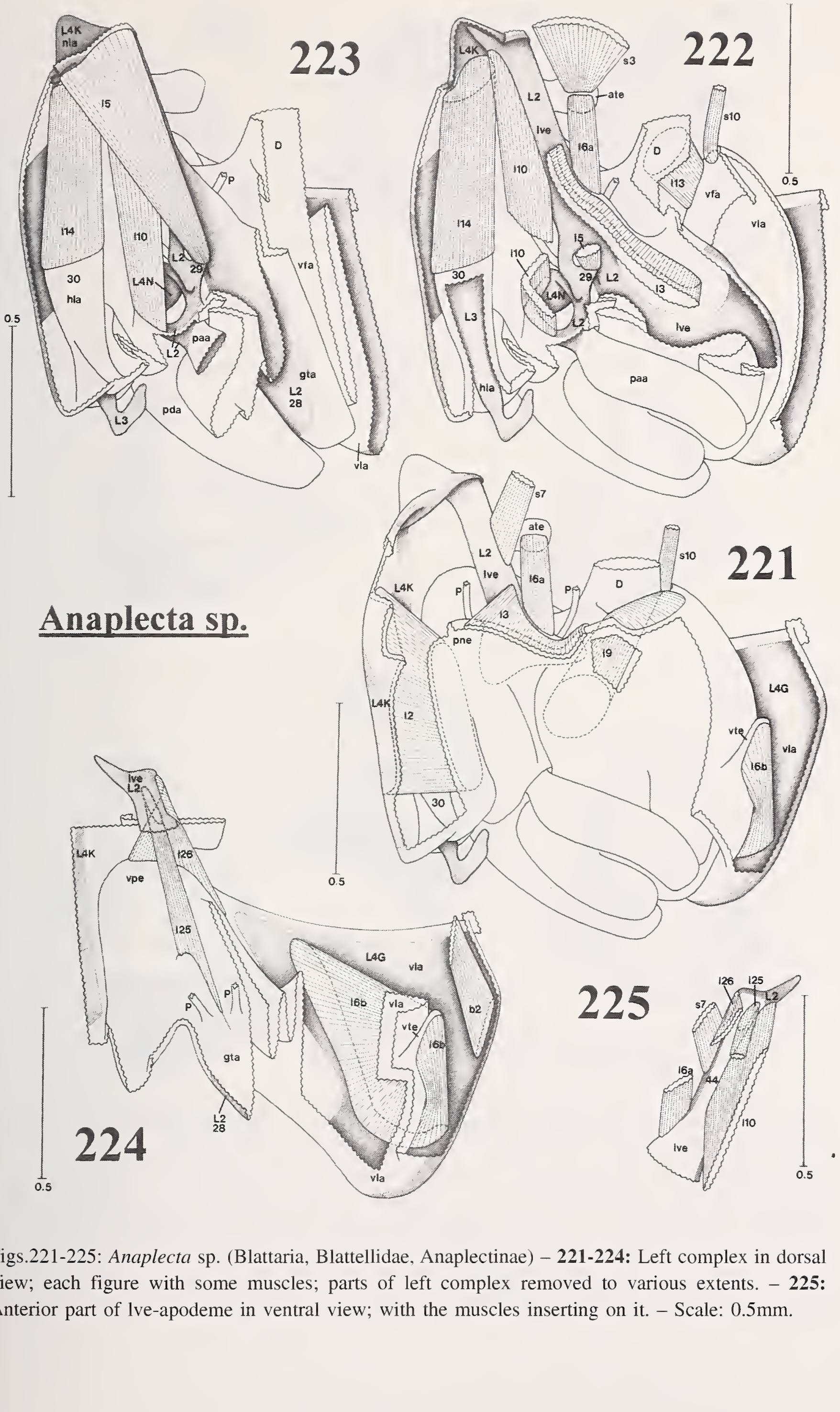
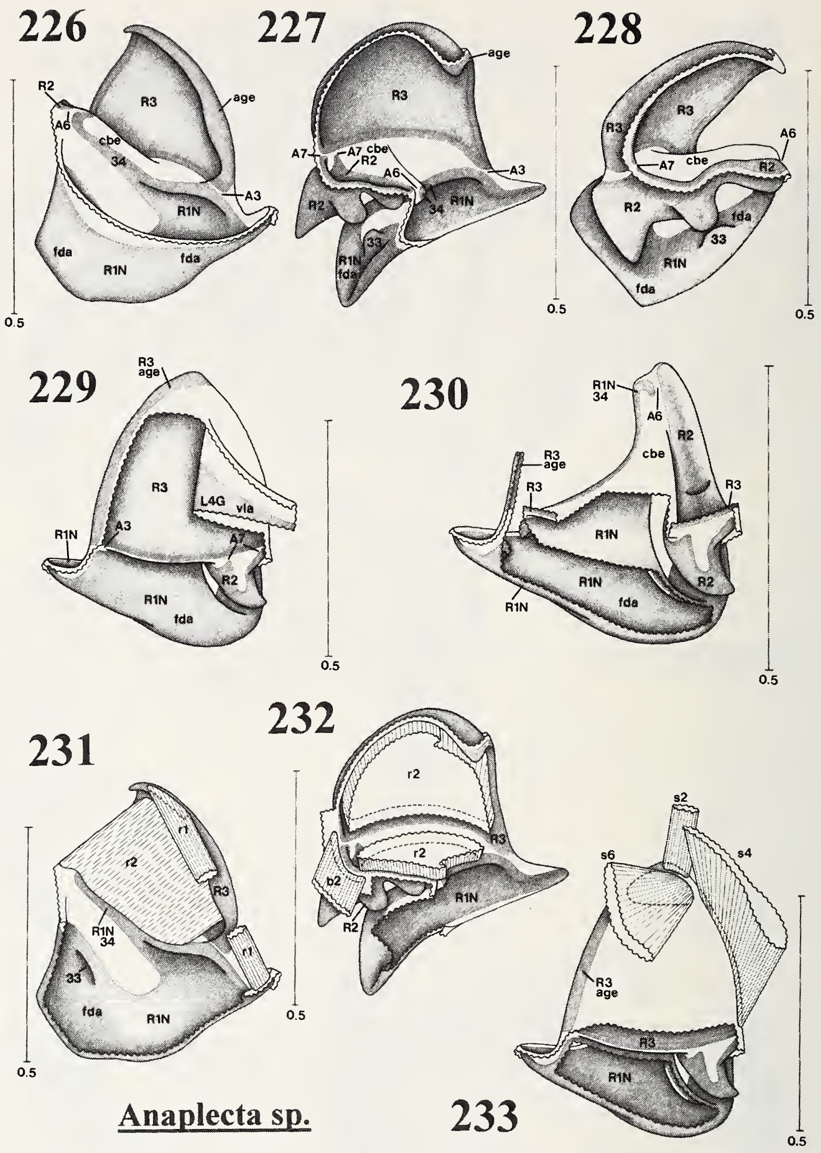
Figs.218-220: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.



Figs.221-225: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **221-224:** Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – **225:** Anterior part of lve-apodeme in ventral view; with the muscles inserting on it. – Scale: 0.5mm.



Figs.226-233: *Anaplecta* sp. (Blattaria, Blattellidae, Anaplectinae) – **226:** Right phallomere in dorsal view. – **227:** Right phallomere in left-dorsal (somewhat anterior) view. – **228:** Right phallomere in left-ventral view. – **229:** Right phallomere in right-ventral view; with transition to left complex. – **230:** Right phallomere in right-ventral view; most elements shown in fig.229 removed. – **231:** Right phallomere in dorsal view; with some muscles; some dorsal elements removed. – **232:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles; some dorsal elements removed. – **233:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.229. – Scale: 0.5mm.

Musculature

Muscles	Positions of insertions	in fig.
l2	Left dorsal wall of left complex (left part of **pne**-"pouch") – **L4K** (posterior part)	221
l3	Anterior central dorsal wall of left complex (anterior part of **pne**-"pouch") – **L2** and membrane to the right of **L2** (right dorsal wall of **lve**-pouch)	201, 221, 222
l5	**L4K** (anterior part, dorsal base of **nla**-process) – **L2** (on apodeme **29**)	222, 223
l6a	**ate**-tendon – **L2** (right edge of **lve**-apodeme)	221, 222, 225
l6b	**L4G** – **vte**-tendon in right dorsal wall of **vla**-lobe	221, 224
l9	Transversely within right dorsal wall of left complex	221
l10	**L2** (anterior left edge of **lve**-apodeme) – sclerite ring with **L4N** and **L2** at common base of processes **paa** and **pda**	222, 223, 225
l13	Ejaculatory duct **D** next to its opening (ventral wall) – bottom of infolding between lobes **vfa** and **vla**	222
l14	**L4K** (anterior part, ventral base of **nla**-process) – **hla**-hook (anterior margin of **L3**)	222, 223
l25	**L2** (anterior ventral wall of **lve**-apodeme) – **ipe**-infolding between openings of phallomere-gland ducts **P**	224, 225
l26	**L2** (anterior right edge of **lve**-apodeme) – anterior edge of **vpe**-infolding	224, 225
r1	**R3** (anterior right margin) – **R1N** (rightmost dorsal wall of **fda**-lobe)	200, 231
r2	**R3** – **cbe**-invagination: **R1N**-extension **34** (anterior margin), membrane, and **R2** (dorsal margin)	231, 232
b2	**L4G** (right margin) – membrane ventral to **R2** and **R3**	224, 232
s2	**S9** right side (laterally and anteriorly) – **R3** (central anterior margin)	201, 204, 207, 233
s3	**S9** left side (medially and anteriorly) – **ate**-tendon	201, 204, 207, 222
s4	**S9** right side (entire anterior margin) – **R3** (left margin)	201, 204, 207, 233
s5	**S9** left side (laterally and anteriorly) – left wall and left ventral wall of genital pouch	201, 204, 207
s6	**S9** right side (lateral margin) – anteriormost right ventral wall of genital pouch	201, 204, 207, 233
s7	**S9** left side (medially and most anteriorly) – **L2** (right edge of **lve**-apodeme)	200, 204, 207, 221, 225
s10	**S9** right side (medially and most anteriorly) – bottom of infolding between lobes **vfa** and **vla** (ventral to ejaculatory duct)	200, 204, 207, 221, 222
p1 (pair)	**S9** – membrane anterior to (right muscle) or median to (left muscle) **Pv**-sclerite; very delicate; left muscle in most cases divided into two bundles	200, 204
p3 (pair)	**S9** – rectum (ventral wall)	200, 204
p4 (pair)	**T9** (lateralmost anterior margin, also extending onto paratergite **T9p**) – membrane anterior to (right muscle) or anteromedian to (left muscle) **Pv**-sclerite; muscles on both sides divided into three bundles (except for their ventralmost parts)	200, 201

p5 (pair)	**T10** (lateralmost anterior margin) – on (right muscle) or median to (left muscle) **Pv**-sclerite	200
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral margin)	200, 203

5.12. *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae)

All figures are side-reversed and show mirror-images of the original structures. In the subsequent descriptions and in the homology discussions (chapter 6.) the terms “left” and “right” will also be exchanged. (This will be practised in other Plectopterinae, too: *Euphyllodromia, Supella*). The natural orientation is shown in fig.236b and 239b.

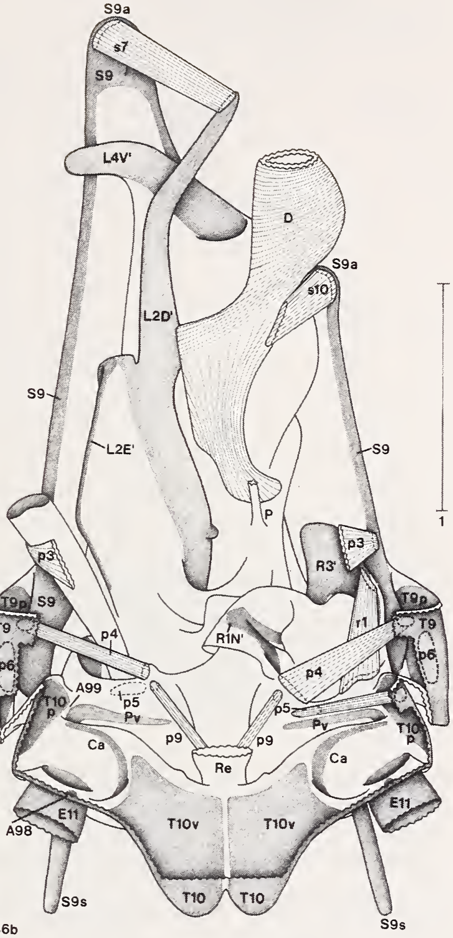
Left complex

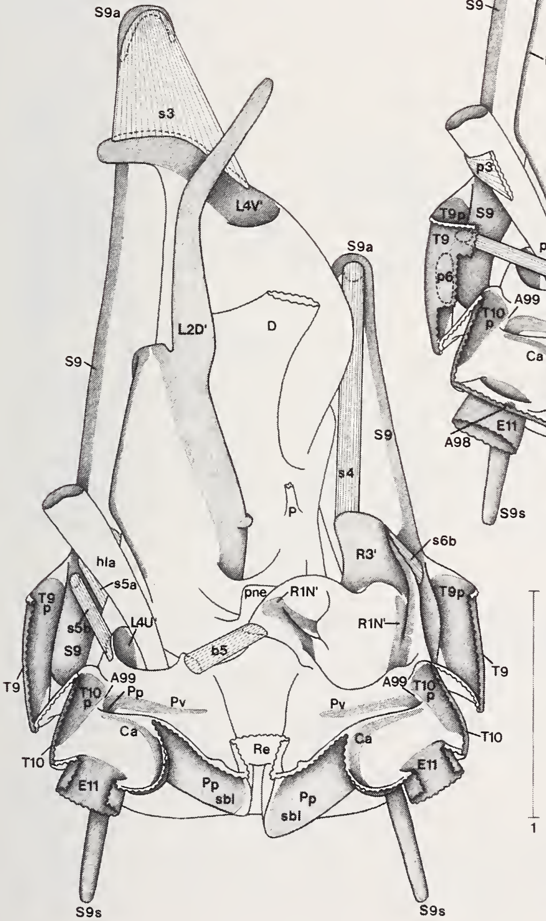
Sclerite **L1’** lies in the posterodorsal wall (fig.243). The **L2’**-sclerotisations (**L2D’, L2E’**) are in the center of the left complex (fig.242-244). The anterior part of **L2D’** forms a tube-like apodeme (**lve**-apodeme = anterior part of **lve**-pouch), to the right of which the ejaculatory duct (**D** in fig.242) opens. At the left base of this apodeme, **L2E’** forms, together with a **L4’**-sclerotisation (**L4N’**), a large trifid process **via** (fig.244, 245). In the anteriormost ventral wall of the left complex lies sclerite **L4V’**, which bears the whip-like process **nla** (fig.239a, 247). The left posterior edge of the left complex bears a long hook **hla** with its sclerite **L3’** (fig.242-244). The base of the hook is partly enclosed by the lateral sclerite **L4U’**.

The left posterior part of the left complex resembles a bulge whose left wall is sclerotised by **L4U’** (fig.242-244). The **hla**-hook is evaginated from the posterior wall of this bulge; its distal half is sclerotised by **L3’**. The membrane of the basal half (**30** in fig.242-244) can be introverted, and **hla** can be retracted in the same way as in *Anaplecta* (all figures show **hla** in its retracted state). Right-ventral to the **hla**-base the posterior wall of the left complex folds inwards (**fpe** in fig.242-245): This **fpe**-fold separates the area of **hla** from the other parts of the left complex. The dorsal wall to the right of **hla** contains a bristle area (**35** in fig.242). Ventral to this area there is a flat pouch invaginated to the anterior (**pne** in fig.242, 243). The ventral wall of the **pne**-pouch is sclerotised by the anterior part of **L1’**. The cup-shaped posterior part of **L1’** occupies a bulge-like process (**dca** in fig.243, 244) beset with setae. Beneath the **dca**-process there is a membranous lobe (**cla** in fig.244). Anteroventral to the **cla**-lobe the cuticle is again evaginated: The posterior end of sclerite **L2D’** forms a bifid process (**psa** in fig.244-246).

Figs.234,235: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – **234:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, subanal lobes (covered), paraprocts (covered), Pv-sclerites, distal part of rectum, basal parts of cerci, and part of musculature. – **235:** Same as in fig.234, after removal of further parts of abdominal tergites 9 and 10 (especially T10v). Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Scale: 1mm.

234





Nahublattella sp.

235

The whole central part of the left complex is invaginated anteriad to form a large pouch (**lve** in fig.242-246; the edges along the bottom of this **lve**-pouch are labelled **7** in fig.242). This invagination contains the **lve**-apodeme (middle part; with the **L2D'**-sclerotisation), the **via**-process (left side), and the terminal part of the ejaculatory duct **D** (right side). The **lve**-apodeme is completely sclerotised by **L2D'** – except for a membranous stripe (**44** in fig.239a, 243, 245) in its ventral wall. At the base of the **lve**-apodeme the **lve**-pouch broadens. Here, **L2D'** has a short extension to the left (**36** in fig.239a, 243-246) and a long ventral extension to the posterior (**28** in fig.245, 246, which lies in the ventral wall of the **lve**-pouch). The main part of **L2D'**, however, extends far posteriad within the dorsal wall of the **lve**-pouch (fig.242); it bears a small apodeme (**37** in fig.242, 245), and its posteriormost part sclerotises the **psa**-process. Along its right margin this main part of **L2D'** folds ventrad and back to the left (towards edge **38** in fig.245; compare fig.244) to form a shallow sclerite groove. Along edge **38** the cuticle turns to the right again and continues into the dorsal wall of the ejaculatory duct (**D** in fig.244, 245). The ejaculatory duct opens from the right side into the **lve**-pouch (fig.242-246). The phallomere-gland (**P** in fig.242) opens posterior to the dorsal wall of the ejaculatory duct.

The **via**-process evaginates posteriad from the left wall of the **lve**-pouch (fig.244; in fig.241 **via** is isolated and shown in ventral view). Distally **via** branches into three spines **paa**, **pda**, and **vsa**. **via** has a basal and a distal sclerite separated by a membranous ring (**39** in fig.241, 244, 245; sclerites not termed separately). The basal sclerite is roughly cylindrical (fig.244), with a deep recess at its ventral anterior margin (fig.241, 245). Ventrally it bears the **vsa**-spine. At its right anterior margin it articulates with extension **36** of sclerite **L2D'**

——→ p.137

Figs.236-238: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures except 236b show mirror-images of the original preparations. – **236a:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **236b:** Same as in fig.236a but smaller scale and natural orientation. – **237:** Subgenital plate in dorsal view; with insertion areas of muscles (including p6). – **238:** Dorsal sclerotisation S9d of subgenital plate; the part of the cuticle shown has been cut off from the subgenital plate along the line between the points labelled x (compare x in fig.237). – Scale: 1mm.

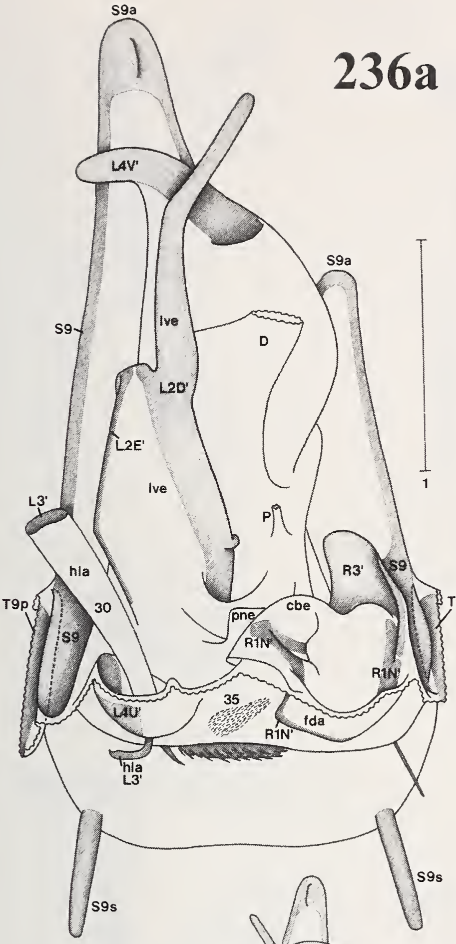
——→ p.138

Figs.239-241: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures except 239b show mirror-images of the original preparations. – **239a:** Phallomere complex in ventral view. – **239b:** Same as in fig.239a but smaller scale and natural orientation. – **240:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch completely retained (compare fig.239a), including dorsal sclerotisation S9d of subgenital plate and its muscles. – **241:** via-process (including paa, pda, and vsa, and sclerotisations L2E' and L4N') in ventral view. – Scale: 1mm.

——→ p.139

Figs.242-244: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – **242:** Left complex in dorsal view. – **243,244:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.244: hook hla and adjacent areas as well as retained parts of process dca with sclerite L1' separated from remainder of left complex. – Scale: 1mm.

Nahublattella sp.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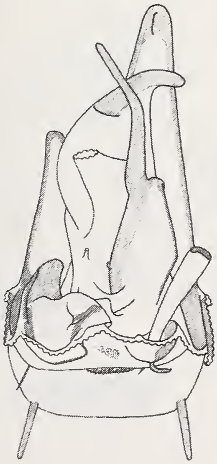
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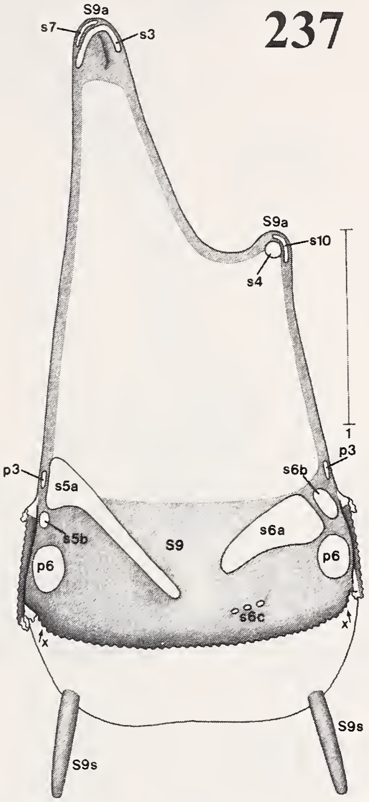
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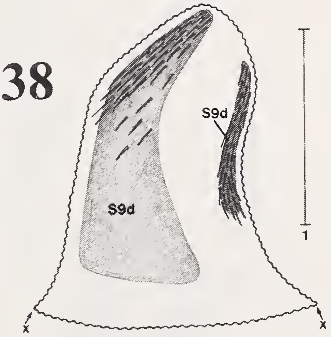
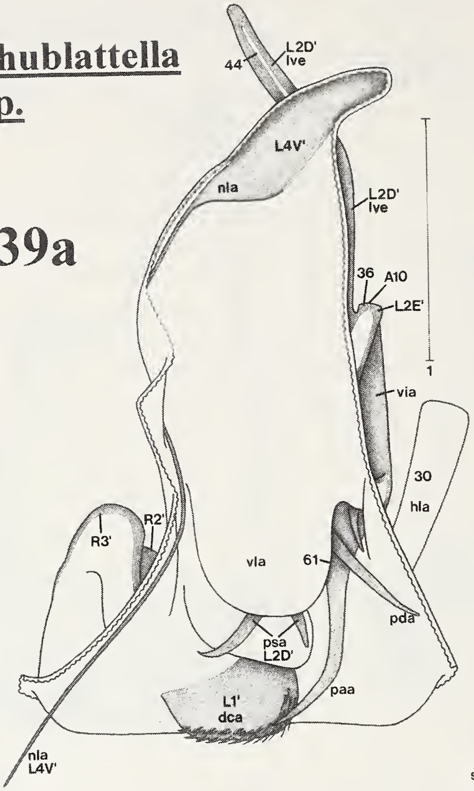


Nahublattella sp.

239a



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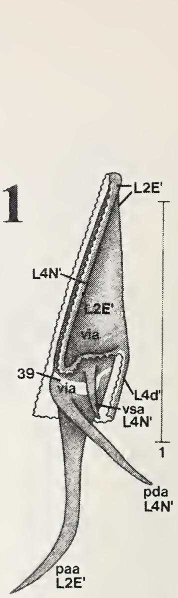

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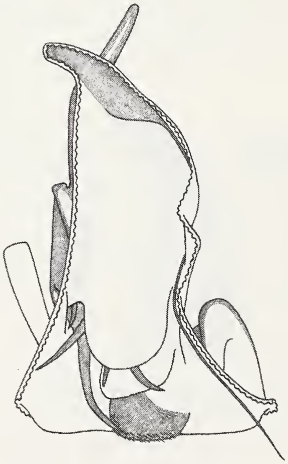

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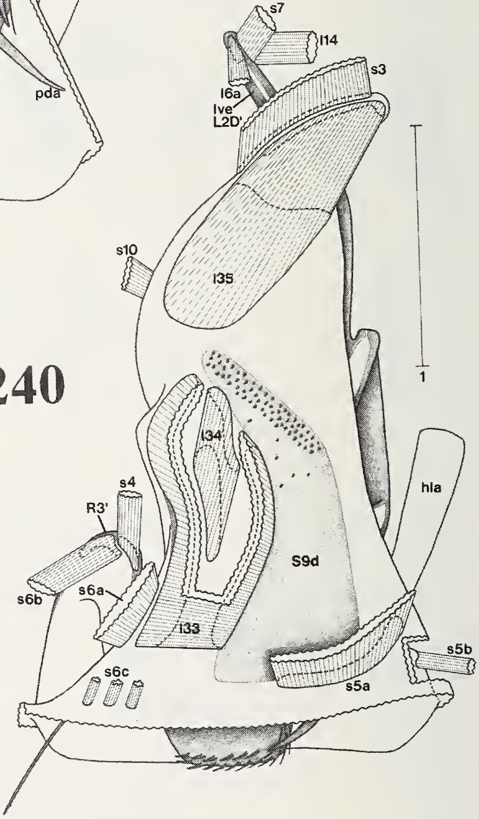

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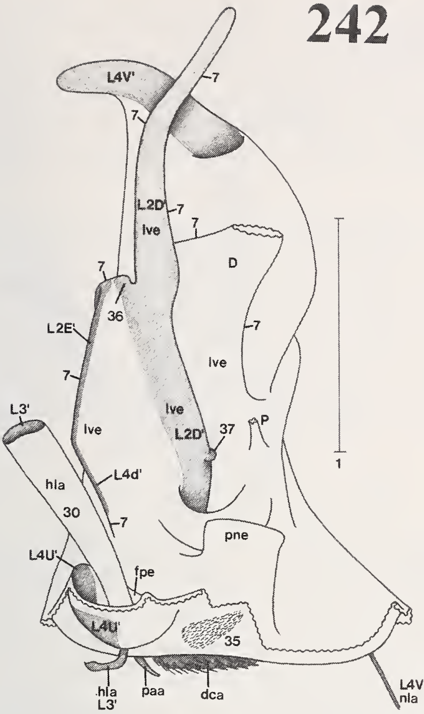

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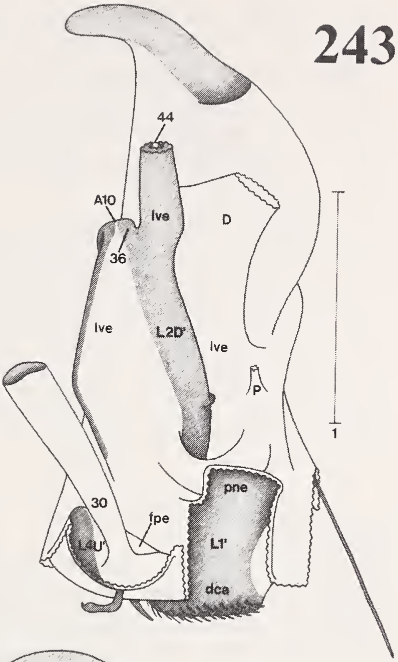

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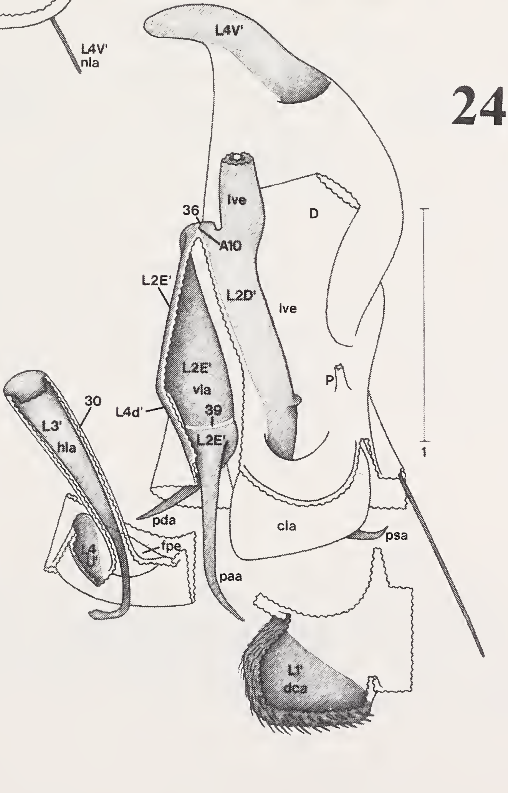


Nahublattella sp.

(**A10** in fig.243-245). At its left anterior margin it has a ribbon-like extension (**L4d'** in fig.241, 242, 244, 245) running posteriad along the left edge of the **lve**-pouch (**7** in fig.242). The distal sclerite branches into the sclerotisations of **paa** and **pda**. According to their assumed origin, the right-dorsal parts of the **via**-sclerotisation (including **A10** and **paa**) are designated **L2E'**, the left-ventral parts (including **L4d'** and **pda**) are designated **L4N'**. (The boundary between **L2E'** and **L4N'** is perpendicular to the division into a basal and a distal sclerite).

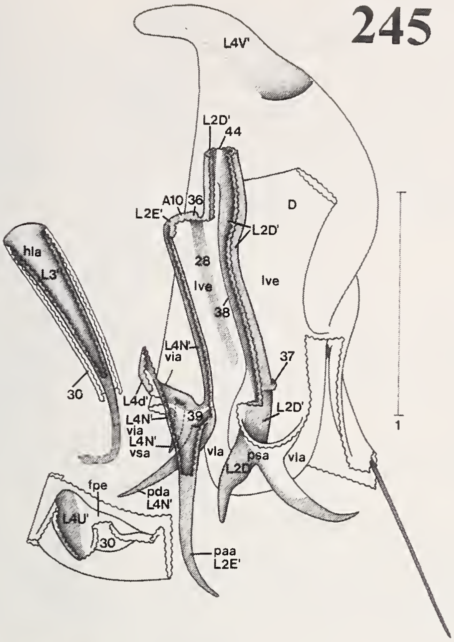
The ventral wall of the **lve**-pouch (fig.246, including the ventral wall of the ejaculatory duct **D**) is, except for the **L2D'**-extension **28** and the sclerotisations within the **lve**-apodeme, membranous. To the posterior it continues into the dorsal wall of a completely membranous lobe (**vla** in fig.245-247, 239a). The ventral wall of **vla** is part of the ventral wall of the left complex (fig.239a, 247). Sclerite **L4V'** (fig.239a, 247) occupies the anteriormost ventral wall; its right part extends onto and completely sclerotises the very long process **nla** (fig.239a, 247, 248). **nla** has a broad base but soon narrows to become whip-shaped.

Right phallomere

Sclerite **R3'** occupies the anterior (right-)ventral wall (fig.253-257); its lateral and anterior margins form a groove-like apodeme (**age** in fig.253, 256, 257). At its left and right ends **R3'** has extensions to the posterior (**40** and **41** in fig.253-257). Posterior to the left part of **R3'** sclerite **R2'** adjoins; the two sclerites have a broad articulation (**A7** in fig.255, 257). **R2'** is a plate of irregular shape, which as a whole slightly bulges posteriad (fig.254-257). It bears a tooth (**42** in fig.254, 255, 260) projecting dorsad and a horseshoe-shaped bulge with small spines (**43** in fig.254, 255, 260; seen from inside in fig.256, 258). Posterior to the central part of **R3'** the ventral wall of the right phallomere curves dorsad and slightly anteriad to form a narrow, groove-like central invagination (**cbe** in fig.253-256; compare fig.257 and 258), whose left-ventral wall is completely sclerotised by **R2'**.

Sclerite **R1N'** broadly articulates with the right posterior part of **R3'** (**A3** in fig.253, 255, 257). From the **A3**-articulation **R1N'** extends like an arch posteriad, leftward, and anteriad again; it occupies the margins of a broad dorsal lobe **fda** (fig.253), which is the posterior part of the right phallomere. The left anterior part of **R1N'** articulates with the left margin of **R2'** (**A6** in fig.253-255, 258); at **A6** **R1N'** turns sharply back to the right (**34** in fig.253), and its bristled terminal part lies on a bulge in the posterior dorsal wall of the **cbe**-invagination (**34** in fig.253, 255, 259).

Figs.245-248: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.245: hook hla and its base (with sclerite L4U') separated from remainder of left complex and from each other (compare fig.244); fig.248: only sclerite L4V' and process nla retained. – Scale: 1mm.



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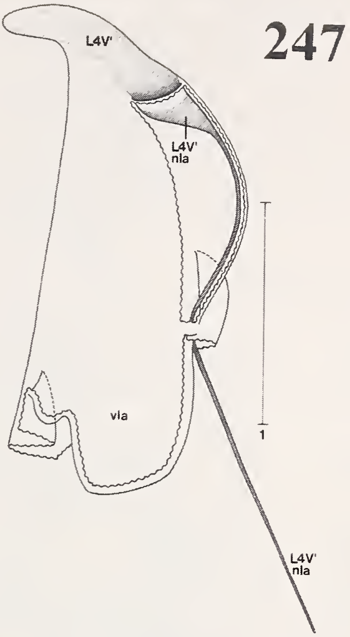

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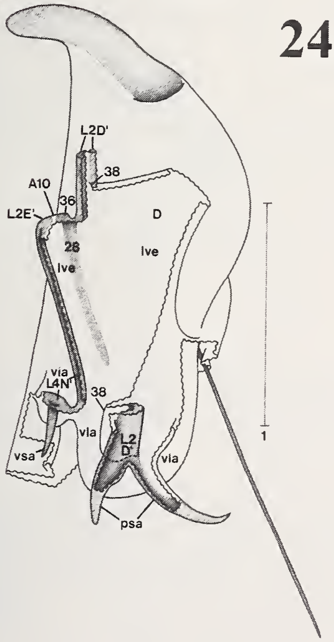

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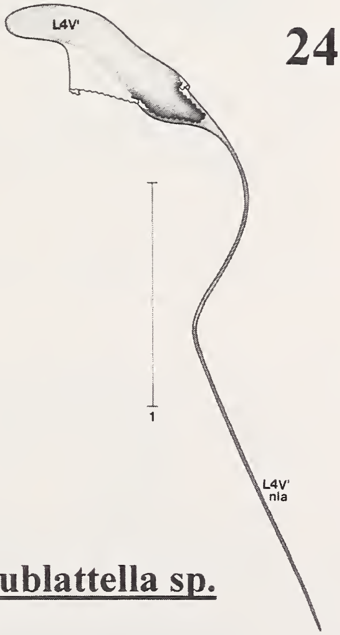


248

Nahublattella sp.

Subgenital plate and posterior abdominal segments

Fig.234, 235 (posterior segments); fig.237, 238 (subgenital plate **S9**). The dorsal sclerotisation **S9d** of the subgenital plate comprises two isolated sclerites (fig.238), which are asymmetrical and beset with stout setae. The entire tergite 10 **T10**, including its ventral part **T10v**, is divided along its midline. **T10v** is rather extensive. Strip-like **Pv**-sclerites are present; they are laterally connected with the paraprocts **Pp**. The **Ca**-sclerites are very long and lie on curved bulges immediately median to the cercal bases. **Cb**- and **Cc**-sclerites are missing. The articulations **A98** and **A99** are well-developed.

Musculature

Muscle	Positions of insertions	in fig.
l1	**L1'** (anteriorly on **pne**-pouch) – **L4d'** (= part of **L4N'**)	249
l2	Membranous basal part **30** of **hla**-hook – **L4U'** (dorsal part)	249
l3	**L1'** (anteriorly on **pne**-pouch) – **L2D'** (posteriormost part, on apodeme **37**)	250
l4	**L2D'** (posteriormost part, on apodeme **37**) – **L4U'** (ventral part)	249
l5	**L4V'** (left posterior margin) – **L2D'** (extension **28** in ventral wall of **lve**-pouch)	251
l6a	**L4V'** (right part) – **L2D'** (most anteriorly on **lve**-apodeme)	240, 250
l6b	Ventral wall of **vla**-lobe – dorsal wall of **vla**-lobe	251, 252
l9a	**L1'** (right wall of **pne**-pouch) – membrane to the right of **pne**-pouch	249
l9b	Transversely in dorsal wall of left complex (including bristle area **35**)	249, 261
l10	**L2D'** (anterior left edge of **lve**-apodeme) – left base of **via**-process (with **L4N'** and **L2E'**)	250
l14	**L2D'** (most anteriorly on **lve**-apodeme) – **hla**-hook (anterior margin of **L3'**)	240, 249, 250
l15	**L2D'** (anteriorly on **lve**-apodeme) – ejaculatory duct **D** next to its opening (dorsal wall)	249
l27	Outlet channel of phallomere-gland **P** – membrane to the right of **P**	249
l28	**L1'** (anterior right ventral wall of **pne**-pouch) – **L1'** (ventral anterior margin)	250
l29	Outlet channel of phallomere-gland **P** – ejaculatory duct **D** next to its opening (dorsal wall)	249
l30	Longitudinally in ventral wall of left complex	251

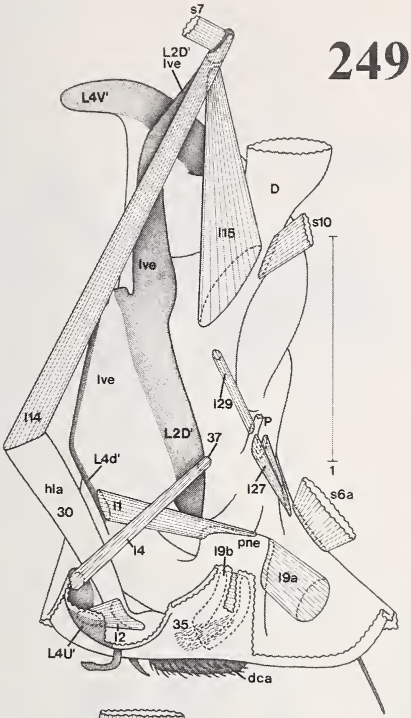
——→ p.143

Figs.249-252: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents. – Scale: 1mm.

——→ p.144

Figs.253-258: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – **253:** Right phallomere in right-dorsal view. – **254:** Right phallomere in right-dorsal view; dorsal elements largely removed. – **255:** Right phallomere in dorsal (somewhat anterior) view; membrane of cbe-invagination cut open to show parts of R2' lying beneath it (42, 43). – **256:** Right phallomere in left view. – **257:** Right phallomere in ventral view. – **258:** Right phallomere in ventral view; most elements shown in fig.257 removed. – Scale: 0,5mm.

249



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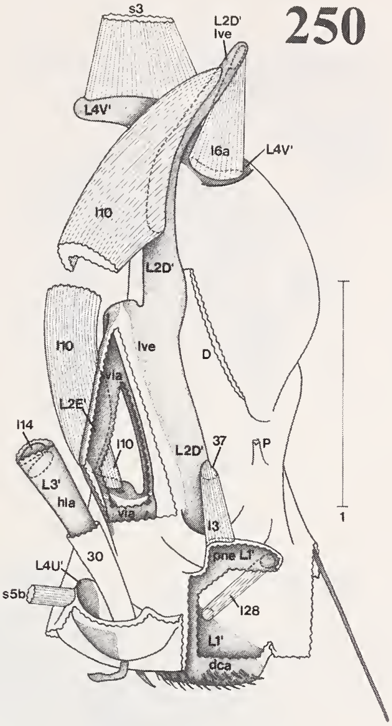

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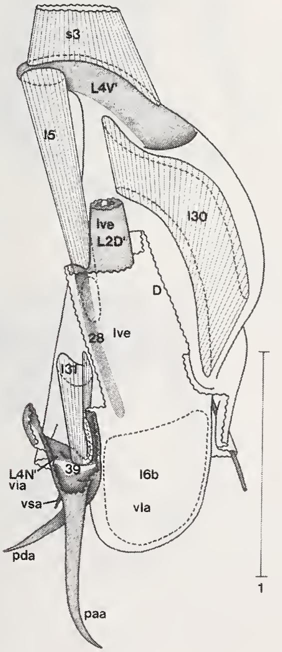

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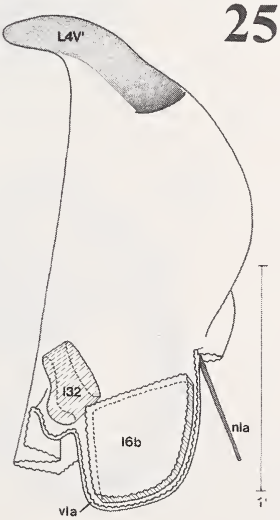
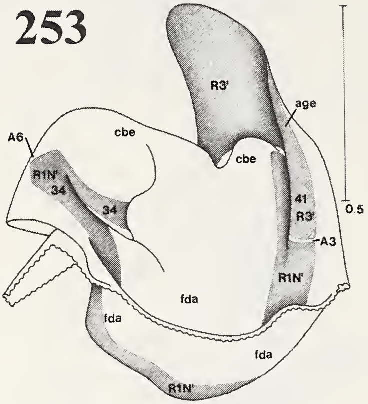


Nahublattella sp.

Nahublattella sp.

253



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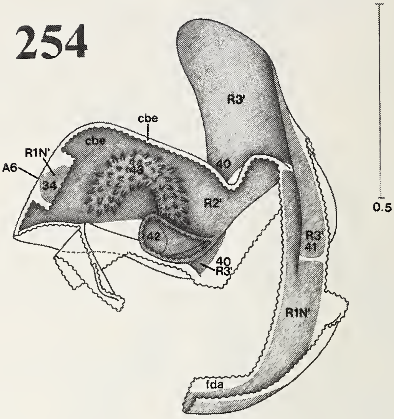

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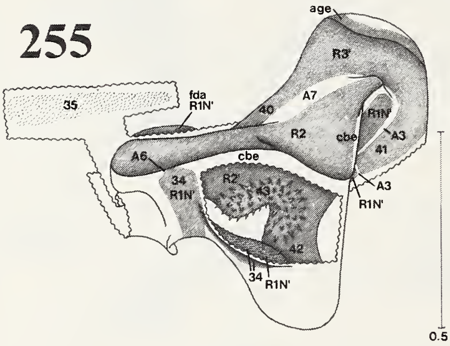

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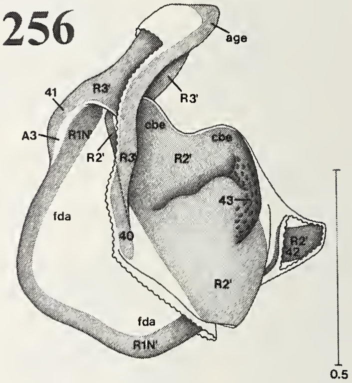

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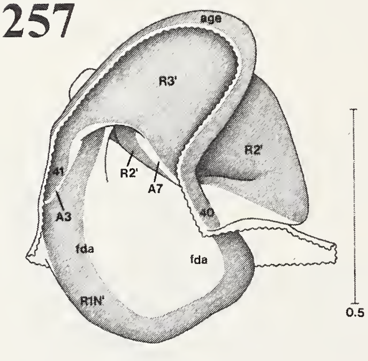

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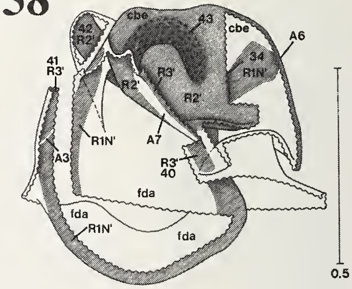

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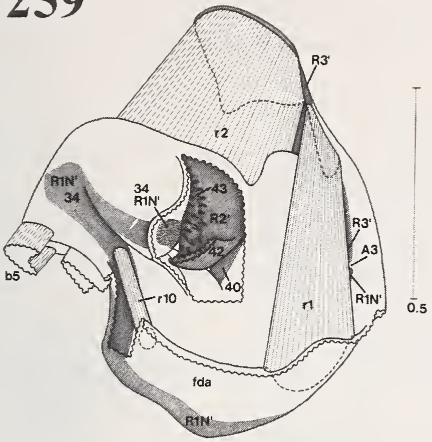

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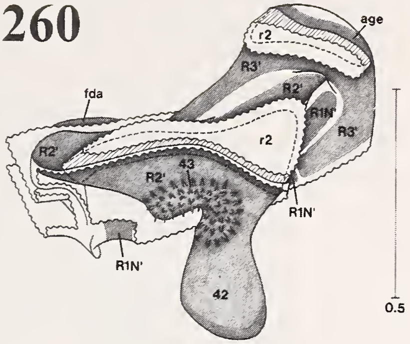

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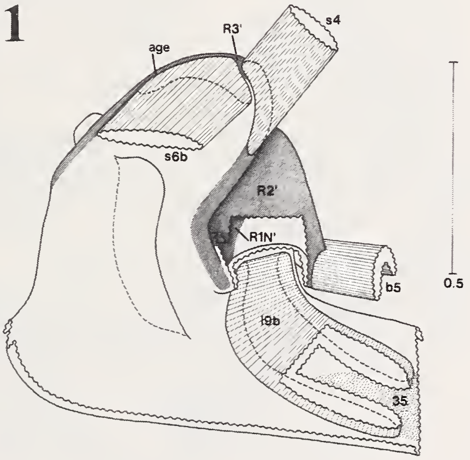


Nahublattella sp.

Figs.259-261: *Nahublattella* sp. (Blattaria, Blattellidae, Plectopterinae) – All figures show mirror-images of the original preparations. – **259:** Right phallomere in right-dorsal view; with some muscles; some dorsal elements removed; membrane of cbe-invagination cut open to show parts of R2' lying beneath it (42, 43). – **260:** Right phallomere in dorsal (somewhat anterior) view; with muscle r2; dorsal elements removed. – **261:** Right phallomere in ventral view; with some muscles; ventral wall of genital pouch much more complete than in fig.257 (compare fig.239a). – Scale: 0,5mm.

l31	Left ventral wall of left complex – ventral base of **via**-process (with **L4N'** and **L2E'**)	251
l32	Both insertions in left posterior ventral wall of left complex	252
l33	**S9d** (right sclerite) – **S9d** (left sclerite)	240
l34	Longitudinally in posterior ventral wall of genital pouch (membrane in between the two **S9d**-sclerites)	240
l35	Longitudinally in anterior ventral wall of genital pouch	240
r1	**R3'** (right margin) – membrane anterior to **R1N'** (rightmost dorsal wall of **fda**-lobe)	234, 259
r2	**R3'** – **cbe**-invagination: membrane and **R2'** (dorsal margin)	259, 260
r10	**R1N'** (left ventral wall of **fda**-lobe) – left dorsal wall of **fda**- lobe	259
b5	Anterior dorsal wall of left complex – leftmost part of right phallomere (to the left of and posterior to **R1N'**-part **34**)	235, 259, 261
s3	**S9** left side (most anteriorly on apophysis **S9a**) – **L4V'** (anterior margin)	235, 237, 240, 250, 251
s4	**S9** right side (most anteriorly on apophysis **S9a**) – **R3'** (anterior left margin)	235, 237, 240, 261
s5a	**S9** left side (far posteriorly; laterally and medially) – left ventral wall of genital pouch	235, 237, 240
s5b	**S9** left side (far posteriorly and laterally) – left wall of genital pouch, next to **L4U'**	235, 237, 240, 250
s6a	**S9** right side (far posteriorly) – right ventral wall of genital pouch, near right margin of left complex	237, 240, 249
s6b	**S9** right side (far posteriorly and laterally) – **R3'** (anterior right margin)	235, 237, 240, 261
s6c	**S9** right side (very far posteriorly and medially) – right ventral wall of genital pouch; composed of several delicate bundles	237, 240
s7	**S9** left side (most anteriorly on apophysis **S9a**) – **L2D'** (most anteriorly on **lve**-apodeme)	234, 237, 240, 249
s10	**S9** right side (most anteriorly on apophysis **S9a**) – ejaculatory duct **D** (right wall)	234, 237, 240, 249
p3 (pair)	**S9** – rectum (ventral wall)	234, 237
p4 (pair)	**T9** (lateral anterior margin) – membrane far anterior to **Pv**-sclerite (far medially)	234
p5 (pair)	**T10** (lateralmost anterior margin) – membrane anterior to **Pv**-sclerite	234
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral part)	234, 237
p9 (pair)	Membrane anterior to **Pv**-sclerite – membrane beneath posterior part of rectum	234

5.13. *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae)

Left complex

The left complex is not as complicated as in the previous species and contains only few sclerotisations. A deep infolding from the posterior (**fpe** in fig.268-271) divides the left complex into a left part with the retractable **hla**-hook and its **L3**-sclerite and a right part with the long **L2**-sclerite.

The left part has the shape of a bulge. The **hla**-hook evaginates from the posterior wall of the bulge; when retracted, **hla** lies in the center of the bulge (fig.268, 269; all figures show **hla** in the retracted state). The distal half of **hla** is sclerotised by **L3**, which becomes

262

Parcoblatta lata

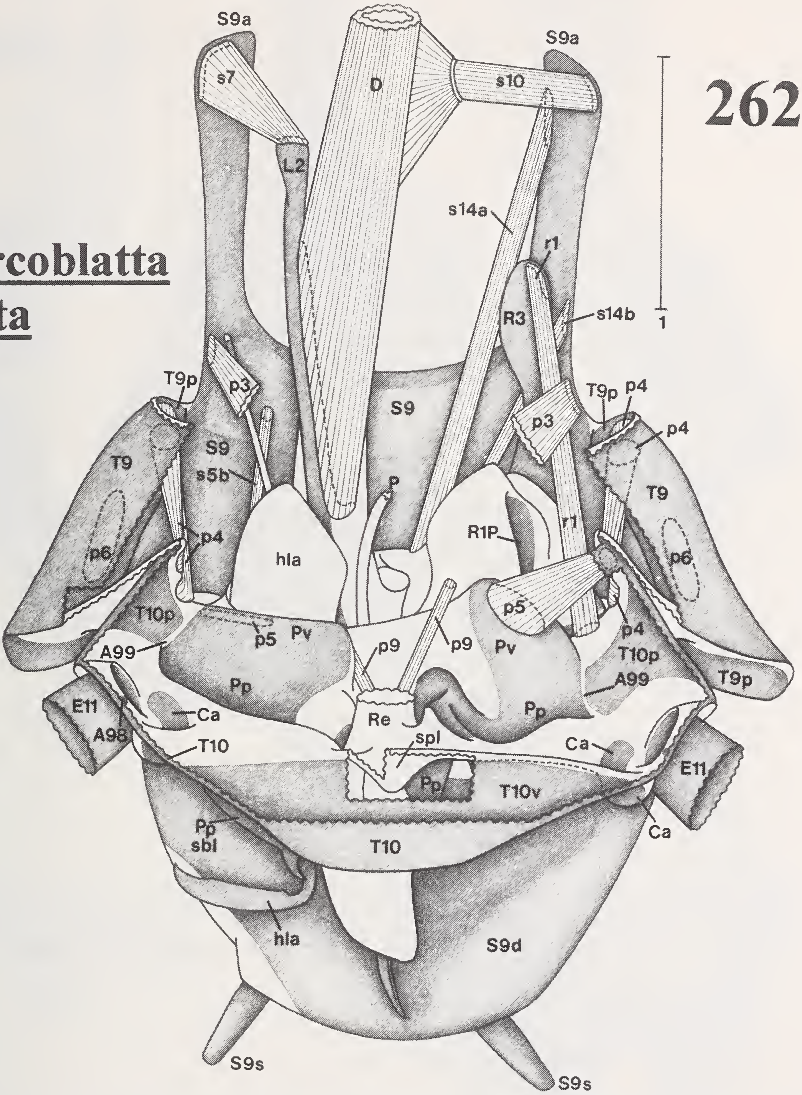
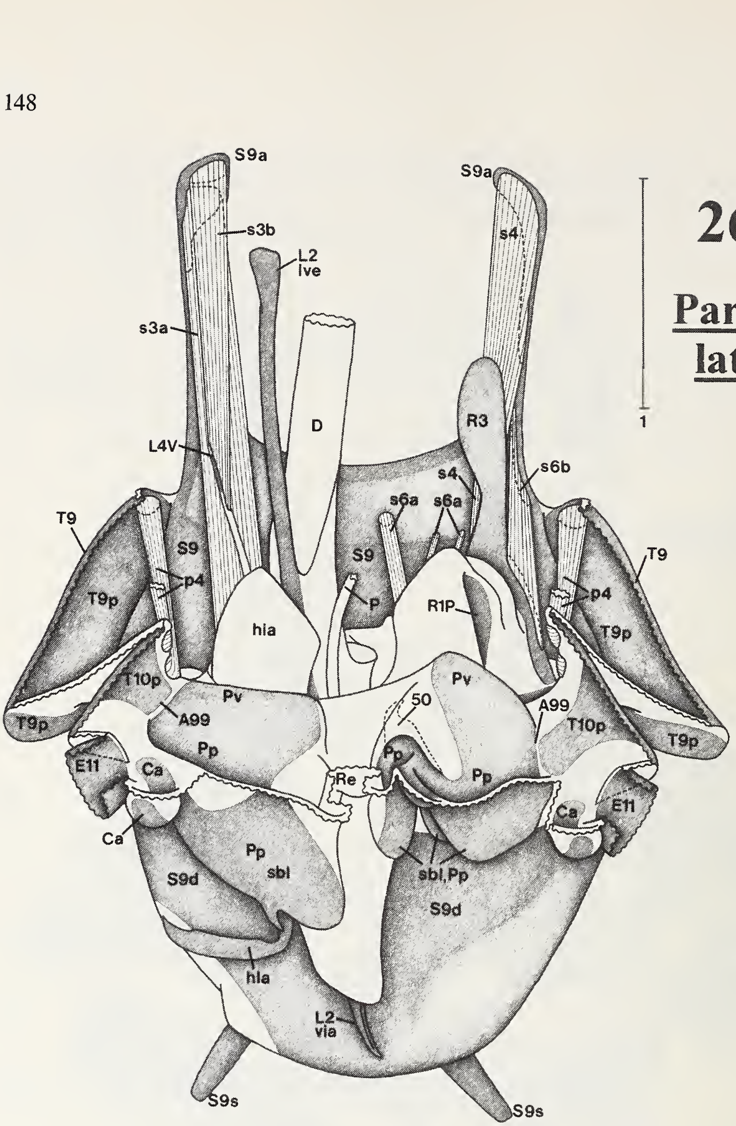


Fig.262: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, subanal lobes, paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. Supraanal lobe shown through a window cut into ventral sclerotisation of abdominal tergite 10 T10v. – Scale: 1mm.



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Parcoblatta lata

Fig.263: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – Male postabdomen as in fig.262, after removal of further parts of abdominal tergites 9 and 10 (especially T10v) and supraanal lobe. Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Scale: 1mm.

⟶ p.149

Figs.264,265: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **264:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **265:** Subgenital plate in dorsal view; with insertion areas of muscles (including p6). Insertion areas of s5a and s6a shown through two windows cut into dorsal sclerotisation S9d of subgenital plate. – Scale: 1mm.

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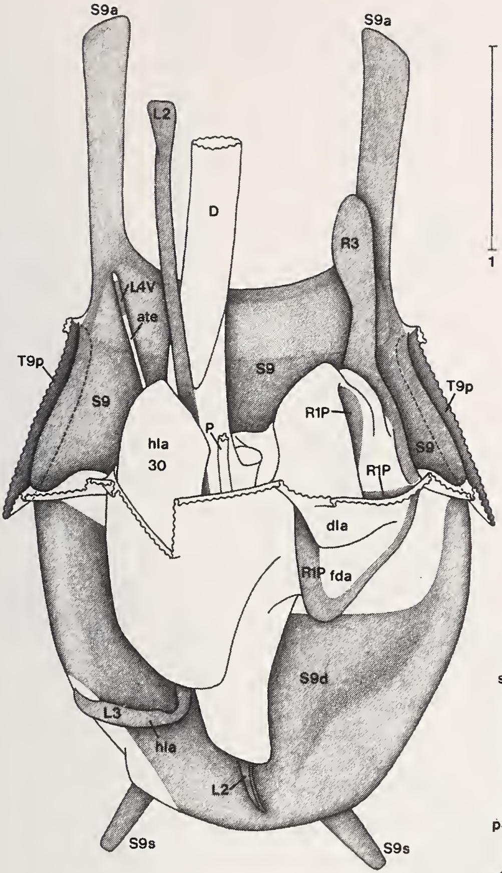

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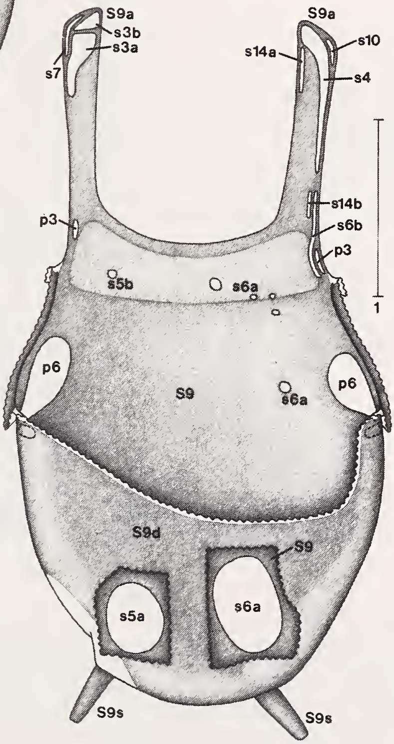
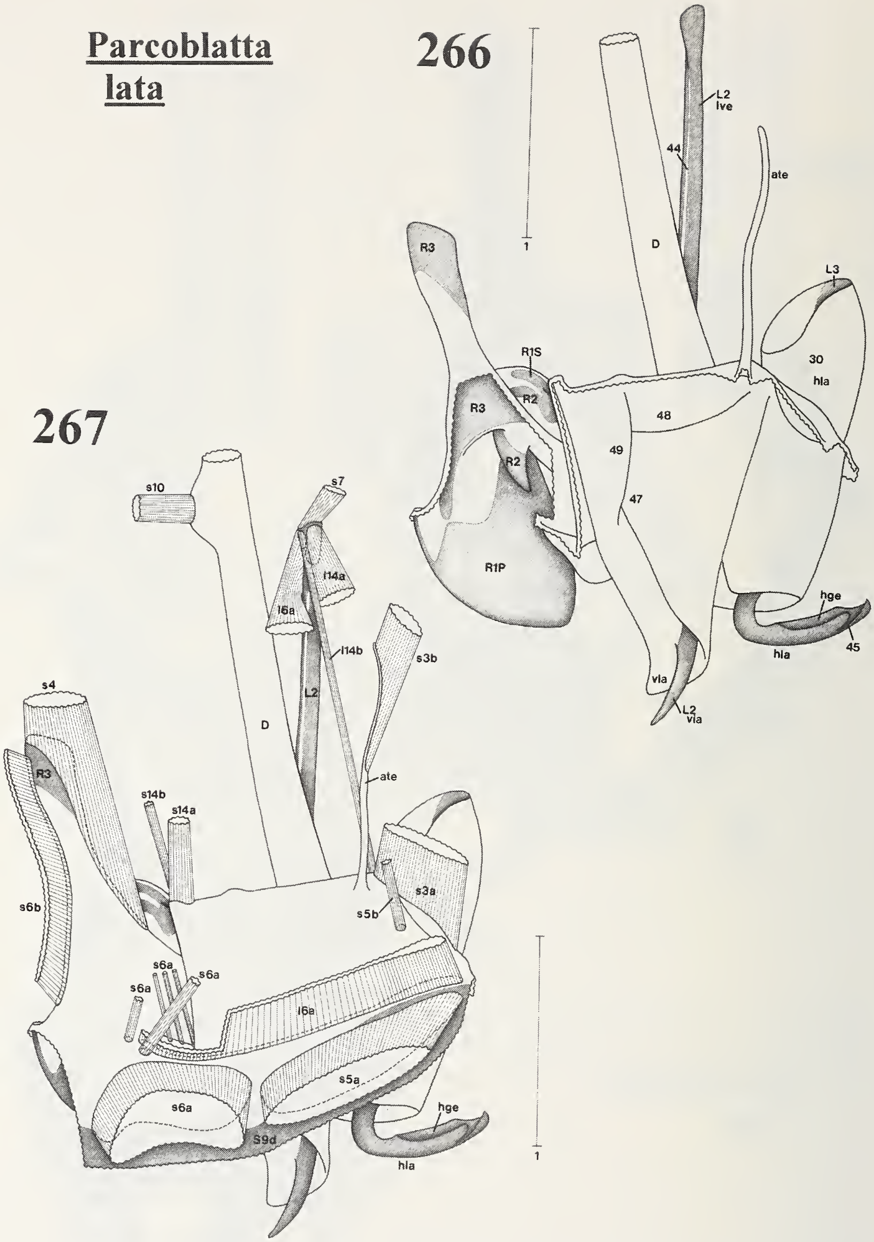


Parcoblatta
lata

Parcoblatta lata



Figs.266,267: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **266:** Phallomere complex in ventral view. – **267:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.266, with parts of dorsal sclerotisation S9d of subgenital plate in its posterior part (compare fig.265). – Scale: 1mm.

heavier distally. The membranous basal half (**30** in fig.268-270) of **hla** becomes introverted in the retraction of **hla** (fig.270, 271). The terminal leftward-bent part of **hla** has a groove along its anterior surface (**hge** in fig.266), whose ventral wall has a distinct notch (**45** in fig.266).

The part to the right of the **fpe**-infolding has in its center a deep invagination to the anterior (pouch **lve** in fig.268, 269) and a spine to the posterior (**via** in fig.268); both contain parts of sclerite **L2**. The anterior part of the **lve**-pouch is a narrow tube-like apodeme (**lve**-apodeme) with a flattened and broadened top. It is completely sclerotised by **L2** – except for a membranous stripe (**44** in fig.266) in its right-ventral (more anteriorly) or right (more posteriorly) wall, which does not reach the top of the apodeme. Roughly in the middle of **L2**, the ejaculatory duct joins the **lve**-pouch from the right (fig.268), and **lve** becomes much broader. At this point, the right edge of the **lve**-apodeme (with the membranous stripe **44**) bends anteriad to continue into a dorsal fold of the ejaculatory duct **D** (fig.268, 269). The ventral main part of the ejaculatory duct extends to beneath the **lve**-pouch (fig.268, 269; cross-section in fig.270) and wraps partly around it from ventrally (fig.270-272). In the area posterior to the confluence of the **lve**-apodeme and the dorsal part of the ejaculatory duct, **L2** is a groove-shaped sclerotisation in the left edge of the **lve**-pouch (cross-sections in fig.270-272). This groove-shape of **L2** extends posteriad as far as to the posterior end of edge **7** (fig.270, 273), where **L2** becomes completely restricted to the dorsal wall of the **lve**-pouch.

Posterior to this point **L2** forms the sclerotisation of the **via**-spine (fig.272-275). **via** has a longitudinal groove in its right-dorsal wall (**vge** in fig.272-275), whose anterior end deepens to form a small, bulb-like, and heavily sclerotised apodeme (**vge**, **tve** in fig.273). The phallomere-gland **P** opens to the right of the **tve**-apodeme. The ventral wall of the left complex has some outfoldings in the area beneath the ejaculatory duct (**47, 48, 49** in fig.266, 271, 272). In between these outfoldings and posterior to them the ejaculatory duct opens to the outside, and this area can be regarded as the genital opening. Dorsal to and to the left of the **via**-process there is a dorsoventrally curved membranous lobe (**vla** in fig.266, 268, 270).

The tendon **ate** (fig.266, 268, 271) has its origin in the anteriormost ventral wall of the genital pouch; it is a long and thin invagination of the cuticle with sclerite **L4V** in its anterior dorsal wall.

⟶ p.152

Figs.268-270: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **268:** Left complex in dorsal view. – **269,270:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones). – Scale: 1mm.

⟶ p.153

Figs.271-275: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **271,272:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.271: hla-hook separated from remainder of left complex (compare fig.270). – **273-275:** Posteriormost part of sclerite L2 on process via, phallomere-gland P, and surrounding membranes in dorsal view (scale larger than in fig.272); with successive removal of parts of the cuticle (mainly of dorsal ones). – Scale: 1mm.

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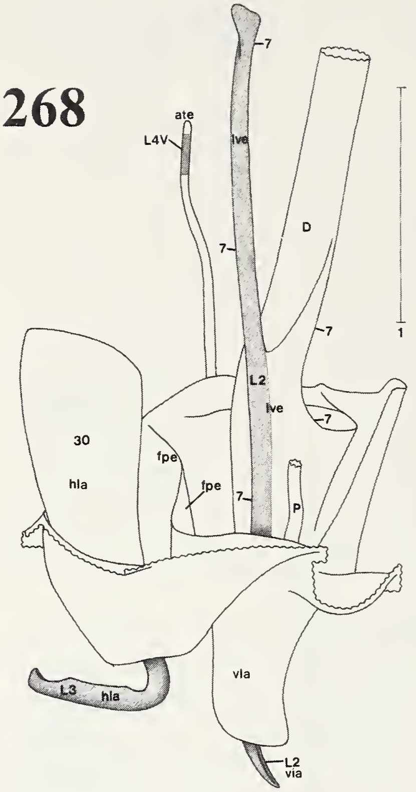

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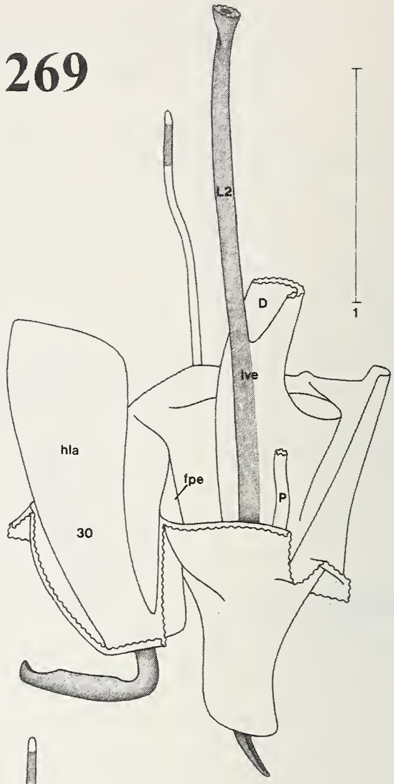

Parcoblatta
lata

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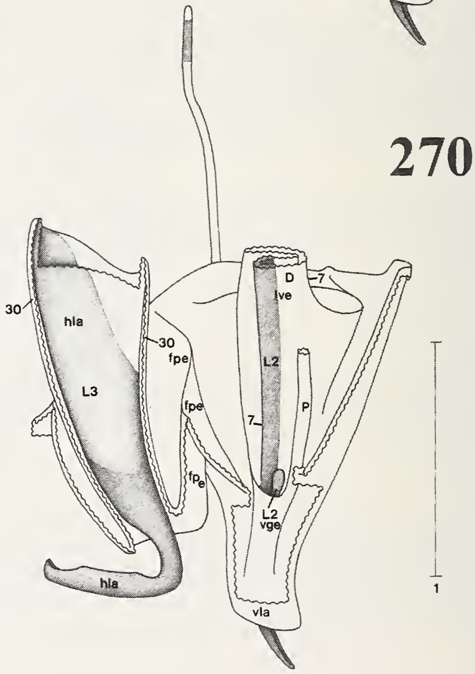
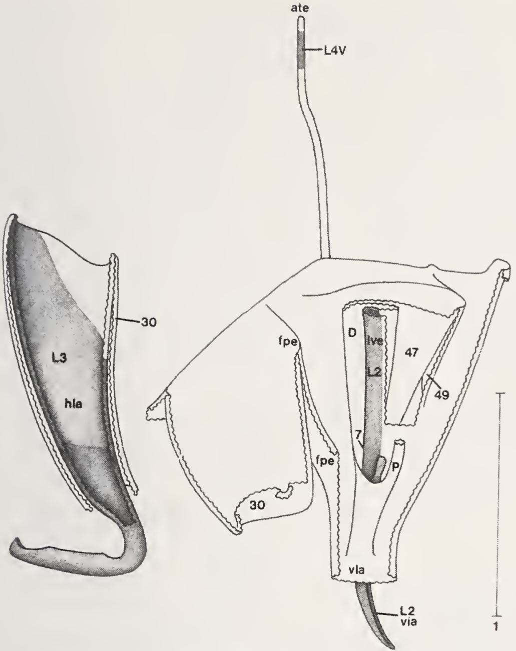


Parcoblatta lata



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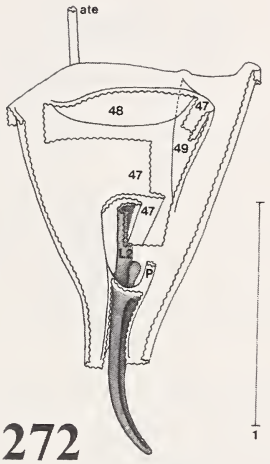

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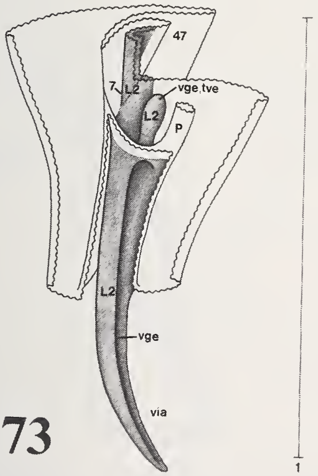

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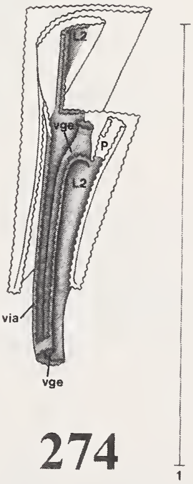

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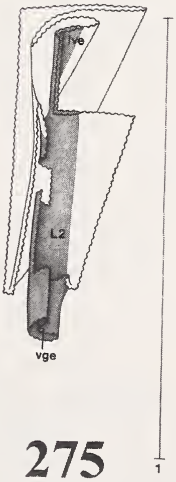

275

Right phallomere

The long, spatulate **R3**-sclerite occupies the anterior ventral wall (fig.280-284). Its right part has a long extension to the posterior (fig.280, 284). The **age**-groove or -apodeme is very broad at the anteriormost margins of **R3**; to the posterior it soon decreases and ends on both sides (fig.266, 284). Sclerite **R2** adjoins posterior to the left part of **R3**; the two sclerites are broadly separated by membrane (at **A7** in fig.282-284). From posterior to **A7**, **R2** extends anteriad and then curves to the left (fig.281, 283, 285). Most ventrally **R2** has a strong tooth (fig.283, 284); in its other parts it forms a very low ridge (fig.285). At its left end **R2** is fused to sclerite **R1S** (at **A6*** in fig.281, 283, 285). **R1S** likewise forms a low ridge (**pva** in fig.281, 282), and next to its fusion with **R2** it has a bulge-like cuticular thickening to the interior (**cwe** in fig.282, 283, 285). Posterior to the central part of **R3** the ventral wall of the right phallomere curves dorsad and anteriad to form a central invagination (**cbe** in fig.280, 281, 283; compare fig.284 and 285) with **R2** and **R1S** in its left-ventral wall.

Sclerite **R1P** adjoins posterior to the right part of **R3** (fig.281, 284), and the two sclerites articulate (**A3** in fig.281, 282, 284). **R1P** occupies the ventral wall and the margins of the dorsal wall of a large lobe **fda** (fig.281, 284). The left anterior tip of **R1P** closely approaches the free end of **R1S** (fig.281, 282). Above the **fda**-lobe there is another, smaller and membranous lobe (**dla** in fig.280).

Subgenital plate and posterior abdominal segments

Fig.262, 263 (posterior segments); fig.265 (subgenital plate **S9**). The ventral part of tergite 10 **T10v** is rather extensive. There are no separate **Pv**-sclerites; the **Pv**-sclerotisations are assumed to be incorporated into the anterior parts of the paraprocts **Pp** (fig.263; a deep indentation at the median margin of each paraproct possibly marks the border between **Pp** and **Pv**). The **Ca**-sclerites lie on curved bulges immediately median to the cercal bases. **Cb**- and **Cc**-sclerites are missing. The articulations **A98** and **A99** are well-developed. The asymmetrical subanal lobes **sbl** are highly elaborated (fig.263): The left **sbl** bears a small spine on its posterior edge. The right **sbl** bears some posteriad-directed bulge-like processes and an anteriad-directed small hook (**50** in fig.263, veiled by membrane).

Musculature

Muscle	Positions of insertions	in fig.
l2	Membranous basal part **30** of **hla**-hook – posterior left dorsal wall of left complex	276
l4	**L2** (posteriormost part, on **tve**-apodeme) – anterior left dorsal wall of left complex	276
l6a	Ventral wall of genital pouch – **L2** (anteriormost right edge of **lve**-apodeme)	267, 277

Figs.276-279: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents; fig.279: of muscle l6b only ventral insertion area shown. – Scale: 1mm.

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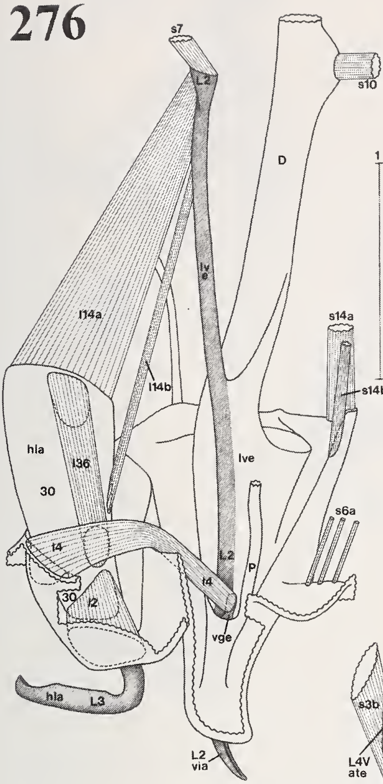

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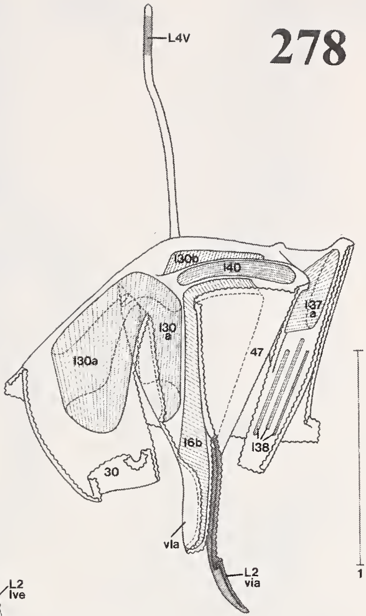

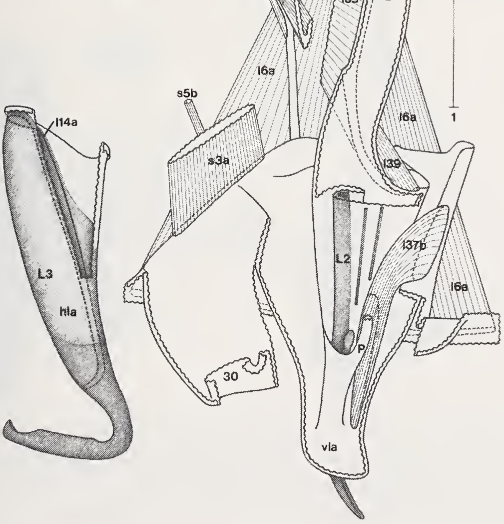

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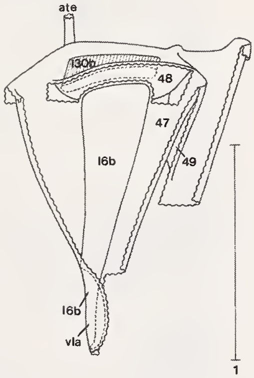

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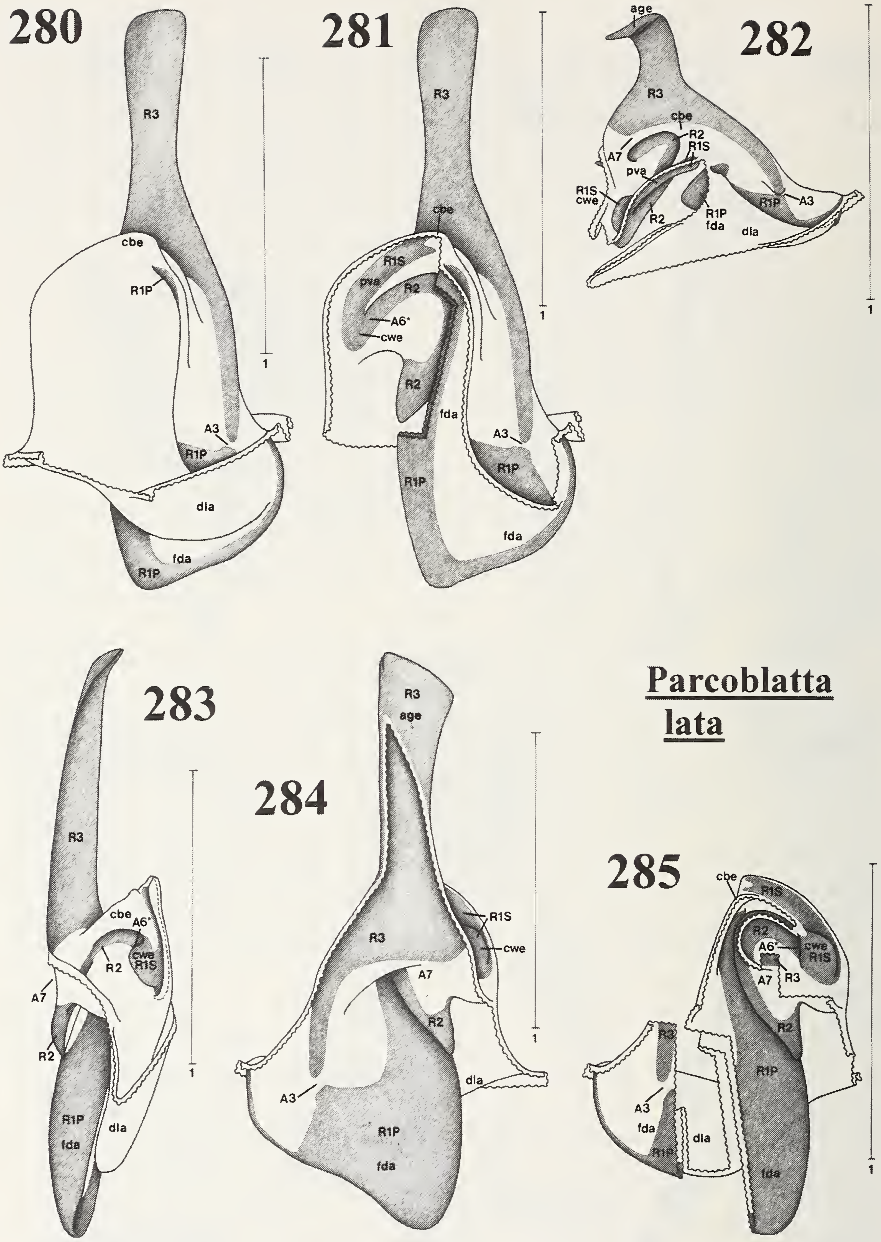
Parcoblatta lata



Figs.280-285: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **280:** Right phallomere in dorsal view. – **281:** Right phallomere in dorsal view; some dorsal elements removed. – **282:** Right phallomere in left-dorsal (somewhat anterior) view. – **283:** Right phallomere in left-ventral view. – **284:** Right phallomere in right-ventral view. – **285:** Right phallomere in right-ventral view; most elements shown in fig.284 removed. – Scale: 1mm.

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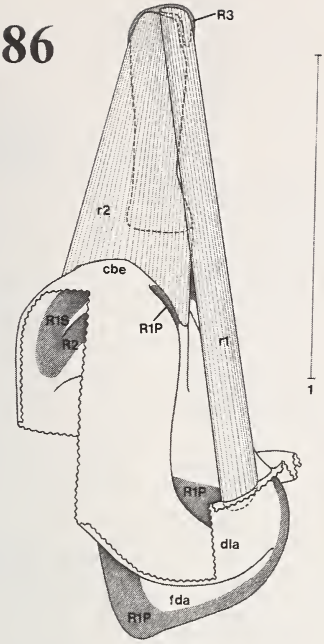

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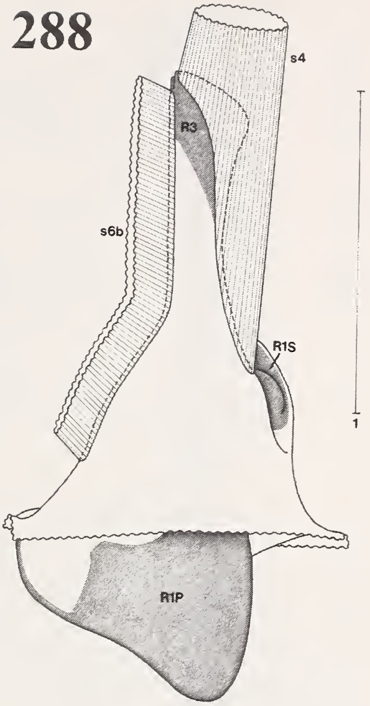

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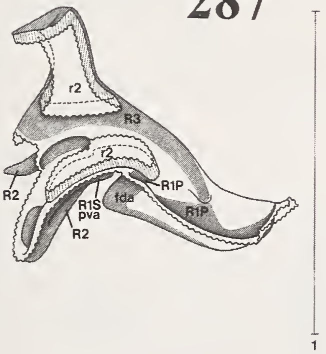


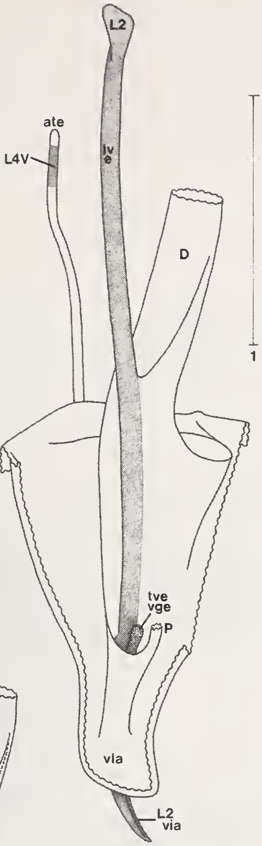
Parcoblatta lata

Figs.286-288: *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **286:** Right phallomere in dorsal view; with some muscles; some dorsal elements removed. – **287:** Right phallomere in left-dorsal (somewhat anterior) view; with muscle r2; some dorsal elements removed. – **288:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.284. – Scale: 1mm.

l6b	Central ventral wall of left complex – posterior ventral wall of **lve**-pouch; diffuse	278, 279
l14a	**L2** (most anteriorly on **lve**-apodeme) – **hla**-hook (left part of **L3**)	267, 276, 277
l14b	**L2** (most anteriorly on **lve**-apodeme) – right part of membranous basal part **30** of **hla**-hook	267, 276
l30a	Longitudinally in ventral wall of left complex (on both sides of **fpe**-infolding); diffuse	278
l30b	Ventral wall of outfolding **48** – dorsal wall of outfolding **48**; diffuse	278, 279
l36	Longitudinally in membranous basal part **30** of **hla**-hook	276
l37a	Transversely in anterior right ventral wall of left complex	278
l37b	Longitudinally in posterior right ventral wall of left complex	277
l38	Some isolated fibers in right ventral wall of left complex	278
l39	**ate**-tendon (anterior part with **L4V**) – ejaculatory duct **D** (ventral wall)	277
l40	Transversely in anterior ventral wall of left complex; diffuse	278
r1	**R3** (right-anteriormost part) – membrane in right anterior dorsal wall of **dla**-lobe	262, 286
r2	**R3** – **cbe**-invagination: **R1S** (right part), **R1P** (leftmost anterior part), and membrane	286, 287
s3a	**S9** left side (far anteriorly on apophysis **S9a**) – left ventral basal line **Bl** of left complex	263, 265, 267, 277
s3b	**S9** left side (most anteriorly on apophysis **S9a**) – **ate**-tendon	263, 265, 267, 277
s4	**S9** right side (anteriorly and posteriorly on apophysis **S9a**) – **R3** (anterior and left margin)	263, 265, 267, 288
s5a	**S9** left side (very far posteriorly) – left ventral wall of genital pouch (very far posteriorly, in part on **S9d**)	265, 267
s5b	**S9** left side (medially) – anterior left ventral wall of genital pouch; very delicate	262, 265, 267, 277
s6a	**S9** right side (main part inserting very far posteriorly, some smaller bundles more anteriorly) – right ventral wall of genital pouch (very far posteriorly, in part on anterior margin of **S9d**)	263, 265, 267, 276
s6b	**S9** right side (laterally) – **R3** (entire right margin)	263, 265, 267, 288
s7	**S9** left side (most anteriorly on apophysis **S9a**) – **L2** (most anteriorly on **lve**-apodeme)	262, 265, 267, 276

Figs.289-292: **289,290:** *Parcoblatta lata* (Blattaria, Blattellidae, Blattellinae) – **289:** Central part of left complex in dorsal view; with sclerites L2 and L4V, tendon ate, process via, phallomere-gland P, and ejaculatory duct D; stippled area: insertion area of muscle l4. – **290:** Central part of left complex in dorsal view; with posterior part of sclerite L2, process via, phallomere-gland P, and ejaculatory duct D; many parts removed compared with fig.289. – **291,292:** *Blaptica* sp. (Blattaria, Blaberidae) – Mirror-images of the original preparations. – **291:** Central part of left complex in dorsal view; with sclerites L2' and L4V', sclerite-group L10', tendon ate, process via, phallomere-gland P, and ejaculatory duct D; stippled area: insertion area of muscle l4. – **292:** Central part of left complex in dorsal view; with posterior part of sclerite L2, process via, phallomere-gland P, and ejaculatory duct D; many parts removed compared with fig.291. – Scale: 1mm.

289



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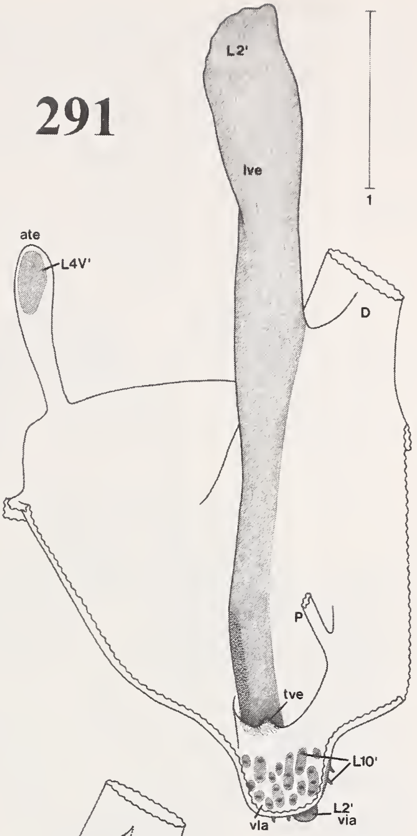

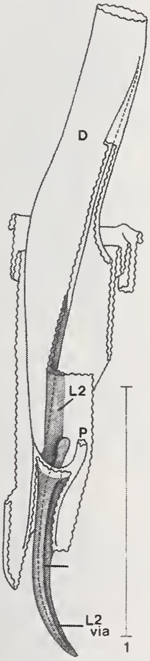

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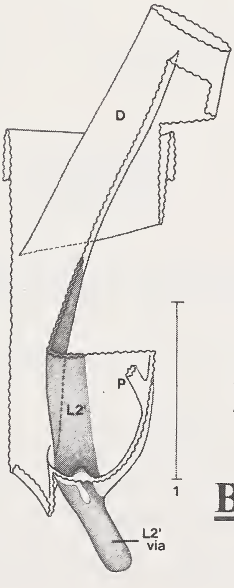
Parcoblatta lata



292

Blaptica sp.

s10	**S9** right side (most anteriorly on apophysis **S9a**) – ejaculatory duct **D** (right wall)	262, 265, 267, 276
s14a	**S9** right side (far anteriorly on apophysis **S9a**) – right ventral basal line **Bl** of left complex	262, 265, 267, 276
s14b	**S9** right side (far anteriorly on apophysis **S9a**) – right ventral basal line **Bl** of left complex	262, 265, 267, 276
p3 (pair)	**S9** – rectum (ventral wall)	262, 265
p4 (pair)	**T9** (lateralmost anterior margin, also extending onto paratergite **T9p**) – paratergite **T10p** (anterior margin); muscles on both sides completely divided into two bundles	262, 263
p5 (pair)	**T10** (lateralmost anterior margin) – anterior margin of **Pv**-sclerotisation	262
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral part, also extending onto dorsal sclerotisation **S9d** of subgenital plate)	262, 265
p9 (pair)	Membrane anterior to **Pv**-sclerotisation – membrane median to paraproct **Pp**, beneath rectum	262

5.14. *Blaberus craniifer* (Blattaria, Blaberidae)

All figures are side-reversed and show mirror-images of the original structures. In the subsequent descriptions and in the homology discussions (chapter 6.) the terms "left" and "right" will also be exchanged. (This will be practised in other Blaberidae, too: *Blaptica, Byrsotria, Nauphoeta*). The natural orientation is shown in fig.295b and 297b.

Left complex

The left complex resembles that of *Parcoblatta*. Again, a deep infolding from the posterior (**fpe** in fig.299-302) divides the left complex into a left part with the retractable **hla**-hook and its **L3'**-sclerite and a right part with the long **L2'**-sclerite.

The left part has the shape of a bulge whose left and ventral walls are occupied by sclerite **L4U'**. The **hla**-hook evaginates from the posterior wall of the bulge; when retracted, **hla** lies in the center of the bulge (fig.295a, 299; all figures show **hla** in a more or less retracted state). Only a small distal part of **hla** is sclerotised by **L3'**. Most of the extensive membranous basal part (**30** in fig.299-302) of **hla** becomes introverted when **hla** becomes fully retracted. **hla** can be retracted more deeply than in the previous species. (Full retraction is shown in fig.295a, with the sclerotised part of **hla** completely veiled by membrane; in the other figures **hla** is only partly retracted – to an extent corresponding to the maximal retraction in *Parcoblatta*). The leftward-bent terminal part of **hla** has a groove along its anterior surface (**hge** in fig.297a), whose ventral wall has a distinct notch (**45** in fig.297a).

The part to the right of the **fpe**-infolding has in its center a deep invagination to the anterior (pouch **lve** in fig.299, 300) and a sclerotised process to the posterior (**via** in fig.299); both contain parts of sclerite **L2'**. The anterior part of the **lve**-pouch is a short tube-like apodeme (**lve**-apodeme) with a flattened and broadened top. Most anteriorly the **lve**-apodeme is sclerotised all around, more posteriorly the right wall is membranous (**44** in fig.297a, 299, 300). Roughly one third down from the top of **L2'**, the ejaculatory duct **D** joins the **lve**-

pouch from the right (fig.299), and **lve** becomes broader. In the area posterior to this confluence, **L2'** is a groove-shaped sclerotisation in the left edge of the **lve**-pouch (cross-section in fig.301). This groove-shape of **L2'** extends posteriad as far as to the posterior end of edge **7** (fig.301), where **L2'** becomes completely restricted to the ventral wall of the **lve**-pouch. The phallomere-gland (**P** in fig.299-301) opens next to this point. The posteriormost part of **L2'** sclerotises the **via**-process (fig.299-302).

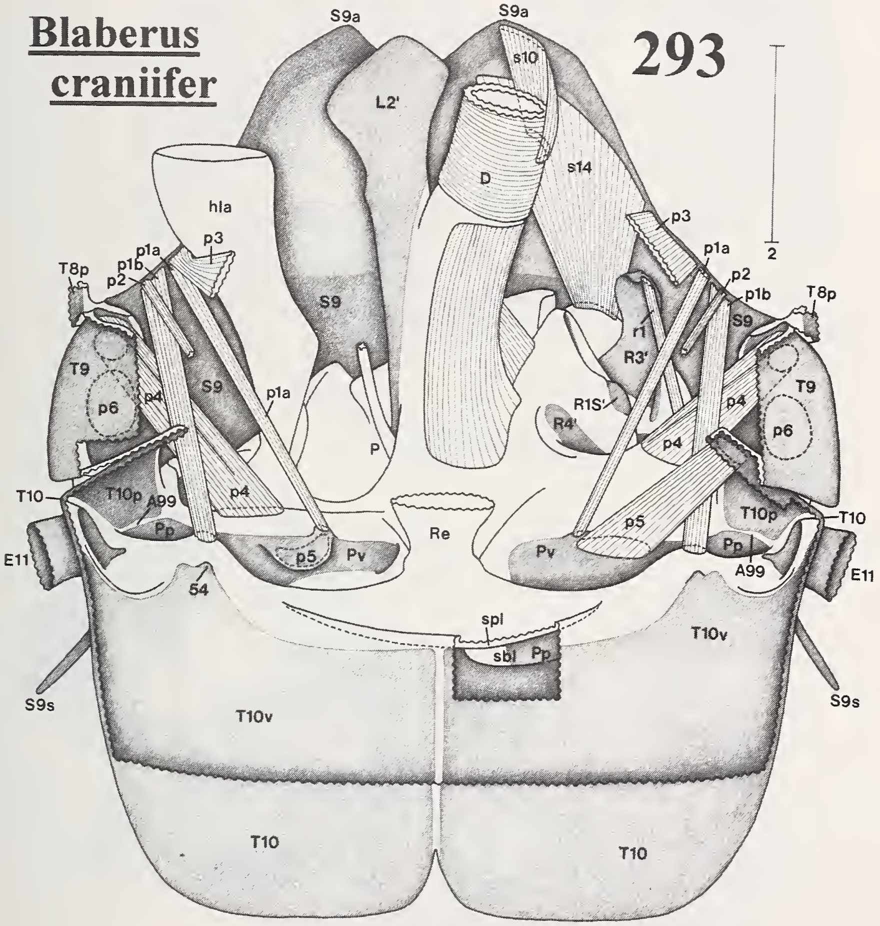
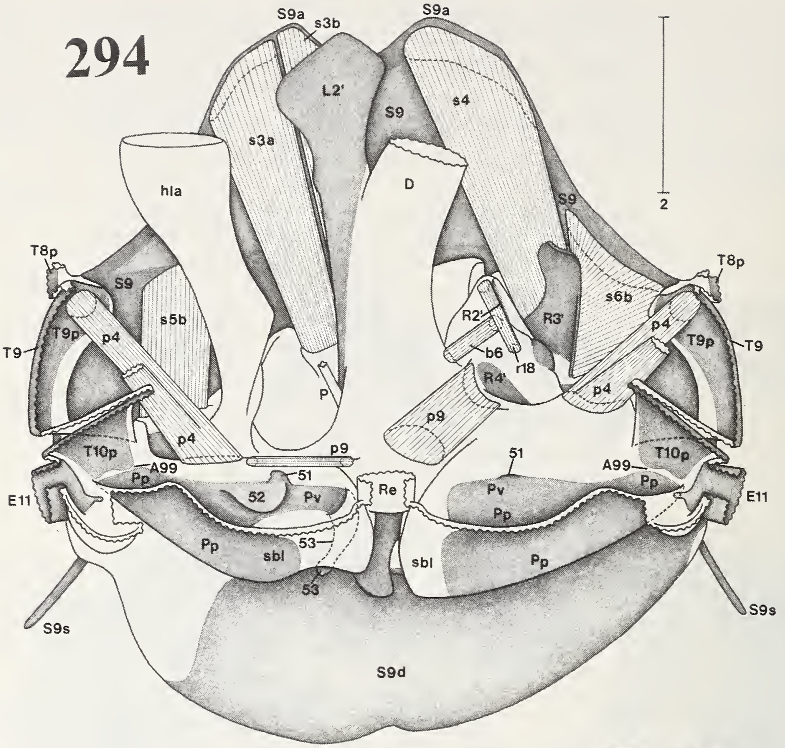
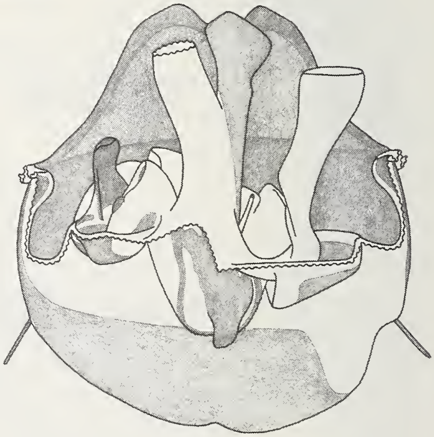


Fig.293: *Blaberus craniifer* (Blattaria, Blaberidae) – Mirror-image of the original preparations. – Male postabdomen in dorsal view; with phallomere complex, subgenital plate, marginal parts of abdominal tergites 9 and 10, supraanal lobe, subanal lobes (covered), paraprocts, distal part of rectum, basal parts of cerci, and part of musculature. Right part of supraanal lobe shown through a window cut into ventral sclerotisation of abdominal tergite 10 T10v. – Scale: 2mm.

294



Blaberus craniifer

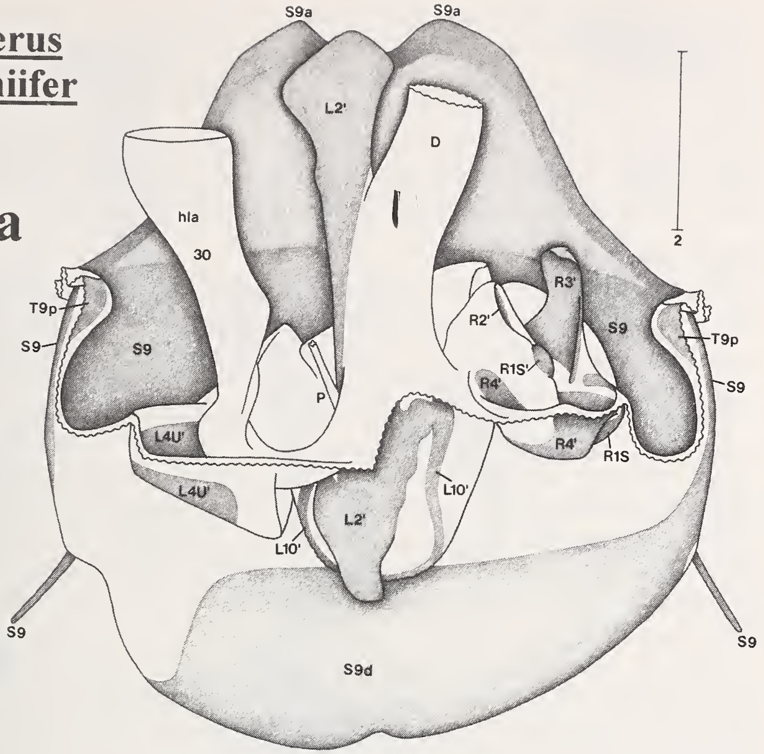


295b

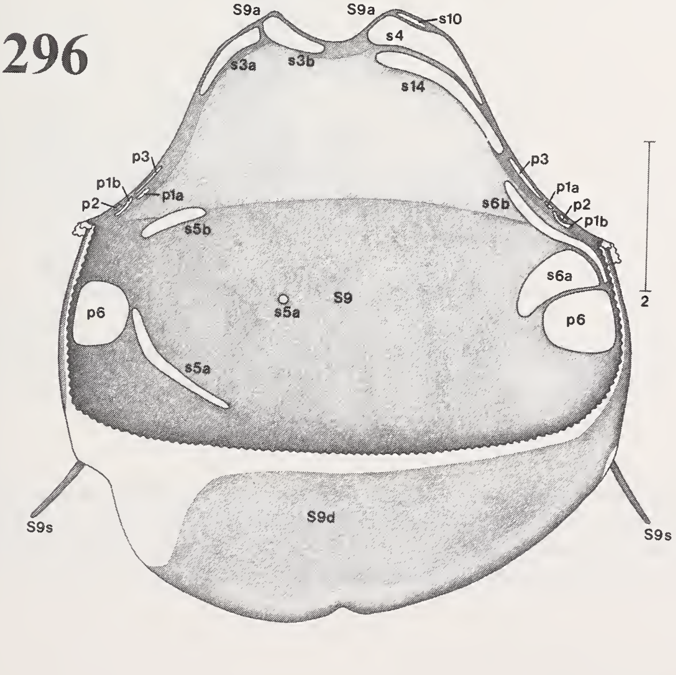
Figs.294,295b: *Blaberus craniifer* (Blattaria, Blaberidae) – **294:** Male postabdomen as in fig.293, after removal of further parts of abdominal tergites 9 and 10 (especially T10 and T10v) and supraanal lobe. Distal part of rectum and basal parts of cerci cut open. Another part of musculature shown. – Mirror-image of the original preparations. – Scale: 2mm. – **295b:** Same as in fig.295a (next plate) but smaller scale and natural orientation (no mirror-image).

Blaberus craniifer

295a



296



Beneath **via**, the ventralmost part of the left complex forms a broad ventral lobe **vla**, whose edges are sclerotised by the tuberculate **L10'**. The right anterior end of **L10'** is connected with **L2'**. The genital opening is more or less right-dorsal to the middle part of sclerite **L2'**, though it is hardly possible to define its exact position.

The membranous tendon **ate** has its origin in the ventral basal line of the left complex (**Bl** in fig.297a, 302); it is a short and broad invagination of the cuticle. To the left of **ate** there is another small membranous invagination (**55** in fig.297a, 302).

Right phallomere

Sclerite **R3'** occupies the anterior (right-)ventral wall (fig.308-312a). Its right part has a short extension to the posterior (fig.308, 312a). The **age**-groove or -apodeme is very broad at the anteriormost margins of **R3'**; to the posterior it soon decreases and ends on both sides (fig.297a, 312a). Sclerite **R2'** adjoins posterior to the left part of **R3'**; the two sclerites are broadly separated by membrane (at **A7** in fig.312a). The ventral anterior tip of **R2'** lies in a small membranous pouch (**56** in fig.308, 312a,b, 313). From here **R2'** extends left-dorsad and forms a ridge (fig.310, 311). At its left end **R2'** is fused to the large sclerite **R1T'** (at **A6*** in fig.310, 313). Next to its fusion with **R2'**, **R1T'** has a bulge-like cuticular thickening to the interior (**cwe** in fig.308-310, 313). Posterior to the central part of **R3'** the ventral wall of the right phallomere curves dorsad and anteriad to form a rather indistinct central invagination (**cbe** in fig.308, 310, 313; compare fig.312a and 313).

The two large sclerites **R1T'** and **R4'** adjoin posterior to the right part of **R3'** (fig.308, 309, 312a). **R1T'** is loosely articulated with **R3'** (**A3** in fig.309, 310, 312a). **R1T'** and **R4'** are the sclerotisations of two lobes lying one above the other, which compose the posterior part of the right phallomere (**fda** and **dla** in fig.308, 309, 313). The left end of the **fda**-lobe is somewhat pointed (**58** in fig.309, 312a), and next to this point **R1T'** is fused to **R2'**. **R4'** mainly occupies the dorsal wall of the **dla**-lobe (fig.308); its right end curves into the ventral wall of the phallomere (**59** in fig.308, 309), where it closely approaches articulation **A3**.

The bulged sclerite **R5'** lies in the left-ventral part of the right phallomere (fig.312a; removed from the other elements in fig.311; cut through in fig.309). The right phallomere can be retracted and protracted, and during this movement **R5'** flaps back and forth (compare fig.312a and 312b).

Subgenital plate and posterior abdominal segments

Fig.293, 294 (posterior segments); fig.296 (subgenital plate **S9**). The entire tergite 10 **T10**, including its ventral part **T10v**, is divided along its midline. **T10v** is very extensive; it has a pair of extensions to the anterior, which bear node-like apodemes (**54** in fig.293).

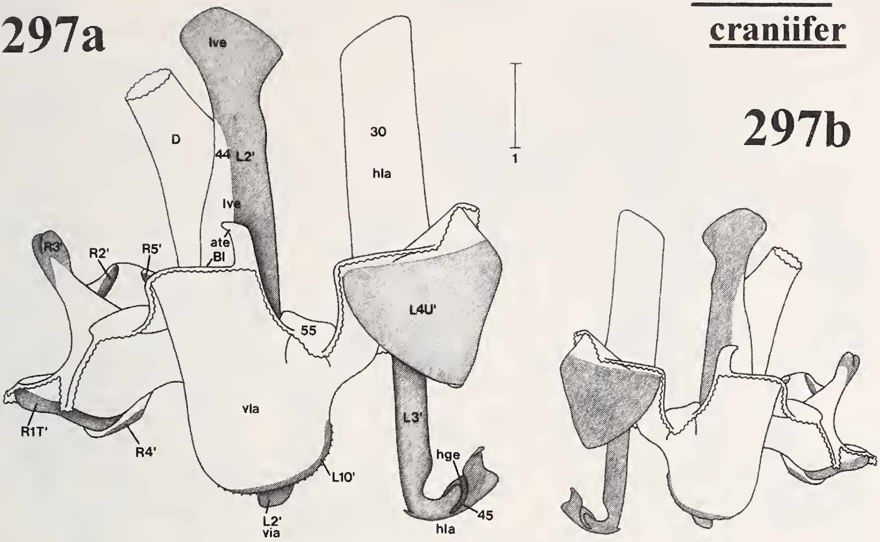
⟵—— p.163

Figs.295a,296: *Blaberus craniifer* (Blattaria, Blaberidae) – All figures show mirror-images of the original preparations. – **295a:** Male postabdomen in dorsal view; with phallomere complex, subgenital plate, and lateral parts of abdominal tergite 9. – **296:** Subgenital plate in dorsal view; with insertion areas of muscles (including p6). – Scale: 2mm.

Blaberus craniifer

297a

297b



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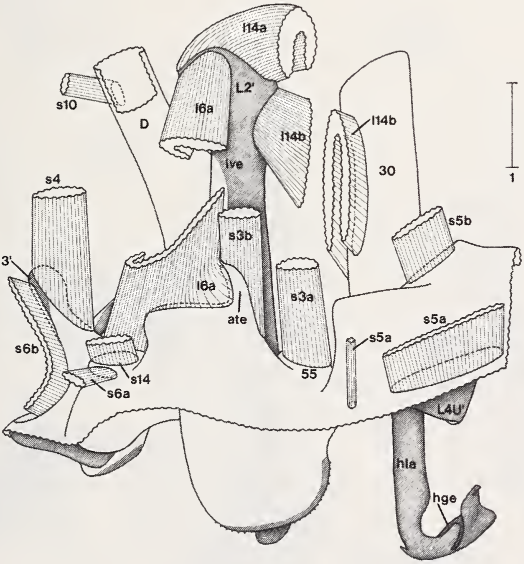
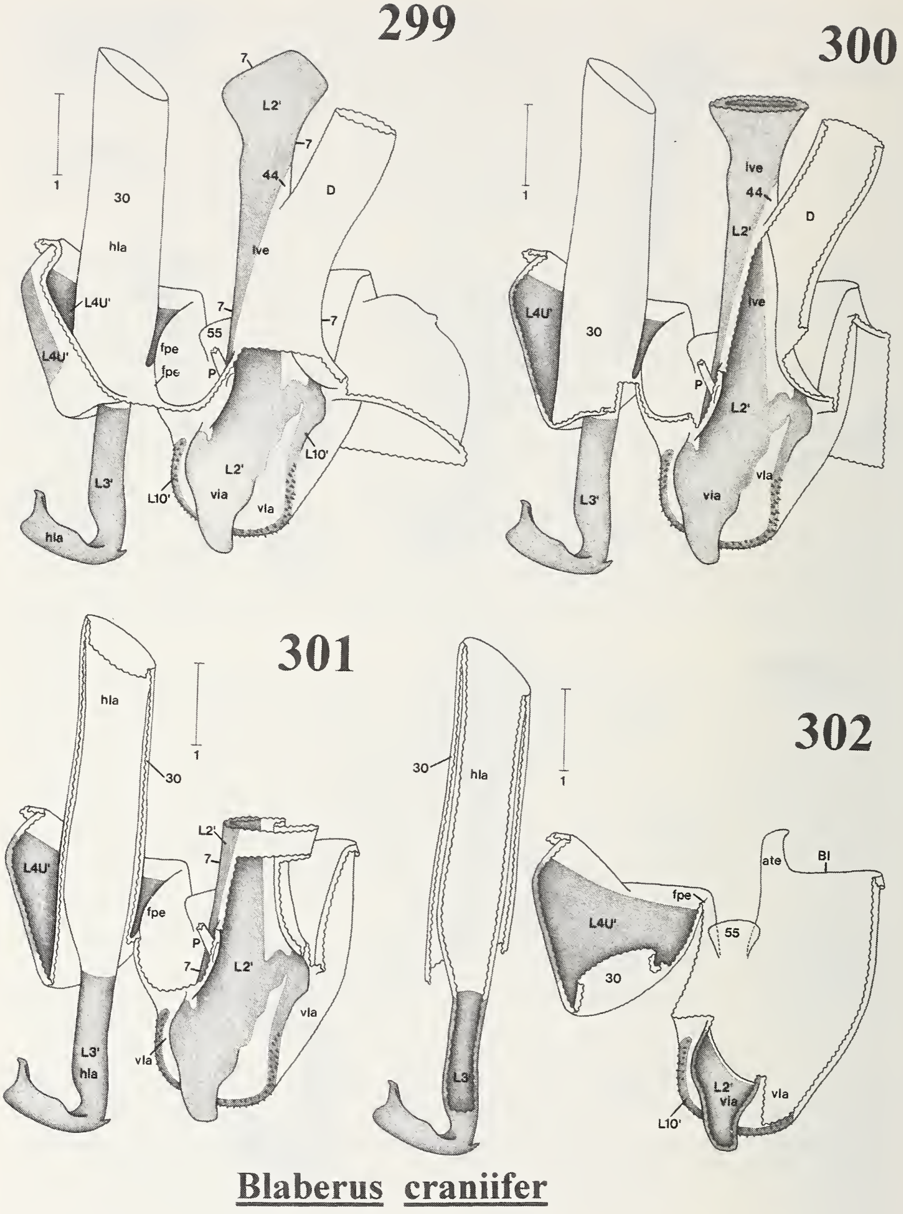


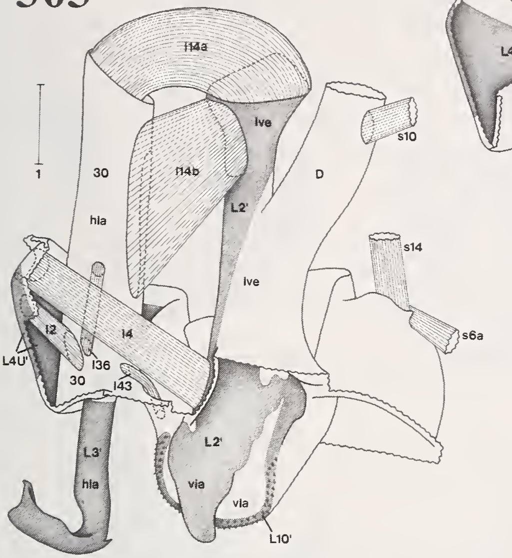
Figs.297,298: *Blaberus craniifer* (Blattaria, Blaberidae) – All figures except 297b show mirror-images of the original preparations. – **297a:** Phallomere complex in ventral view. – **297b:** Same as in fig.297a but smaller scale and natural orientation. – **298:** Phallomere complex in ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.297a. – Scale: 1mm.

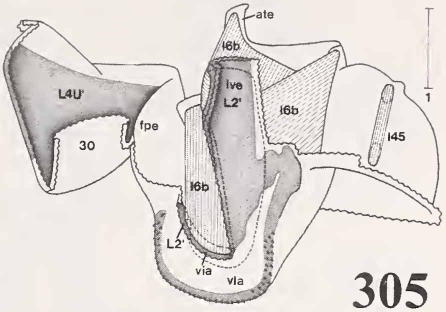


Figs.299-302: *Blaberus craniifer* (Blattaria, Blaberidae) – All figures show mirror-images of the original preparations. – **299:** Left complex in dorsal view. – **300-302:** Left complex in dorsal view; with successive removal of its parts (mainly of dorsal ones); fig.302: hook hla separated from remainder of left complex (compare fig.301). – Scale: 1mm.

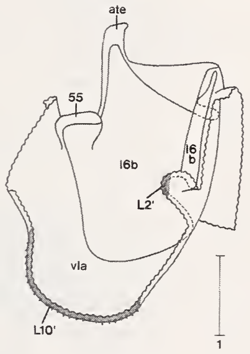
Blaberus craniifer

303



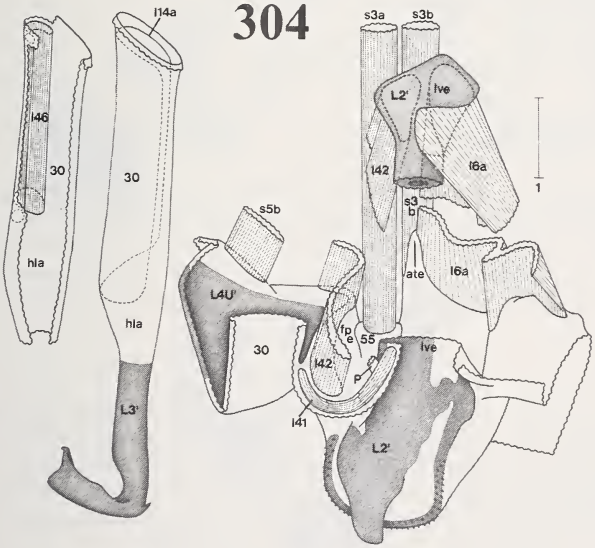


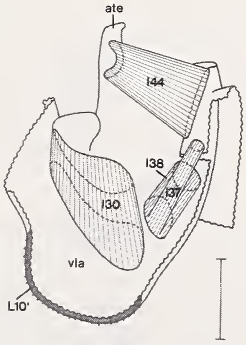
305



306

304





307

There are no separate **Pv**-sclerites; the **Pv**-sclerotisations are assumed to be incorporated into the anterior parts of the paraprocts **Pp** (fig.294; a deep indentation at the median margin of the left paraproct possibly marks the border between **Pp** and **Pv**). On their anterior margins the assumed **Pv**-sclerotisations bear the anteriad-directed node-like apodemes **51** (both sides, smaller on the right) and the posteriad-directed apodeme **52** (left side only). The sclerites **Ca, Cb**, and **Cc** are missing. The bulges next to the cercal bases the **Ca**-sclerites lie upon in the other species, however, are present (compare fig.263). The articulations **A99** are well-developed; the articulations **A98** are missing: The sclerotisations **E11** and **T10** are far away from each other. The left subanal lobe **sbl** bears a finger-like process (**53** in fig.294: mostly veiled by membrane) in its anterior ventral wall.

Musculature

Muscles	Positions of insertions	in fig.
l2	Membranous basal part **30** of **hla**-hook – **L4U'** (dorsal part)	303
l4	**L2'** (left-posterior part) – **L4U'** (anterior part in left edge of left complex) and membrane anterior to **L4U'**	303
l6a	Anteriormost ventral wall of left complex and anteriormost ventral wall of genital pouch – **L2'** (anteriormost right edge of **lve**-apodeme)	298, 304
l6b	Central ventral wall of left complex – **L2'** in posterior ventral wall of **lve**-pouch; diffuse	305,306
l14a	**L2'** (most anteriorly on **lve**-apodeme) – **hla**-hook (left wall anterior to **L3'**)	298, 303, 304
l14b	**L2'** (anterior left wall of **lve**-apodeme) – right part of membranous basal part **30** of **hla**-hook (insertion area horseshoe-shaped)	298, 303
l30	Longitudinally in ventral wall of left complex (only to the right of **fpe**-infolding); diffuse	307
l36	Longitudinally in membranous basal part **30** of **hla**-hook	303

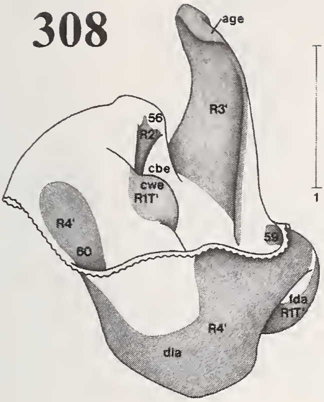
⟵ p.167

Figs.303-307: *Blaberus craniifer* (Blattaria, Blaberidae) – All figures show mirror-images of the original preparations. – Left complex in dorsal view; each figure with some muscles; parts of left complex removed to various extents; fig.304: hook hla separated from remainder of left complex; of muscle l14a only posterior insertion area on hla shown; left picture shows part of the membranous base of hla (part of membrane 30) together with muscle l46; fig.306: of muscle l6b only ventral insertion area shown. – Scale: 1mm.

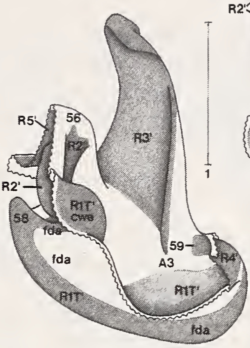
⟶ p.169

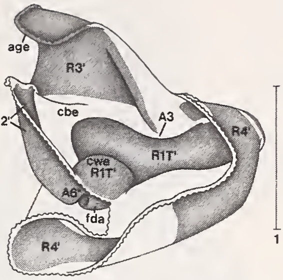
Figs.308-313: *Blaberus craniifer* (Blattaria, Blaberidae) – All figures show mirror-images of the original preparations. – **308:** Right phallomere in dorsal view. – **309:** Right phallomere in dorsal view; some dorsal elements removed (mainly lobe dla and sclerite R4'). – **310:** Right phallomere in left-dorsal (somewhat anterior) view; sclerite R5' removed. – **311:** Right phallomere in left-ventral view; sclerite R5' and surrounding membranes separated from remainder of right phallomere (along the undulate line between the points labelled x). – **312a:** Right phallomere in right-ventral view. – **312b:** Left part of right phallomere in right-ventral view; sclerite R5' flapped to the anterior. – **313:** Right phallomere in right-ventral view; most elements shown in fig.312a removed. – Scale: 1mm.

308



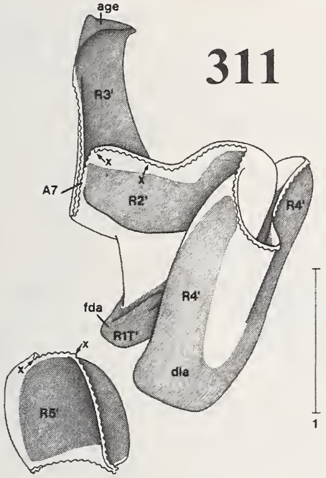
309



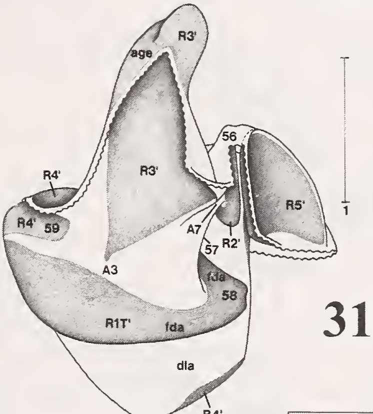


310

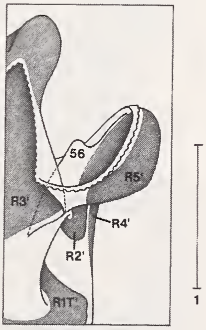
Blaberus craniifer



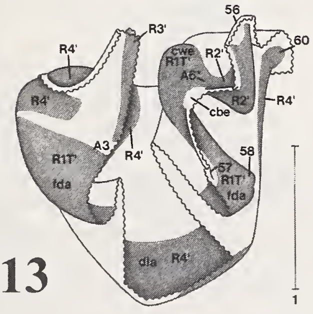
311



312a



312b



313

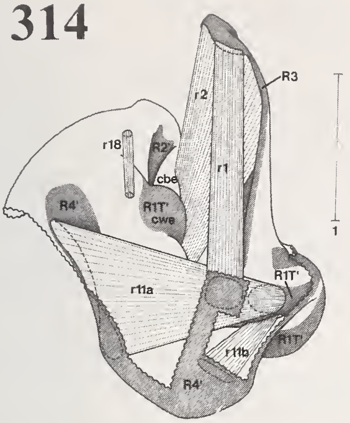
l37	In right ventral wall of left complex	307
l38	In right ventral wall of left complex	307
l41	Transversely in dorsal wall of left complex, between **fpe**-infolding and opening of phallomere-gland **P**; diffuse	304
l42	**L2'** (left anterior ventral wall of **lve**-apodeme) – **fpe**-infolding	304
l43	Membranous basal part **30** of **hla**-hook – membrane to the right of **hla**-base	303
l44	**ate**-tendon – anterior right ventral wall of left complex; diffuse	307
l45	Longitudinally in rightmost part of left complex	305
l46	Longitudinally in membranous basal part **30** of **hla**-hook, distal to **l36**; composed of diffuse fibers running within the insertion area of **l14a**.	304 (left)
r1	**R3'** (right-anteriormost part) – **R4'** in right anterior dorsal wall of **dla**-lobe	293, 314
r2	**R3'** – **cbe**-invagination: **R1T'** (left part) and membrane	314, 316
r11a	**R4'** (left edge of **dla**-lobe) – **R1T'** (right ventral wall of **fda**-lobe); diffuse	314, 315
r11b	**R4'** (right dorsal wall of **dla**-lobe) – **R1T'** (rightmost ventral wall of **fda**-lobe); diffuse	314, 315
r12	**R3'** (right-anteriormost part) – **R4'** (leftmost part); very delicate	315
r13	**R3'** (right-anteriormost part) – membrane posterior to **cwe**-thickening; anterior part of **r13** running within muscle **r2** (compare fig.314), posterior part abruptly leaving **r2** and running to **cwe**; very delicate	315
r14	**R3'** (anterior right margin) – membrane to the right of right posterior end of **R3'**; very delicate	315
r15	Membrane posterior to **cwe**-thickening – **R1T'** (right ventral wall of **fda**-lobe); diffuse	315
r16	**R4'** (leftmost part) – membrane to the right of left part of **R4'**; very delicate, diffuse	315
r17	Longitudinally in ventral wall of genital pouch beneath right phallomere; several delicate and diffuse bundles	317
r18	Membrane to the left of **R2'** – membrane to the left of **cwe**-thickening	294, 314

Fig.315 shows the muscles **r12, r13, r14, r15**, and **r16**. However, none of these muscles was present in all of the investigated specimens, and in none of the specimens these muscles were present all together.

b6	Membrane to the left of **R2'** – ejaculatory duct **D** (posterior right dorsal wall)	294, 316

Figs.314-319: **314-317:** *Blaberus craniifer* (Blattaria, Blaberidae) – Figures 314-317 show mirror-images of the original preparations. – **314,315:** Right phallomere in dorsal view; each figure with some muscles; dorsal elements removed to various extents. – **316:** Right phallomere in left-dorsal (somewhat anterior) view; with some muscles; some dorsal elements removed. – **317:** Right phallomere in right-ventral view; with some muscles; ventral wall of genital pouch more complete than in fig.312a. – **318:** *Byrsotria fumigata* (Blattaria, Blaberidae) – Mirror-image of the original preparations. – Right phallomere in dorsal view. – **319:** *Nyctibora* sp. (Blattaria, Blattellidae, Nyctiborinae) – Right phallomere in dorsal view. – Scale: 1mm.

314



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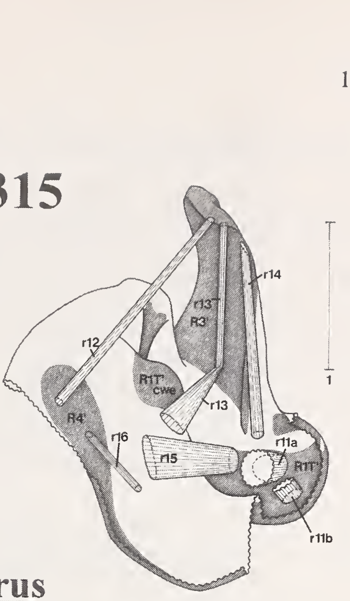
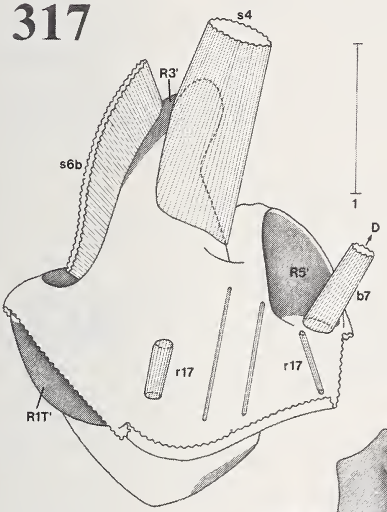
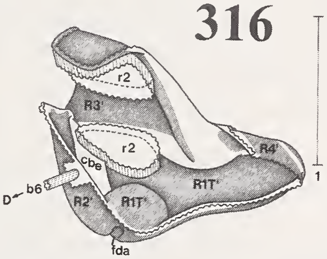


Blaberus craniifer

317



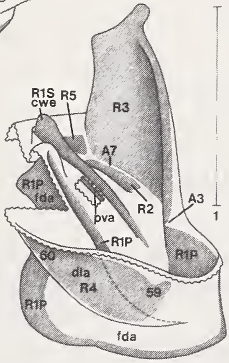
316



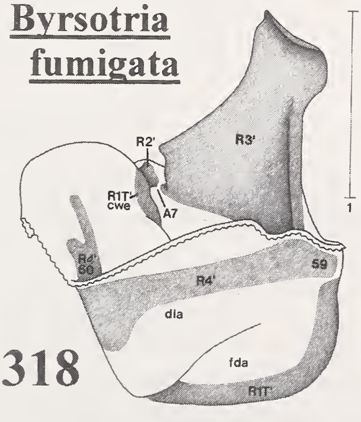
Byrsotria fumigata

Nyctibora sp.

319



318



b7	Membrane posterior to **R5'** – ejaculatory duct **D** (posterior right ventral wall)	317
s3a	**S9** left side (far anteriorly on apophysis **S9a**) – ventral basal line of left complex, on infolding **55**	294, 296, 298, 304
s3b	**S9** left side (most anteriorly on apophysis **S9a**) – **ate**-tendon	294, 296, 298, 304
s4	**S9** right side (most anteriorly on apophysis **S9a**) – **R3'** (anterior and left margin)	294, 296, 298, 317
s5a	**S9** left side (far posteriorly) – left ventral wall of genital pouch (far posteriorly); an additional delicate bundle runs more medially	296, 298
s5b	**S9** left side (laterally) – left ventral basal line **Bl** of left complex	294, 296, 298, 304
s6a	**S9** right side (far posteriorly and laterally) – right ventral wall of genital pouch	296, 298, 303
s6b	**S9** right side (laterally) – **R3'** (entire right margin)	294, 296, 298, 317
s10	**S9** right side (on apophysis **S9a**) – ejaculatory duct **D** (right wall)	293, 296, 298, 303
s14	**S9** right side (posterior to apophysis **S9a**) – right ventral basal line **Bl** of left complex	293, 296, 298, 303
p1a (pair)	**S9** – anterior margin of **Pv**-sclerotisation, on apodeme **51**; very delicate	293, 296
p1b (pair)	**S9** – posterior (!) margin of paraproct **Pp**, in anteriormost dorsal wall of subanal lobe **sbl**	293, 296
p2 (pair)	**S9** – **T9** (lateral anterior margin); very delicate	293, 296
p3 (pair)	**S9** – rectum (ventral wall)	293, 296
p4 (pair)	**T9** (lateralmost anterior margin, also extending onto paratergite **T9p**) – membrane far anterior to **Pv**-sclerotisation; muscles on both sides divided into two bundles in their dorsolateral parts	293, 294
p5 (pair)	**T10** (lateralmost anterior margin) – anterior margin of **Pv**-sclerotisation (left muscle on apodeme **52**)	293
p6 (pair)	**T9** (lateralmost part) – **S9** (lateral part)	293, 296
p9 (pair)	Membrane anterior to **Pv**-sclerotisation – membrane median to anterior margin of **Pv**-sclerotisation, beneath rectum; very asymmetrical	294

5.15. Further species

In some further species only certain parts or elements of the phallomere complex have been investigated. These will be described within the respective sections of the following chapter 6.

For *Blatta orientalis*, *Deropeltis* sp., *Periplaneta americana* (Blattidae, Blattinae) and *Ergaula capucina* (Polyphagidae, Polyphaginae): Sclerites and most muscles of left complex (no figures for Blattinae; for *Ergaula capucina* the morphology of the leftmost part of the left complex is shown in fig.326d, 327d).

For *Tryonicus angustus* (Blattidae, Tryonicinae) and *Ergaula capensis* (Polyphagidae, Polyphaginae): Sclerite **L1**, **pne**-pouch (with opening of phallomere-gland), and **dca**-

processes (shown in fig.105-108). Only in *E. capensis*: morphology of right phallomere (shown schematically in fig.330m).

For *Euphyllodromia angustata* and *Supella longipalpa* (Blattellidae, Plectopterinae), *Loboptera decipiens* (Blattellidae, Blattellinae), *Ectobius sylvestris* (Blattellidae, Ectobiinae), *Nyctibora* sp. (Blattellidae, Nyctiborinae), and *Byrsotria fumigata, Blaptica* sp. and *Nauphoeta cinerea* (Blaberidae): Central part of left complex with sclerite **L2**, **lve**-pouch, and **via**-process (all species; shown in fig.328c,d,f,g,h,i and 291, 292; no figures for *Byrsotria*). Morphology of right phallomere (all species except *Ectobius*, *Loboptera*, *Nauphoeta*; shown in fig.330o,r and 318, 319; no figures for *Supella*). Presence and special condition of some further elements of left complex: **hge**-groove, notch **45** (elements of **hla**-hook, compare fig.266), **ate**-tendon with its sclerite **L4V** (no figures).

6. HOMOLOGY RELATIONS AND CHARACTER STATES

In this chapter a homology hypothesis will be elaborated for the phallomere and postabdominal elements of the investigated species. This hypothesis should be as detailed as possible, and it should be provided with as many arguments as possible. The following list gives a survey which elements are discussed in which section. For the first five sections (left complex I-V) the discussed elements are listed. Which elements are contained in the

320

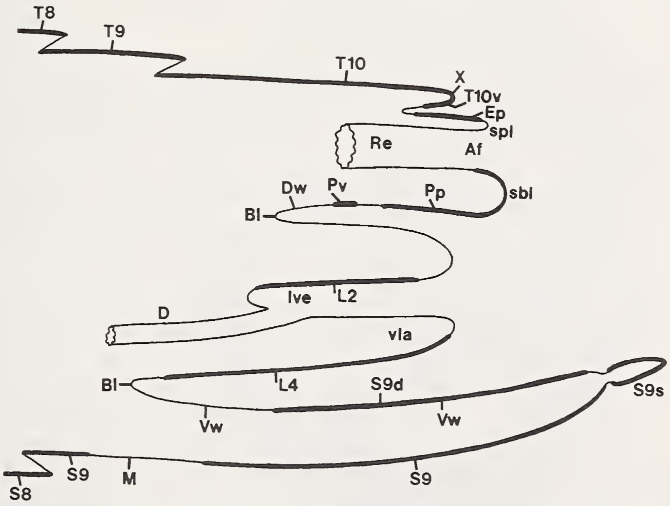


Fig.320: Male postabdomen and phallomere complex in median sagitto-longitudinal section. Left view; anterior←, posterior→. Only the cuticle is shown: Thin lines are membranous, thick lines are sclerotised cuticle. Styles and paraprocts are shown though they are not visible in a median section. Abbreviations in 4.7.

remaining sections is evident from the headlines. Some elements will be discussed in more than one section – according to the various aspects of their relative position.

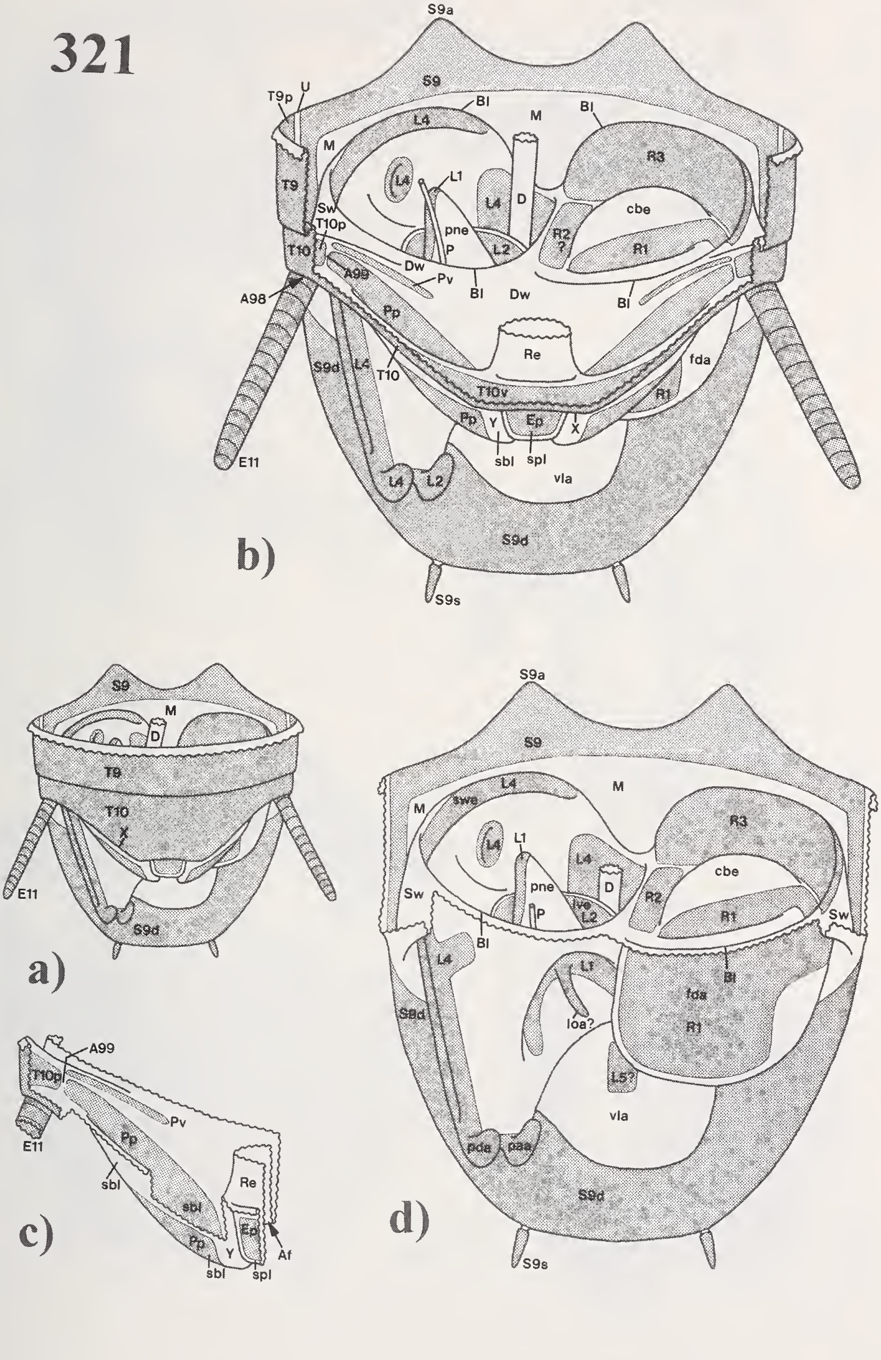
6.1. Left complex I: Main sclerites L1 and L6 and associated elements (**L1, L6 / pne, dca, loa, afa / l1, l2, l3, l9, l28, b4** / phallomere-gland **P**)
6.2. Left complex II: Main sclerite L2 and associated elements (**L2 / lve, vla, pda, paa, via, gta, psa / l4, l5, l6, l8, l10, l12, s7** / ejaculatory duct **D**)
6.3. Left complex III: Main sclerites L4 and L10 and associated elements (**L4, L10 / swe, pda, paa, vsa, via, nla, vla / l1, l2, l4, l5, l6, l7, l10, l11, l14, s1, s3, s12**)
6.4. Left complex IV: Main sclerite L3 and associated elements (**L3 / hla, hge, fpe / l14, l19, l22, l23, l36, l46**)
6.5. Left complex V: Further main sclerites and muscles (**L5, L6, L7, L8, L9, L10, L11 / lba / l7, l9, l12, l13, b2**)
6.6. Left complex VI: The position of the phallomere-gland opening
6.7. The elements of the right phallomere

Fig.321: Male postabdomen and phallomere complex corresponding to the hypothetical ground-plan of Blattaria and Mantodea (on pages 175-177).

a) Postabdomen from segment 9 on in dorsal view.
b) Postabdomen from segment 9 on after removal of central parts of abdominal tergites 9 and 10; dorsal view. With marginal parts of tergites 9 and 10, phallomere complex, ejaculatory duct, subgenital plate, paraprocts, epiproct, subanal lobes, supraanal lobe, cerci, and distal part of rectum.
c) Detail from left part of fig.321b after removal of some dorsal parts in dorsal view.
d) Subgenital plate and phallomere complex in dorsal view.
e) Left complex in dorsal view.
f) Right phallomere in dorsal view.
g) Left complex after removal of some dorsal parts in dorsal view.
h) Right phallomere after removal of some dorsal parts in dorsal view. Ridges pia and pva shown through a window cut into ventral wall of lobe fda.
i) Left complex in ventral view.
k) Subgenital plate in dorsal view. Ventral wall of genital pouch with dorsal sclerotisation S9d of subgenital plate retained on left side but removed on right side.
l) Postabdomen from segment 9 on after removal of rectum, supraanal lobe, epiproct, and of large parts of abdominal tergites 9 and 10, subanal lobes, and dorsal wall of genital pouch; dorsal view. With lateral parts of tergites 9 and 10, phallomere complex, ejaculatory duct, subgenital plate, paraprocts, ventral walls of subanal lobes, and basal parts of cerci. Dorsal lobe fda cut open lengthwise in its leftmost part. All ground-plan muscles of categories p (peripheral), s (phallomero-sternal), and b (between left complex and right phallomere) shown. p4 only shown on right side, p6 and p7 only on left side. Dorsal part of p3 (to rectum) removed.
m)-o) Left complex after removal of some dorsal parts in dorsal view. Each figure with some ground-plan muscles of category l (intrinsic muscles of left complex).
p) Right phallomere after removal of some dorsal parts in dorsal view. With the ground-plan muscles of category r (intrinsic muscles of right phallomere). Ridge pia shown through a window cut into ventral wall of lobe fda.

Stippled areas are sclerotised. Abbreviations in 4.7. Elements whose presence in the ground-plan of Blattaria and Mantodea is uncertain are provided with “?”.

321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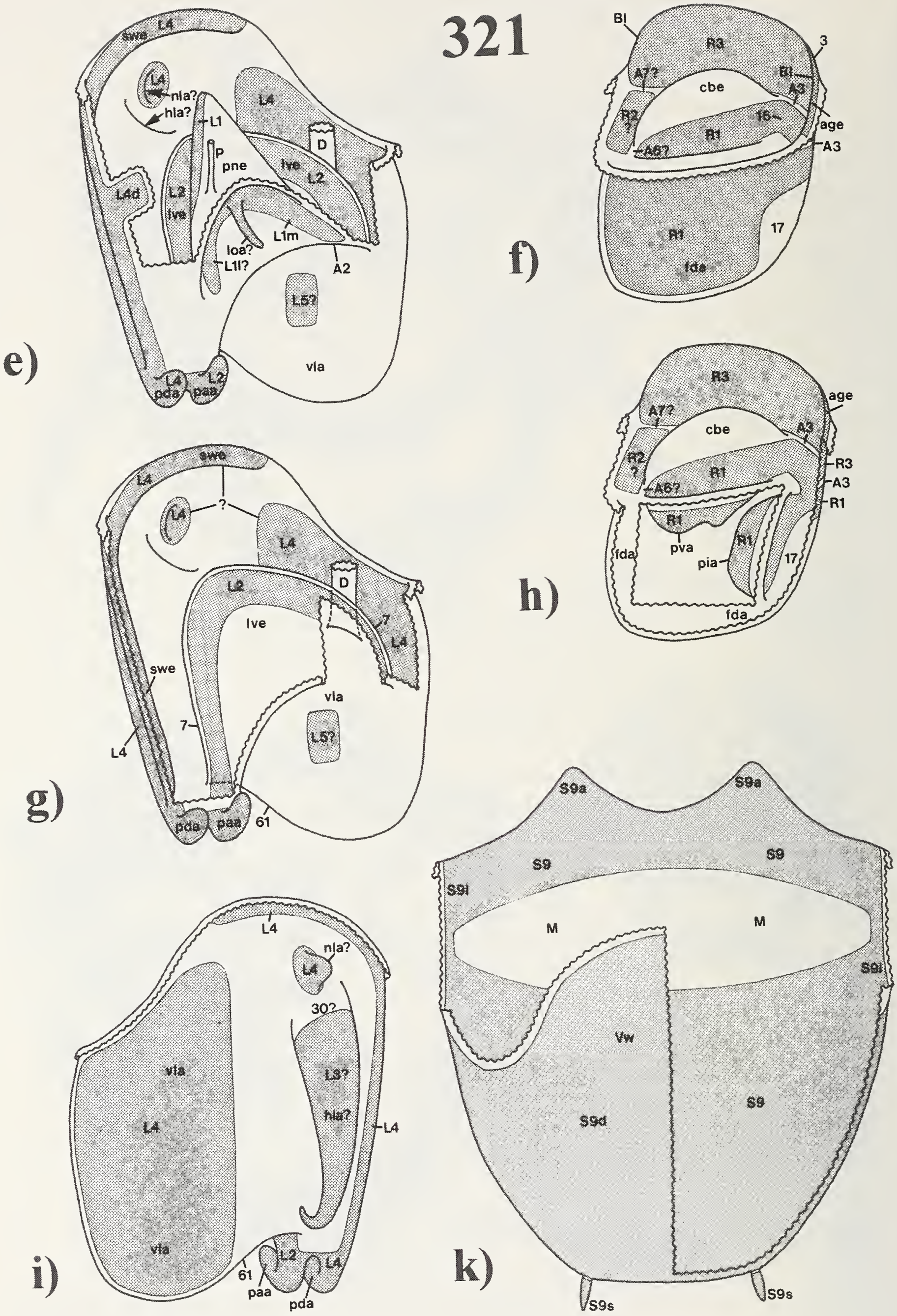
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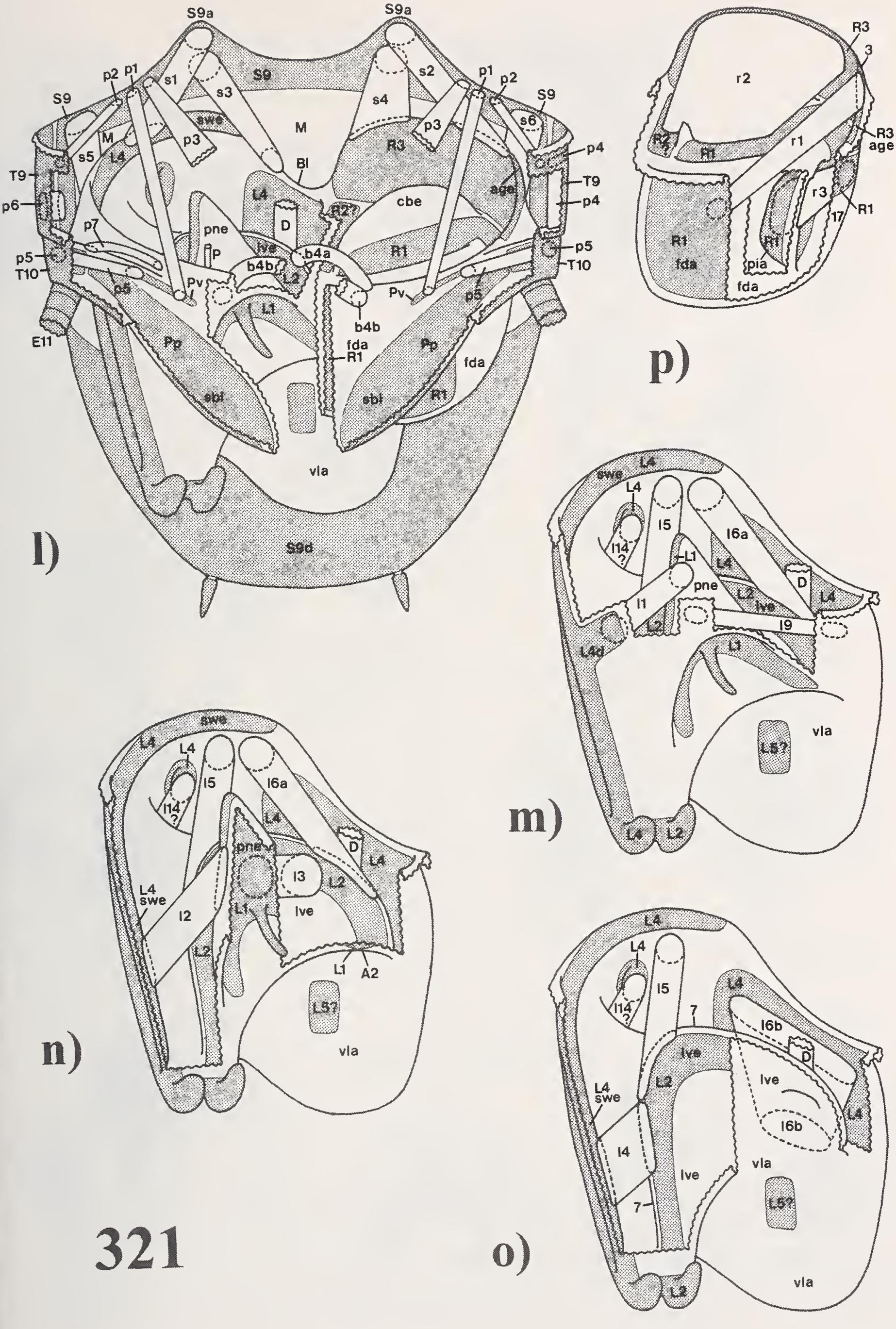
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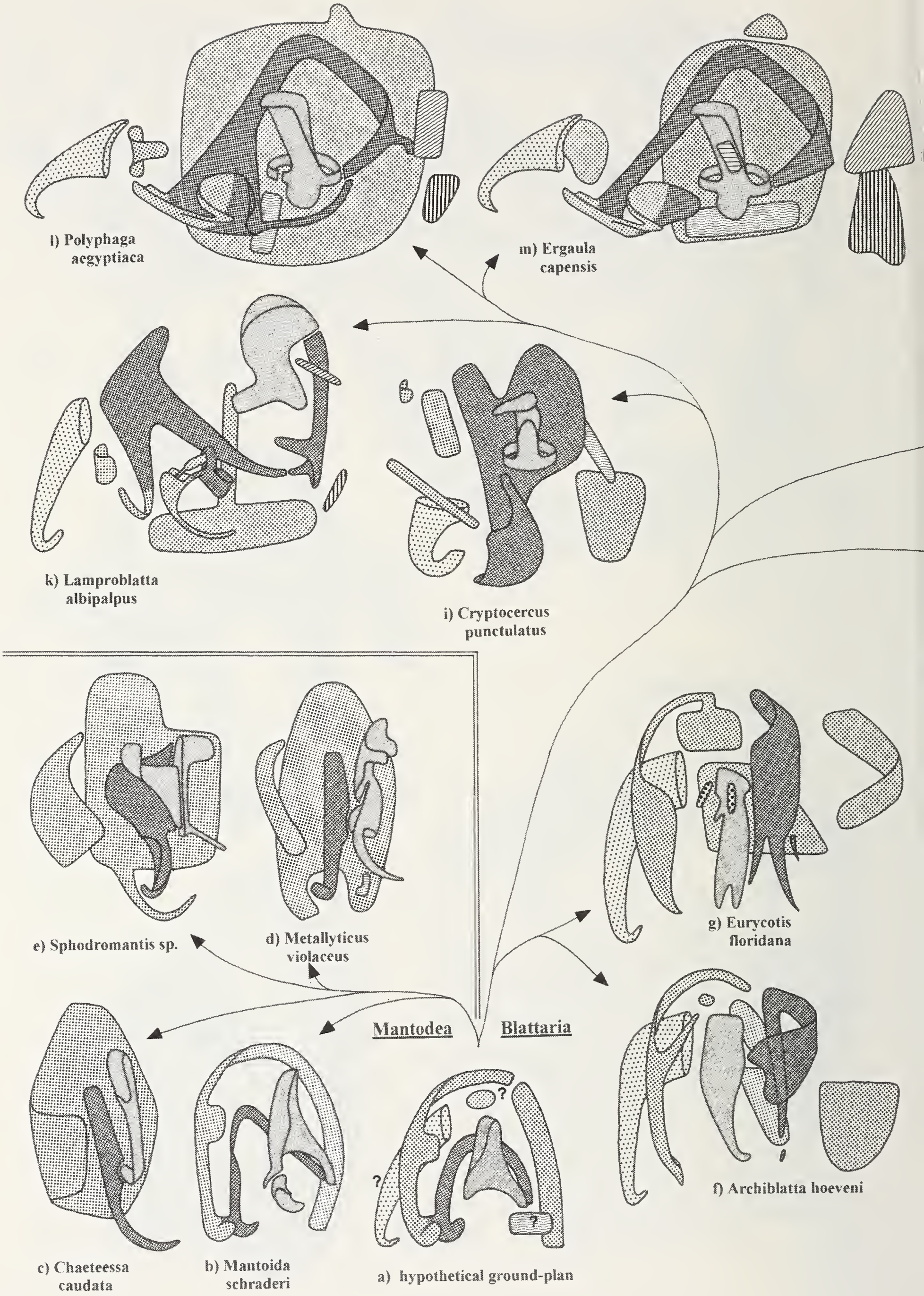
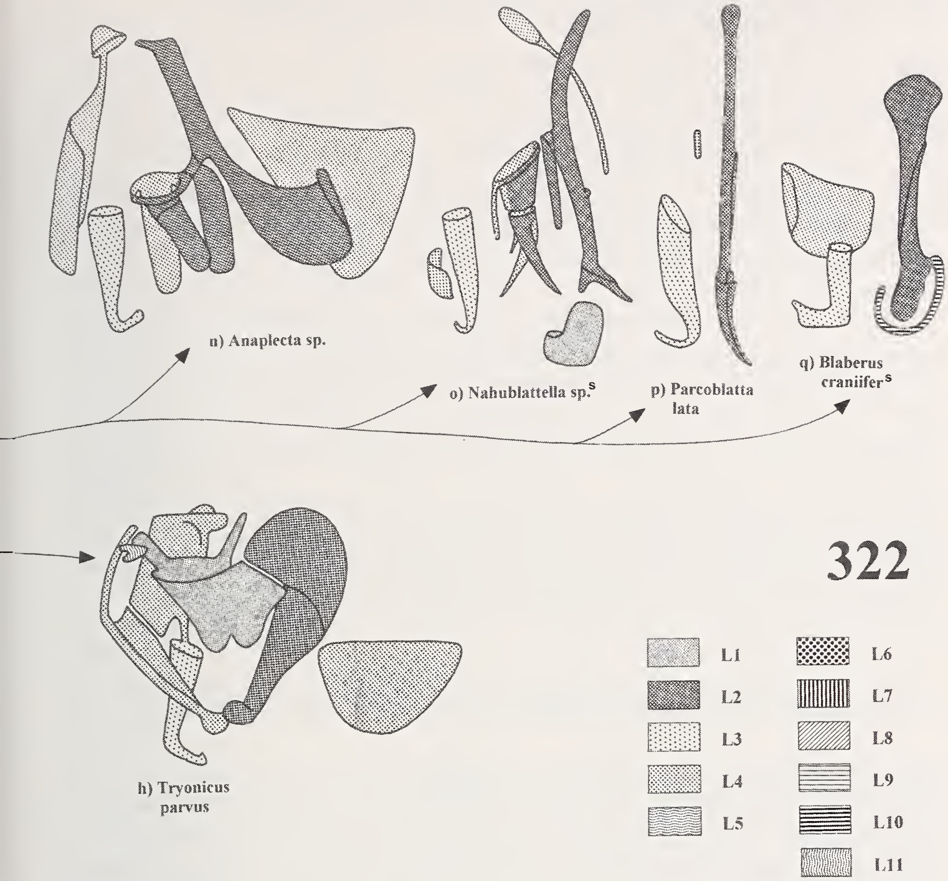

l) Polyphaga aegyptiaca
m) Ergaula capensis
k) Lamproblatta albipalpus
i) Cryptocercus punctulatus
e) Sphodromantis sp.
d) Metallyticus violaceus
g) Eurycotis floridana
f) Archiblatta hoeveni
Mantodea
Blattaria
?
?
?
c) Chaeteessa caudata
b) Mantoida schraderi
a) hypothetical ground-plan



322

Fig.322: Left complex, evolution of main sclerites. – Only the sclerites of the left complex are shown – largely in their natural arrangement. Dorsal views. Species with "S" behind their names have side-reversed phallomeres, and a mirror-image of the original preparation is shown. The branching black lines represent the assumed phylogeny. The ground-plan is in some respects unclear (? in fig.322a, discussions in 6.3.1., 6.4., 6.5.): Presence or absence of sclerites **L3** and **L5**; connection or separation of the **L4**-sclerites in the anterior ventral wall.

In each of the sections 6.1.-6.4. and 6.7., as a first point, the homologies between Blattaria and Mantodea will be analysed. This will be done by a discussion of selected species of both groups which show similarities in the respective elements. Since Mantodea are not a subgroup of Blattaria, and vice versa, this comparison is an outgroup comparison for Blattaria as well as for Mantodea. Thus, it can serve (1) to reconstruct features of the common ground-plan of Blattaria and Mantodea and (2) to determine polarities of characters within Blattaria and within Mantodea. The ground-plan features will be shortly summarised within each section as a second point, and the complete ground-plan will be presented in chapter 7. As the third and fourth points of each section, the homologies, the special conditions, and, in part, the evolution of the respective elements will be discussed for Mantodea and then for Blattaria. The different states of the various characters, their distribution over the taxa, and their polarities will in most cases become clear from these discussions. An evaluation of the results in terms of evolution and phylogeny will be done in 7.2.-7.8.. Fig.322-333 show the homology relations of the elements discussed.

6.1. Left complex I: Main sclerites L1 and L6 and associated elements

6.1.1. Comparison between Blattaria and Mantodea

All Mantodea and most Blattaria have a pouch (**pne**) in the dorsal part of the left complex, the walls of which are largely sclerotised (sclerite **L1**). The membranous part of the **pne**-wall is on the right side in Mantodea (e.g. fig.44, 45) but left-dorsal or dorsal in Blattaria (e.g. fig.151). Arguments for the homology of **L1** and **pne** in Mantodea and Blattaria and indications for the ground-plan morphology of these elements can best be found by comparing *Mantoida* (fig.44, 45) with *Polyphaga* (fig.120, 121), *Ergaula* (fig.105, 106), and *Cryptocercus* (fig.153, 154); other Blattaria can also contribute.

In *Mantoida, Polyphaga, Ergaula* (both species), and *Cryptocercus* **L1** and **pne** show several similarities:

1. The **pne**-pouch lies in the central dorsal wall of the left complex and is an invagination to the anterior.
2. The anterior part of **L1** (region **L1a** in fig.323d,i,l,m) occupies most of the **pne**-wall and is hood-shaped.
3. The right posterior part of **L1** is a distinct arm-like extension (region **L1m** in fig.323d,i,l,m).
4. A stout muscle runs from the posterior or central part of **L1** to **L2** in the dorsal wall of the **lve**-pouch: **l3** (fig.50, 128, 158, 159; *Ergaula*: only *E. capucina* studied, no figure).

5. Another stout muscle runs from the anterior or central part of **L1** to **L4**-sclerotisations in or near the left edge of the left complex: **l2** (fig.49, 128, 156; *Ergaula*: only *E. capucina* studied, no figure).

Mantoida, Polyphaga, and *Cryptocercus* have in common that:

6. The phallomere-gland **P** opens into the membranous part of the **pne**-wall. (In *Ergaula* the opening is beneath the **pne**-pouch and the **dca**-processes.)

Mantoida, Polyphaga, and *Ergaula* have in common that:

7. The extension **L1m** (fig.323d,l,m) articulates with **L2** (**A2** in fig.45, 46, 105, 118). This articulation is rather narrow. (There is no contact between **L1** and **L2** in *Cryptocercus*: **A2** is missing.)

Another feature is present only in *Mantoida* and *Cryptocercus*:

8. A stout muscle runs from the **pne**-pouch to **L4**-sclerotisations in the dorsal wall of the left complex, the latter insertion being right-dorsal to the **l2**-insertion: **l1** (fig.48, 155).

Regarding the **l2**-insertion on **pne**, *Mantoida* is more similar to other Blattarian species (compare feature 5.):

9. In *Mantoida* (fig.49), *Eurycotis* (fig.70), and *Anaplecta* (fig.221) **l2** has its right insertion in the left wall of the **pne**-pouch. (In *Cryptocercus*, *Ergaula*, and *Polyphaga* this insertion is on the anterior face of the **pne**-pouch.)

In *Cryptocercus, Polyphaga*, and *Ergaula* **L1** has, apart from **L1m** on the right side, another distinct extension at its left posterior margin (region **L1l** in fig.323i,l,m). In *Cryptocercus* and *Ergaula* **L1l** joins **L1m** ventrally to form a complete sclerite-ring (region **L1r** in fig.323i,m). *Mantoida* has no **L1l**-extension, but other Mantodea have such an extension:

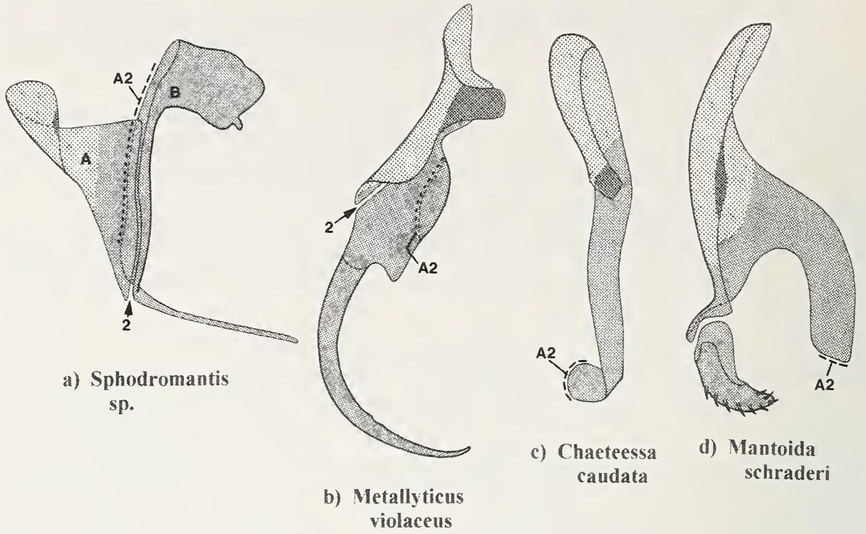
10. In *Metallyticus* (fig.323b) and *Chaeteessa* (fig.323c) **L1** has an extension at its dorsal margin, which could well be homologous with the **L1l** of the respective Blattaria. (In *Mantoida*, fig.323d, the corresponding area of **L1** is designated as a vestigial **L1l**.)

The formation of a sclerite-ring, however, does not seem to be a ground-plan element:

11. In *Mantoida*, *Chaeteessa*, *Metallyticus*, as well as in *Archiblatta* (fig.54, 55, 323f) and *Eurycotis* (fig.67, 68, 323e) the posterior part of **L1** does not form a sclerite-ring.

Many Blattaria and Mantodea have distinct cuticular evaginations behind **L1**, which are either membranous or sclerotised by posterior parts of **L1**: **dca** (e.g. in fig.153) and **loa** (e.g. in fig.45, 54). The exact homology relations can hardly be determined for these formative elements. Only in some cases homology is evident, e.g. for the paired membranous cushions of *Polyphaga*, *Cryptocercus*, *Tryonicus angustus*, and probably *Archiblatta* (**dca** in fig.120, 153, 107, 54). It is unclear whether these **dca**-processes are elements of the common ground-plan of Blattaria and Mantodea and what their morphology was like in this ground-plan. As regards the process **loa**, *Mantoida* resembles *Archiblatta*:

12. At the posterior margin of **L1** there is a completely sclerotised, curved and thorned process (**loa** in fig.45, 54). Its sclerotisation is connected with **L1** in *Archiblatta* but articulated with **L1** in *Mantoida*. However, the homology of these processes is not certain.



a) Sphodromantis sp.

b) Metallyticus violaceus

c) Chaeteessa caudata

d) Mantoida schraderi

323

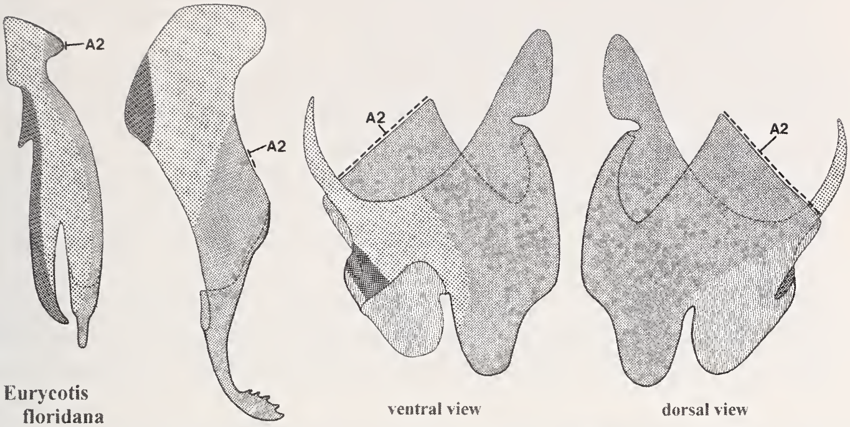
▨ L1a

▩ L1l

▨ L1m

▤ L1r

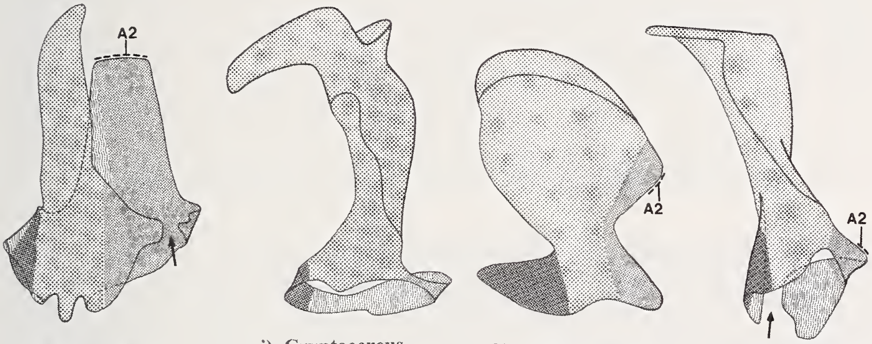
Fig.323: Left complex, homologous regions of main sclerite **L1.** – Only **L1**-sclerotisations are shown. Dorsal views, only left drawing of fig.323g and right drawing of fig.323n in ventral view. **L1** is divided into the four regions **L1a, L1l, L1m**, and **L1r** (definition in 6.1.1.). If **L1** is divided into several sclerites, these are labelled with the capital letters used in the text and in fig.1-319 (e.g. **B** = **L1B**). The part of the sclerite margin which forms articulation **A2** with sclerite **L2** is indicated by dashes; if part of this margin is covered by other parts of the sclerite, the dashes are shorter.



e) Eurycotis floridana

f) Archiblatta hoeveni

g) Tryonicus parvus

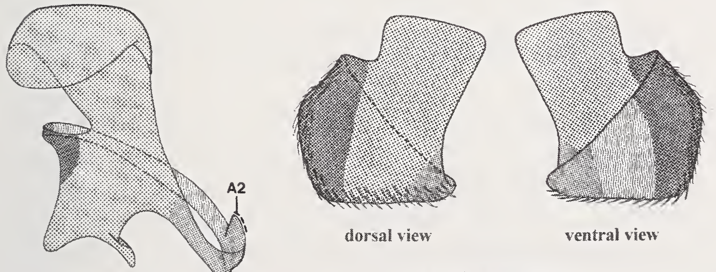


h) Tryonicus angustus

i) Cryptocercus punctulatus

k) Lamproblatta albipalpus

l) Polyphaga aegyptiaca



m) Ergaula capensis

n) Nahublattella sp.

323

The membranous part of the **pne**-wall takes different positions within **pne**:

13. It is right-dorsal in *Mantoida* (fig.44, 45), dorsal in *Archiblatta* (fig.53, 54), left-dorsal in *Polyphaga*, *Ergaula*, and *Cryptocercus* (fig.117, 151). The ground-plan position can be assumed to be somewhere within this span.

This outgroup comparison suggests the similarities 1.-13. to be features of the common ground-plan of Blattaria and Mantodea (rather uncertain as regards 10.-12.).

Main sclerite **L1** is divided into four regions (fig.323):

- **L1a** (anterior): The large anterior part of **L1** within the **pne**-pouch (hood-shaped in most species).
- **L1m** (median): The extension at the median (right) posterior margin of **L1a**. **L1m** has an articulation **A2** with **L2**.
- **L1l** (lateral): The extension at the lateral (left) posterior margin of **L1a**.
- **L1r** (ring): The sclerotisation connecting **L1l** and **L1m** ventrally and giving the posterior part of **L1** the shape of a ring. (The ring can be complete or with a short gap.)

6.1.2. The elements in the common ground-plan of Blattaria and Mantodea

The features 1.-13. in 6.1.1. permit a reconstruction of the ground-plan morphology of **L1**, **pne**, and some adjacent elements (fig.321e,g): Region **L1a** is hood-shaped, is situated within a deep pouch **pne**, and has two posterior extensions: regions **L1l** (not certain) and **L1m** (long and distinct). **L1l** and **L1m** do not join each other ventrally to form a sclerite-ring (no region **L1r**). **L1m** articulates with **L2** (**A2**). The membranous part of the **pne**-wall is more or less dorsal and contains the opening of the phallomere-gland **P**. At the posterior margin of **L1** there is a thorned **loa**-processes (not certain). Muscles **l1**, **l2**, and **l3** are present. **l2** inserts on the left wall of the **pne**-pouch. **l1** is dorsal to **l2**.

6.1.3. Homology relations and character states of the elements in Mantodea

In *Chaeteessa* (fig.32, 34), *Metallyticus* (fig.24, 25), and *Sphodromantis* (fig.10) **L1** and the **pne**-pouch are similar to *Mantoida* (fig.44, 45): The anterior part of **L1** lies in the deep **pne**-pouch and is more or less hood-shaped. The phallomere-gland **P** (not found in *Metallyticus*) opens into the membranous part of **pne**. A large extension **L1m** (fig.323a-d) from the right posterior part of **L1** articulates (**A2**) with the right part of **L2**.

In contrast to *Mantoida*, the membranous part of the **pne**-wall is not right-dorsal but on the right or right-ventral (*Sphodromantis*); this rotation (clockwise as viewed from behind) is regarded as derived.

The articulation area **A2** is elaborated differently: In *Mantoida* **A2** is exactly on the edge **1** between the pouches **pne** and **lve** (fig.45, 46). In the other species the **L1m**-extension bends around edge **1** into the dorsal wall of the **lve**-pouch, and here **L1m** and **L2** lie in the same plane (fig.10, 11, 25, 26, 34, 35; fig.323a-c). This is assumed to be a derived condition. The sclerotisation bending around the edge is narrow in *Chaeteessa* but much broader in *Metallyticus* and *Sphodromantis*. In *Metallyticus*, the right, bending part of **L1m** is partly cut off from the basal part of **L1m** by the stripe of membrane **2** (fig.25, 323b). In *Sphodromantis* this separation is complete (**2** in fig.10, 323a), and **L1** has divided into two sclerites **L1A** and **L1B**. This comparison with *Metallyticus* reveals that in *Sphodromantis* **L1B** is a right part of the **L1m**-region, that the articulation labelled **A2** in fig.11 is the true **A2**, and that the membranous stripe **2** is a derived feature.

The homology relations of the processes behind the **pne**-pouch and on the edge **1** between the pouches **pne** and **lve** (**loa**, **paa**, **afa** in fig.10, 25, 34, 45) are – with the exception of **paa**, which is discussed in 6.2.3. – somewhat difficult: The sclerotisation of **loa** originates in *Sphodromantis* (fig.10) and *Metallyticus* (fig.25) from that part of **L1** to the right of the membranous stripe **2** (fig.323a,b), and the base of **loa** is posterior to the bending part of **L1m**. Thus, homology is assumed for these **loa**-processes. The base of **loa** is far to the right in *Sphodromantis*, but more to the left, in the ventral wall of the **pne**-pouch, in *Metallyticus*. **loa** of *Mantoida* protrudes from the left-dorsal wall of the **pne**-pouch, but homology with the **loa** of the other species seems possible if a shift of **loa** is assumed – with the situation in *Metallyticus* being intermediate. *Chaeteessa* has no **loa**-process. In *Sphodromantis* the sclerotisation of **loa** is reduced to a stripe in the dorsal wall (compare feature 12. in 6.1.1.).

The part of **L1m** bending ventrad around edge **1** sclerotises anteriorly the low bulge **afa** in *Metallyticus* (fig.25, 26) and the hammer-shaped **afa** in *Sphodromantis* (fig.10, 11); these **afa** might be homologous. The membranous lobes of *Mantoida* and *Chaeteessa* (**afa** in fig.34, 45) might be homologous with the **afa** of *Metallyticus* and *Sphodromantis* (not with **loa**), since their bases are anterior (not posterior) to the bending part of **L1m**. If this homology is true, in *Metallyticus* and *Sphodromantis* the **L1m**-region has, while becoming broader, additionally expanded onto the **afa**-processes.

6.1.4. Homology relations and character states of the elements in Blattaria

Ergaula, Polyphaga, and *Cryptocercus*

In *Ergaula* (fig.105, 106, 323m), *Polyphaga* (fig.120, 121, 323l), and *Cryptocercus* (fig.153, 154, 323i) **L1** and **pne** are quite close to the ground-plan but also have some probably derived features: The anterior end of **L1** is plateau-like, and the insertion of **l2** has shifted to this plateau (fig.128, 156; compare 9. in 6.1.1.). The extensions **L1l** and **L1m** curve ventrad and approach each other. However, only in *Ergaula* and *Cryptocercus* the extensions unite to form a complete ring; in *Polyphaga* the ring is open (arrow in fig.323l). The **dca**-processes – with their bases encircled by the **L1**-ring – are very similar in *Cryptocercus* and *Polyphaga*. In *Ergaula* the morphology of **dca** is quite different. Only *Cryptocercus* has a sclerotised peak (**18** in fig.153) in between the **dca**, and the close contact between **L1m** and **L2** (**A2**-articulation) has been lost (fig.151).

Tryonicus angustus and *T. parvus*

In *Tryonicus angustus* (fig.107, 108, 323h) **L1**, **pne**, and **dca** are similar to the previous species: The **pne**-pouch is very distinct and deep. The opening of the phallomere-gland has the same position as in *Polyphaga* and *Cryptocercus* (compare fig.107 and 120, 153). **L1** articulates with **L2** (**A2** in fig.107, 108). The shape of the **dca** resembles *Polyphaga* and *Cryptocercus* (fig.107, 120, 153). The extensions **L1l** and **L1m** are distinct (fig.323h) and form a (open) sclerite ring encircling the **dca**-processes. The sclerotised peak **18** (fig.107, 108) resembles that of *Cryptocercus* (**18** in fig.153), but its sclerotisation is connected with the **L1**-ring dorsally and ventrally.

Some features are certainly derived (compared with the previous species and with the ground-plan): **L1a** (fig.323h) and **pne** are flat (not hood-shaped). The **L1**-ring is not complete since **L1m** has a gap between its base on **L1a** and **A2** (arrow in fig.323h; this situation differs from *Polyphaga* where the ring has a gap ventrally between **L1l** and **A2**: arrow in fig.323l). **A2** has become a broad hinge-like articulation, and the part of **L1m** next to **A2** is strongly enlarged (compare fig.323h and i,l,m). **L1**, **pne**, and **dca** are – compared with *Ergaula*, *Polyphaga*, and *Cryptocercus* – rotated 40° (counterclockwise as seen from behind): The membranous part of the **pne**-wall (removed in fig.107) is on the left.

In *Tryonicus parvus* (fig.94, 95, 323g) **L1**, **pne**, and **dca** are even further rotated, and the membranous part of the **pne**-wall is ventral. Compared with *Polyphaga* or *Cryptocercus*, **L1** and **pne** are rotated 120°; compared with e.g. *Sphodromantis*, where **L1** and **pne** are rotated in the opposite direction, the angle of rotation is 300°. Therefore, in comparing *T. parvus* with the other species, **L1** should be viewed from ventrally (fig.323g, left picture). The anterior part of **L1** (**L1a** in fig.323g) is a flat ribbon in the dorsal wall (rotation! former ventral wall) of the distinct but narrow anterior part of the pouch **pne** (fig.95). The position of the phallomere-gland opening is, having the **L1**-rotation in mind, exactly the same as in *Cryptocercus* or *T. angustus*. The sclerotisation of the two bulges **dca** posterior to **L1a** can be interpreted (fig.323g) as a complete sclerite-ring composed of the regions **L1m**, **L1l**, and **L1r** (like in *Ergaula* and *Cryptocercus*) and an additional expansion of **L1** onto **dca**. The **L1l**-arm runs mesad because of the **L1**-rotation. **L1m** first extends far laterad, then it turns to the left, where it forms, like in *T. angustus*, a large plate and a broad hinge-like articulation **A2** with **L2**.

Archiblatta, other Blattinae, and *Eurycotis*

In *Archiblatta* **L1**, **pne**, and **dca** (fig.53, 54, 323f) can be easily identified: They take a position in the central dorsal wall of the left complex. The anterior part of **L1** (**L1a**-region in fig.323f) lies in a pouch **pne**. At its right margin **L1** articulates with **L2** (**A2** in fig.54). The **dca** are membranous cushions at the left-posterior margin of **L1** (fig.54); however, the **dca** are not very similar to those of e.g. *Cryptocercus* (fig.153). **loa** resembles **loa** of Mantodea (feature 12. in 6.1.1.). Some features can be regarded as derived: The **pne**-pouch is less deep and distinct than in all species discussed before (fig.53, 54). The **L1a**-region has become level as in *Tryonicus*. The phallomere-gland (**P** in fig.56) opens in the same position as in *Ergaula* – beneath the **dca**-processes (fig.54-56, 105, 106). (This situation has certainly been achieved independently in *Ergaula* and *Archiblatta*). There are no distinct arms **L1l** and **L1m** (and also no ring-formation or region **L1r**). The vestiges of **L1l** and **L1m** can be localised according to their characteristic relative positions (fig.323): **L1l** is left-anterior to the **dca**-cushions; **L1m** is right-anterior to the **dca**-cushions and bears articulation **A2**.

In other Blattinae (with *Deropeltis*, *Blatta*, and *Periplaneta* studied) **L1** is similar to *Archiblatta*, but the **dca**-processes are rather variable, and the **pne**-pouch is less distinct (as in *Eurycotis*, see below). The musculature of these species (not studied in *Archiblatta*) confirms the assumed homologies for **L1** and **pne**: Like in e.g. *Mantoida* or *Cryptocercus*, there is a stout muscle from **L1a** to **L4**-sclerotisations (compare fig.53: **L4C**) in the left edge of the left complex (**l2**) and another one to **L2** (compare fig.55) in the dorsal wall of the **lve**-pouch (**l3**). Muscle **l1** is missing. A derived feature peculiar to Blattinae (and *Eurycotis*, fig.70) is the shift of the left insertion of muscle **b4b** to the anterior summit of the **pne**-pouch (discussion in 6.7.1.).

In *Eurycotis* (fig.65-67) the characteristics of **L1a**, **L1l**, **L1m**, and **A2** (fig.323e) and the position of the phallomere-gland opening (**P** and edge **6** in fig.54, 55, 67, 68) are quite the same as in *Archiblatta*. The pouch-shape of **pne**, however, is by far less distinct. The processes posterior to **L1** could be **dca** (as labelled in fig.66, 67) or **loa** (the right one?). The insertion of **l2** (fig.70) is still on the left part of the **pne**-pouch but has shifted from **L1** to the adjacent membrane. (The position of the **l2**-insertion on **L4** is the same as e.g. in *Mantoida*: discussion in 6.3.1.). Like in Blattinae, muscle **l1** is missing. Muscle **l3** from **L1** to **L2** is represented by three bundles (**l3a,b,c** in fig.71), which together occupy the same insertion area as the **l3** of Blattinae, and an apomorphic tripartition can be assumed. Muscle **b4b** inserts, like in the Blattinae, anteriorly on the **pne**-pouch (fig.70). The origin and homology of the sclerites **L6A** and **L6B** (fig.66, 322g) only found in *Eurycotis* is questionable: new sclerites or derivatives of **L1**? Homology with sclerite **L8** of *Ergaula*, *Polyphaga* (fig.117, 322l,m), and *Lamproblatta* (fig.177, 322k) is unlikely (different muscle insertions); homology with **L9** of *Ergaula* (fig.105) is also not very probable.

Lamproblatta

Like in the other species, **L1** lies in the dorsal wall of the left complex, its anterior part **L1a** (fig.323k) is inside a deep pouch (**pne** in fig.177), and its right part articulates with **L2** (**A2** in fig.178). Furthermore, **L1** and **pne** can be identified by the characteristic muscle connections with the area of **L4** in the left edge of the left complex (**l2** in fig.184; the **L4**-sclerotisations are highly modified, discussion in 6.3.4.) as well as with **L2** (**l3** in fig.187; the insertion on **L2** is far posteriorly). Like in *Polyphaga, Ergaula*, and *Cryptocercus*, the **l2**-insertion on **L1** has shifted far anteriad. Muscle **l1** is missing.

As compared with other Blattaria and Mantodea, **L1** and **pne** have shifted right-anteriad. Most of the anterior part of **L1** (**L1a** in fig.323k) is level, but, in contrast to Blattinae, *Eurycotis*, and *Tryonicus*, there is a reminiscence of the hood-shape since the anteriormost part of **L1** bends into the dorsal wall of **pne** (fig.177, 178). This dorsal part of **L1a** may even be regarded as a vestige of an anterior plateau which has been inclined posteriad. Sclerite arms (regions **L1l** and **L1m**) are not distinct. The part of **L1** containing articulation **A2** can be designated as the vestigial **L1m**-region (fig.323k; that **A2** in fig.178 really is **A2** is shown in 6.2.4.). The demarcation of **L1l** in fig.323k is tentative. For the process **dca** (fig.177) the homology with the **dca** (or **loa**, fig.54?) of the other species is questionable. Region **L1r** is missing (no sclerite ring). The phallomere-gland opens, like in *Archiblatta* or *Ergaula*, into the membrane extending ventrad from the posterior margin of **L1** (**P** in fig.178); however, parts of **L2** and **L4** (with the processes **paa** and **pda**, fig.178) have shifted into the interspace between **L1** and the opening (compare in 6.6.4.).

Anaplecta

In the previous species **L1** and **pne** are in the central dorsal wall. In *Anaplecta* the corresponding area is membranous and just somewhat depressed (fig.209). This area is interpreted as the vestige of a **pne**-pouch, with **L1** completely lost. This assumption is supported by the muscles **l2** and **l3** (fig.201, 221), which run to **L4**-sclerotisations in the left edge of the left complex (**l2**) and to **L2** in the dorsal wall of the **lve**-pouch (**l3**). These are the same connections as in the species discussed before. **l1** is, like in some other species, missing. (The homology of **L4** and **L2** is discussed in 6.2.4. and 6.3.4). Further support comes from McKittrick (1964): She identifies in another species of *Anaplecta* ("sp. *C*") a sclerite **L1** (McKittrick's fig.112), which has the same position as the assumed **pne**-vestige in the species I studied.

Nahublattella

L1' and **pne** (fig.242, 243) show some characteristic features: They take a dorsal position. The level anterior part of **L1'** (**L1a** in fig.323n) occupies the ventral wall of a pouch **pne**. The posterior part of **L1'** completely sclerotises a bulge-like process (**dca** in fig.243, 244). This is interpreted as a sclerite-ring (regions **L1l**, **L1m**, and **L1r** in fig.323n) encircling the **dca**-process which has spread posteriad over the whole **dca** (similar to but more complete than in *Tryonicus parvus*, compare fig.323g and n). Further arguments for homology come from the muscles on **pne**: **l1** (fig.249) runs leftward to the sclerite-ribbon **L4d'** (which is probably homologous with **L4d** of *Mantoida*, fig.44, and *Cryptocercus*, fig.150: discussion in 6.3.4.; compare **l1** of *Mantoida*, fig.48, and *Cryptocercus*, fig.155). **l3** (fig.250) runs to **L2** in the dorsal wall of the **lve**-pouch (compare **l3** of e.g. *Mantoida*, fig.50, *Polyphaga*, fig.128, *Cryptocercus*, fig.158, 159, and *Anaplecta*, fig.221); the homology relations of **L2** and **lve** are discussed in 6.2.). **l9a** (fig.249) runs to the membrane to the right of **L1'** – as do **l9** in *Anaplecta* (fig.221) and the posterior part of **l9** in *Polyphaga* (fig.127, 129).

The right insertion of **l2** (fig.249) has shifted away from the **pne**-pouch (discussion in 6.3.4.). Muscle **l28**, with both insertions on **L1'**, is peculiar to *Nahublattella* (fig.250). Like in *Cryptocercus*, but in contrast to the other species, **L1** and **L2** are no longer in contact (articulation **A2** lost).

Parcoblatta and *Blaberus*

There are no vestiges of **L1** and **pne**. Muscles **l1** and **l3** have been lost. **l2** has shifted in the same way as in *Nahublattella* (discussion in 6.3.4.).

6.2. Left complex II: Main sclerite L2 and associated elements

6.2.1. Comparison between Blattaria and Mantodea

In the Mantodean and in several Blattarian species the **L2**-sclerotisations, the **lve**-pouch, the **vla**-lobe, the processes **paa** and **pda**, and the genital opening show the same principal arrangement and similar positions relative to **pne** and **L1**. The proportions of these elements, however, can be very different. To determine the homology relations between Blattaria and Mantodea and to reconstruct the ground-plan a comparison between *Mantoida, Polyphaga, Tryonicus, Archiblatta*, and *Eurycotis* is most useful. Some **L4**-sclerotisations and the **pda**-process will be considered in this section, but the homology discussion of these elements will be completed in 6.3.

The right parts of **L2** and of the **lve**-pouch are level in Mantodea (fig.11, 26, 34, 46) but curve dorsad and back to the left in most Blattaria (fig.54, 55, 94, 95, 118, 122). If this up- and recurved area is extensive, the walls of the **lve**-pouch cannot be designated as dorsal and ventral: The wall corresponding to the dorsal **lve**-wall of Mantodea (containing **L2**) is the inner **lve**-wall; the wall corresponding to the ventral **lve**-wall of Mantodea (mostly membranous) is the outer **lve**-wall (compare in 5.5.-5.7.). The respective walls of **lve** are homologous, the absence or presence of a curvature being the only difference. The **vla**-lobe usually shows the same curvature (in the figures **vla** is often pulled to the right), but the walls of **vla** will be designated throughout as dorsal and ventral.

Mantoida and *Polyphaga* have a lot of features in common:

1. The pouch **lve** (fig.46, 122) is flat and lies ventral to the pouch **pne**. However, in *Polyphaga* **lve** spans almost the whole width of the left complex and is on the whole very large, whereas in *Mantoida* **lve** is restricted to the right part and much smaller.
2. Sclerite **L2** (fig.46, 122) is arch-shaped and extends along the anterior and lateral edges of the **lve**-pouch (edges **7** in fig.46, 122). However, in *Mantoida* **L2** is mainly restricted to the dorsal **lve**-wall (only its leftmost part bends into the ventral wall, compare fig.46, 47), whereas in *Polyphaga* **L2** bends into the ventral wall all along the edge **7** (compare **7** and **L2** in fig.122 and 123).
3. The left part of **L2** leaves the **lve**-pouch posteriorly, bends around the posterior edge of the left complex into the dorsal wall, and sclerotises a process (**paa** in fig.46, 117).
4. This **L2**-sclerotisation on **paa** is on its left connected with the sclerotisation of a closely adjacent process (**pda** in 44, 117). However, the shapes of both **paa** and **pda** are quite different in *Mantoida* and *Polyphaga*.
5. The right end of **L2** articulates with the **L1m**-region (**A2** in fig.45, 46, 118). However, the right parts of **L2** are up- and recurved in *Polyphaga* but level in *Mantoida*.
6. A muscle (**l3** in fig.50, 128) runs from the dorsal wall of **lve** to **pne** (compare in 6.1.1.).
7. A muscle (**l4** in fig.50, 132) runs from the left edge of **lve** to sclerotisations in the left part of the left complex. However, the latter sclerotisations are very different in *Polyphaga* and *Mantoida*.
8. Ventral to the **lve**-pouch there is a broad ventral lobe (**vla** in fig.47, 123). The anterior part of the dorsal **vla**-wall is at the same time the ventral **lve**-wall.
9. The dorsal **vla**-wall is mostly membranous. The ejaculatory duct (**D** in fig.46, 47, 123, 124) opens into the right anterior part of this membrane.
10. The ventral **vla**-wall is part of the ventral wall of the left complex (fig.41, 115) and is largely sclerotised (by **L4** or **L4M**, respectively).
11. Two or three muscles inserting in the anterior ventral wall of the left complex run to the **lve**-pouch: The leftmost one inserts on the left anterior edge of **lve** (**l5** in fig.50, 133).

12. The anterior right muscle (or the anterior part of the right one in *Mantoida*) inserts on the right anterior edge of **lve** (anterodorsal part of **l6** in fig.50; **l6a** in fig.133).
13. The posterior right muscle (or the posterior part of the right one in *Mantoida*) runs to the ejaculatory duct near its opening (posteroventral part of **l6** in fig.52, **l6b** in fig.132). Muscle **l6** is undivided in *Mantoida*; in *Sphodromantis*, however, **l6** is divided in the same way as in *Polyphaga* (compare **l6a** and **l6b** in fig.132, 133 and 16, 18).

All features listed for *Polyphaga* are also true of *Ergaula* (both species, muscles only investigated in *E. capucina*) – with the exception that the **pda**-process is missing.

Homology is assumed for all these similarities between *Mantoida* and *Polyphaga* and for all elements given the same name. 1.-13. are regarded as features of the common ground-plan of Blattaria and Mantodea. Some of the mentioned differences between *Polyphaga* and *Mantoida* are bridged by various other Blattaria, which will be discussed subsequently; these species, however, are in some features rather different from *Mantoida* and/or *Polyphaga*.

The **lve**-pouch and **L2** of *Tryonicus* (fig.95) are, like **lve** and **L2** of *Polyphaga*, ventral to and to the right of the **pne**-pouch, and the right parts of **L2** and **lve** curve dorsad and back to the left (compare fig.95 and 94). In contrast to *Polyphaga*, this up- and recurved part is by far more extensive, and it is directed anteriad and conceals the **pne**-pouch from dorsally. Some features correspond with both *Mantoida* and *Polyphaga*: The relative position of articulation **A2** is the same; the dorsal **lve**-wall is largely sclerotised by **L2**; the left posterior part of **L2** leaves the **lve**-pouch and provides the sclerotisation of a process (**paa** in fig.94, 97), which is to the left connected with the sclerotisation of another process (**pda** in fig.94); the outer (= ventral) **lve**-wall is membranous; this membrane is at the same time the dorsal **vla**-wall (fig.87, 91) and contains the genital opening (**D** in fig.91, 92) anteriorly; the ventral **vla**-wall is part of the ventral wall of the left complex and is largely sclerotised (by **L4G** in fig.87).

In some features *Tryonicus* is more similar to *Mantoida* than *Polyphaga* is, and these similarities are regarded as further features of the common ground-plan of Blattaria and Mantodea:

14. The **lve**-pouch of *Tryonicus* does not extend as far to the left as in *Polyphaga* but is restricted to the right part of the left complex as in *Mantoida* (compare feature 1.; fig.46, 97, 122).
15. **L2** does not, in contrast to *Polyphaga*, occupy the margins of the outer = ventral **lve**-wall but is restricted to the inner = dorsal **lve**-wall (fig.92, 94-98); this situation approximates that in *Mantoida* (compare feature 2.).
16. The shapes of both **paa** and **pda** are quite similar in *Mantoida* and *Tryonicus* (fig.44, 96; compare feature 4.): both are short and bulge-like, and **paa** is somewhat upcurved.

As a consequence, some features of *Polyphaga* (and *Ergaula*) are assumed to be derived: (1) the extension of the **lve**-pouch almost to the left edge of the left complex; (2) the **L2**-sclerotisation in the marginal ventral **lve**-wall; (3) the special shapes of **paa** and **pda**.

In some other features *Tryonicus* is certainly derived: (1) **L2** is much broader than in *Mantoida* and *Polyphaga* and has lost the arch-shape of the ground-plan since its dorsal part is directed anteriad (fig.94-97; compare feature 2). (2) Another feature concerns the left parts of the **vla**-lobe and the **lve**-pouch. In all three species the invagination of the **lve**-pouch (edge **7** in e.g. fig.96-98) and the free left edge of the **vla**-lobe (edge **61** in e.g. fig.87, 98) start at the same point in the ventral wall of the left complex. Anterior to this point the ventral **vla**-wall is confluent with the remaining ventral wall of the left complex (e.g. fig.87). This point takes a different position in the three species. In *Tryonicus* it is far anteriorly (fig.87): The left edge **61** of **vla** extends far anteriad, and the invagination of the **lve**-pouch begins far anteriorly. In *Mantoida* this point is by far more posteriorly (**7** and **61** in fig.41, 47): The left edge **61** of **vla** does not extend so far anteriad, the ventral **vla**-wall is except for its posteriormost part confluent with the remaining ventral wall of the left complex, and the invagination of the **lve**-pouch begins far posteriorly. In *Polyphaga* this point is at the posterior edge of the left complex (fig.122, 123): The **vla**-lobe does not have a free left edge **61** at all, the ventral **vla**-wall is completely confluent with the remaining ventral wall of the left complex (fig.115), and the invagination of the **lve**-pouch begins most posteriorly. The ground-plan state of this feature is assumed to be somewhere in between the situation of *Mantoida* and that of *Polyphaga*:

17. The ventral **vla**-wall is for most or all of its length confluent with the remaining ventral wall of the left complex, the left edge **61** of the **vla**-lobe ends far posteriorly or is missing, and the invagination of the left(-ventral) part of the **lve**-pouch begins far posteriorly.

Archiblatta likewise has a second pouch (**lve** in fig.54, 55) in the right part of the left complex. Like in *Polyphaga* and *Mantoida*, the sclerotisation **L2** (fig.55) runs like an arch along the edges of the pouch (**7** in fig.55). To the same extent as in *Tryonicus*, the right parts of **L2** and **lve** curve dorsad and back to the left, and in this area **L2** is very broad. Similar to *Mantoida* (fig.46, 47), **L2** is mostly restricted to the inner = dorsal **lve**-wall but bends into the outer = ventral **lve**-wall in the posterior left part of **lve** (at the posterior end of edge **7** in fig.55, 56). In some features *Archiblatta* corresponds with all previous species: **L2** articulates with **L1** (**A2** in fig.54, compare fig.94, 118, 45, 46). The left posterior part of **L2** leaves the **lve**-pouch and runs onto a process (**paa** in fig.55, 56), which thus corresponds to the **paa** of the other species in this aspect of its relative position.

The outer = ventral **lve**-wall is the dorsal **vla**-wall (fig.53; **vla** is pulled to the right), is membranous, and receives the ejaculatory duct (**D** in fig.53). The ventral **vla**-wall is a right part of the ventral wall of the left complex and is largely sclerotised (by **L4G** in fig.54). Like in *Polyphaga* only, the **vla**-lobe does not have a left edge **61** but its ventral wall is entirely confluent with the remaining ventral wall of the left complex.

Derived features of *Archiblatta* are (1) that **paa** is mostly membranous, (2) that there is no connection between the sclerotisations of **paa** (**L2**) and **pda** (**L4**), and (3) that **paa** is quite far removed from **pda** (compare fig.44 and 53). The two latter features are probably correlated with a derived feature of the **lve**-pouch: (4) The posteroventral part of **lve** has strongly receded to the right (compare edges **7** in fig.122, 46, and 55) and is restricted to a narrow right part of the left complex. The anteroventral part of **lve** is still deeply invaginated to the left and has become tongue-like.

Eurycotis is similar to *Archiblatta* but in some features more derived (compare fig.67, 68 and 54, 55): (1) **L2** is not an arch but a plate (probably the arms of the arch have fused).

(2) The posteroventral part of the **lve**-pouch is even more reduced than in *Archiblatta* (compare fig.55 and 68). (3) A deep notch (**9** in fig.63, 69) separates the right main part of the **vla**-lobe from the remaining parts of the left complex. This notch lies within the **vla**-lobe and does not correspond to the left edge **61** of **vla** in *Tryonicus* (compare fig.63 and 87). Like in the other species, the posterior part of **L2** extends onto a process (**paa** in fig.67, 68), which might thus be regarded as **paa** (compare fig.55). That **paa** is completely sclerotised is primitve compared with *Archiblatta*, but, like in *Archiblatta*, **paa** and its **L2**-sclerotisation have been far removed from **pda** and its **L4**-sclerotisation (fig.65).

The muscles of *Eurycotis*, compared with *Polyphaga* and *Mantoida*, confirm the assumed homologies: *Eurycotis* also has a muscular connection **l3** from **L2** to the posterior part of **L1** (**l3a,b,c** in fig.71, **l3** in fig.50, 128; compare in 6.1.) and a muscle **l4** from **L2** to the left edge of the left complex (fig.71, 50, 132). The **l4** of *Eurycotis* and *Mantoida* and their insertion areas are extremely similar and reveal an additional feature of the common ground-plan of Blattaria and Mantodea:

18. **l4** (fig.50, 71) runs from **L2** in the **lve**-pouch to the **swe**-apodeme on **L4**-sclerotisations in the left edge of the left complex (sclerites **L4** or **L4H**), where it inserts immediately ventral to muscle **l2** (fig.49, 70) coming from the **pne**-pouch.

Several muscles of *Eurycotis* run from the ventral wall of the left complex to the **lve**-pouch: **l6b** (fig.70, 71) runs to the ejaculatory duct near its opening, like **l6b** in *Polyphaga* (fig.132) and the ventral part of **l6** in *Mantoida* (fig.52). Another muscle (**l6a** in fig.73) runs to the anterior ventral wall of **lve**, and homology with either **l5** or **l6a** of *Polyphaga* (fig.133) and *Mantoida* (**l6a** = dorsal part of **l6** in fig.50) seems possible. Two other muscles (**l5a,b** in fig.72) insert on the ventral left edge of the **lve**-pouch, somewhat like **l5** in *Polyphaga* (fig.133); however, the ventral insertions of **l5a** and **l5b** are far posteriorly. Thus, for **l5a,b** and **l6a** of *Eurycotis* the homologies are not completely clear, but I suppose that the relations expressed by the designations are the most probable.

Concerning the common ground-plan of Blattaria and Mantodea, one question remains open: It is not decidable whether the right parts of **L2** and **lve** are level (like in Mantodea) or up- and recurved (like in Blattaria).

The definition of the regions of main sclerite **L2** (fig.324) is based on the primitive arch-shape of **L2**, which is present in its typical form in *Mantoida*, *Archiblatta*, and *Polyphaga*. From the left to the right four **L2**-regions are distinguished:

- **L2d** (dorsal): The sclerotisation of the process **paa**.
- **L2p** (posterior): The part of the **L2**-arch in the left posterior part of the **lve**-pouch.
- **L2a** (anterior): The part of the **L2**-arch in the anterior part of the **lve**-pouch.
- **L2m** (median): The part of the **L2**-arch in the right part of the **lve**-pouch. **L2m** has an articulation **A2** with **L1**.
- **L2v** (ventral): This is not defined as a separate region of **L2**. This term is used (mainly in fig.324) if large parts of **L2** have invaded the ventral wall of the **lve**-pouch; these parts of **L2** are not necessarily homologous in the species concerned.

The up- and recurved right parts of **L2** of Blattaria belong to the regions **L2m** and **L2a**.

6.2.2. The elements in the common ground-plan of Blattaria and Mantodea

The features 1.-18. in 6.2.1. permit a reconstruction of the ground-plan morphology of **L2**, **lve**, **paa**, and **vla**, and of the genital opening (fig.321e,g): The **lve**-pouch lies ventral to the **pne**-pouch; it is quite broad but does not reach the left edge of the left complex (and does not have a recess to the right in its posterior part). **L2** is largely restricted to the dorsal **lve**-wall and runs like an arch along the lateral and anterior edges of the **lve**-pouch. The left part (**L2p**-region) of the arch leaves the pouch posteriorly, and the posteriormost part (**L2d**-region) sclerotises the short, somewhat upcurved process **paa**. **L2d** is connected with the sclerotisation of the process **pda**, and **paa** and **pda** are close to each other. The right end of **L2**, or the dorsal left end in the case of **L2**-upcurving (**L2m**-region), articulates with **L1m** (**A2**). The ventral **lve**-wall is mostly membranous and is at the same time an anterior part of the dorsal **vla**-wall. The ejaculatory duct **D** opens into the right anterior part of this membrane. The ventral **vla**-wall is largely sclerotised and almost completely confluent with the ventral wall of the remaining left complex (i.e. the left edge **61** of **vla** is missing or does not extend far anteriad). Muscles **l3, l4, l5, l6a**, and **l6b** are present.

6.2.3. Homology relations and character states of the elements in Mantodea

In *Chaeteessa, Metallyticus*, and *Sphodromantis*, the main features of **L2, lve**, and **paa** are like in *Mantoida* (fig.11, 26, 34, 45, 46): **lve** lies ventral to the **pne**-pouch. **L2** is restricted to the dorsal **lve**-wall. The right parts of **L2** and **lve** are level. Posteriorly **L2** leaves the **lve**-pouch to provide the sclerotisation of a process which is therefore regarded as **paa**. The right margin of **L2** articulates with **L1** (**A2**; compare in 6.1.3.).

In contrast to *Mantoida, Metallyticus* and *Sphodromantis* have separated the sclerotisations of **paa** (**L2**) and **pda** (**L4**), and the processes are more distinct from each other and more prominent (fig.10-12, 23-26, 44-46). In *Chaeteessa* (fig.31, 32, 34) **paa** is very prominent, too, but a process **pda** is missing. Nevertheless, in this species, too, **L2** and **L4** are completely separated in the area concerned.

L2 of *Chaeteessa, Metallyticus*, and *Sphodromantis* has become plate- or ribbon-like and has spread over most of the dorsal **lve**-wall. Like in *Eurycotis*, the arms of the arch (regions

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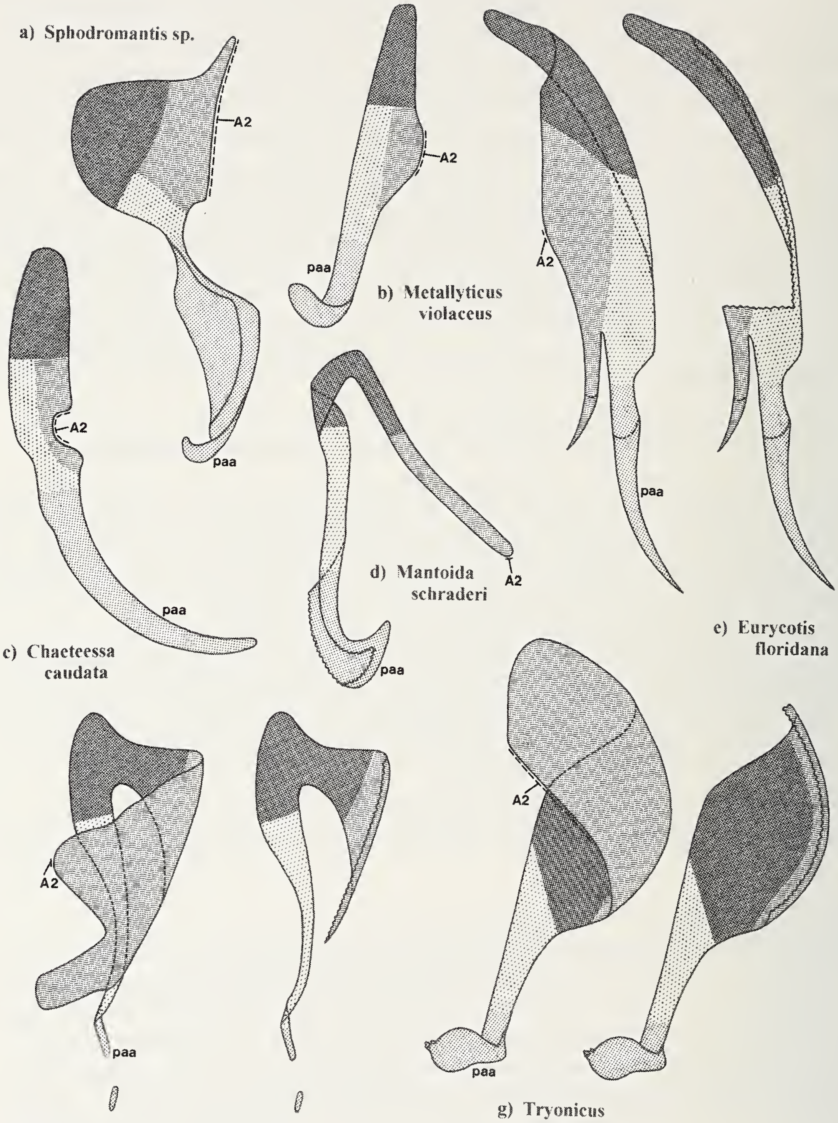
Fig.324: Left complex, homologous regions of main sclerite **L2** (on pages 194, 195). – Only **L2**-sclerotisations are shown. Dorsal views. **L2** is divided into the four regions **L2a, L2d, L2m**, and **L2p** (definition in 6.2.1.); the extensive parts of **L2** in the ventral wall of pouch **lve** in *Polyphaga* are labelled **L2v** (not defined as a region of **L2**). If **L2** is divided into several sclerites, these are labelled with the capital letters used in the text and in fig.1-319 (e.g. **B = L2B**). Undulate lines are cutting lines through sclerotisations (if **L2** is fused with parts of other main sclerites, e.g. **L4**). In fig.324e,f,g the left drawing shows the complete **L2**, the right drawing shows **L2** after removal of its dorsal parts. The part of the sclerite margin which forms articulation **A2** with sclerite **L1** is indicated by dashes. **A4** and **A10** are articulations between **L2**-sclerites. **paa** and **via** are processes occupied at least partly by **L2**-sclerotisations. The sclerite of *Parcoblatta* (fig.324n) and *Blaberus* (fig.324o) which is termed **L2** in the text has to be designated correctly **L2D+(L2E+L4N)**, compare in 6.2.4.; the **L4N**-part has been removed from the sclerite.



a) Sphodromantis sp.

b) Metallyticus violaceus

c) Chaeteessa caudata

d) Mantoida schraderi

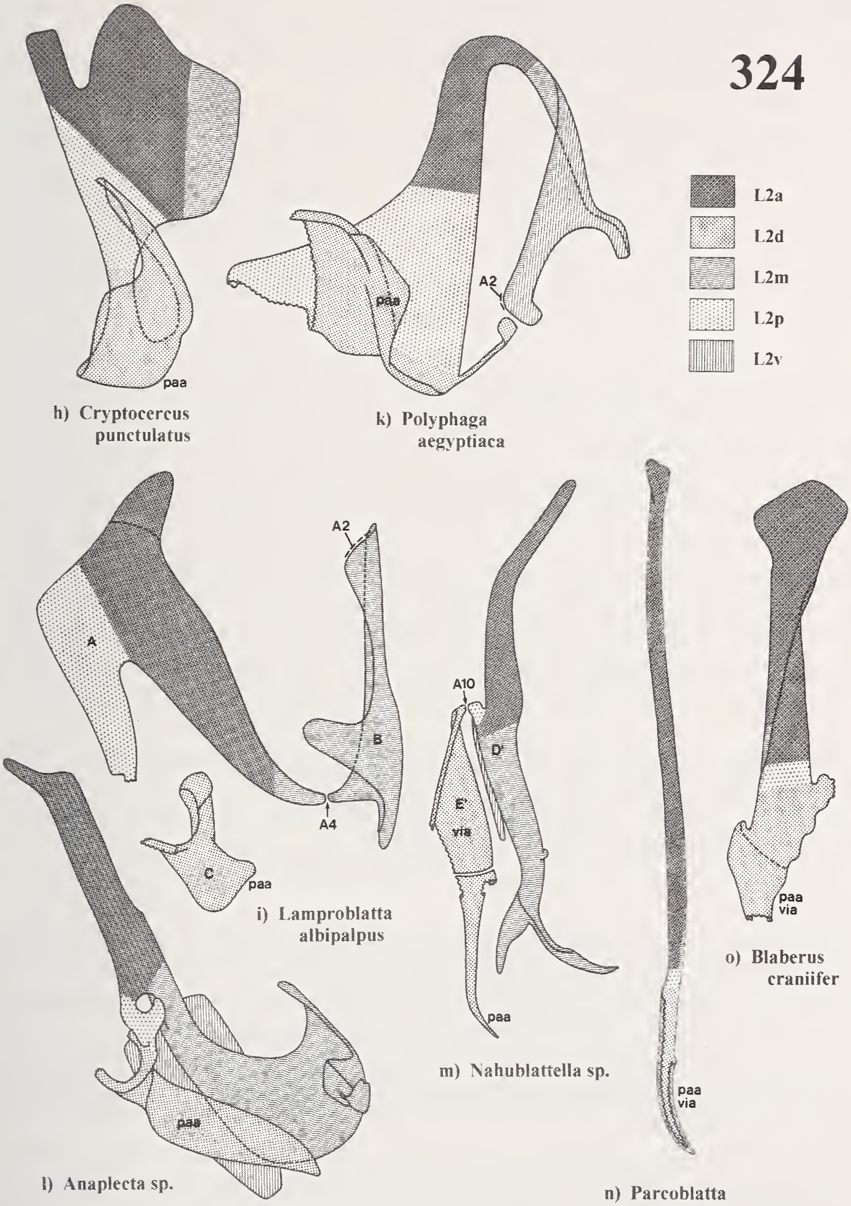
e) Eurycotis floridana

324

f) Archiblatta hoeveni

g) Tryonicus parvus

324



h) Cryptocercus punctulatus

k) Polyphaga aegyptiaca

i) Lamproblatta albipalpus

l) Anaplecta sp.

m) Nahublattella sp.

n) Parcoblatta lata

o) Blaberus craniifer

L2p and **L2m**) have probably fused (fig.324a-c, compare fig.324d). In *Chaeteessa* and *Metallyticus*, as compared with *Mantoida*, the **lve**-pouch has strongly narrowed (compare fig.26, 34 and 46), and **L2** is also narrow. In *Sphodromantis* the anterior part of the **lve**-pouch is deeply invaginated to the left, and **L2** forms a broad transverse tongue (fig.11). This resembles the situation in *Archiblatta* (compare the course of edge **7** in fig.11 and 55) – certainly a case of parallel evolution.

As in *Mantoida,* in *Chaeteessa, Metallyticus*, and *Sphodromantis* the membranous ventral **lve**-wall is a (left) anterior part of the dorsal **vla**-wall (fig.12, 27, 35), the ejaculatory duct (**D** in fig.11, 12, 26, 32) opens far anteriorly into the dorsal **vla**-wall, and the ventral **vla**-wall is part of the ventral wall of the left complex and is largely sclerotised (by **L4** or **L4A** in fig.6, 20, 28). The genital opening lies in *Sphodromantis* within the **lve**-pouch (like in *Mantoida* and *Polyphaga*); in *Metallyticus* and *Chaeteessa* it is a bit, or far, respectively, to the right of the pouch and outside of it.

The homology of **lve** and **L2** of *Mantoida* and *Sphodromantis* is confirmed by the musculature: **l5**, **l6a**, and **l6b** of *Sphodromantis* (fig.15, 16, 18) show the same arrangement as **l5** and **l6** in *Mantoida* (fig.50, 52). Both species have a stout muscle **l3** from **L2** to **L1** (fig.16, 50). Muscle **l4** inserts on the left edge of **lve** (fig.15, 50) and has its opposite insertion (on **L4**-sclerotisations) immediately to the left of the dorsal **l2**-insertion. However, the latter insertions of both **l2** and **l4** are in *Sphodromantis* by far more to the right than in *Mantoida*. This topic will be taken up again in 6.3.3.. Muscle **l8** of *Sphodromantis* (fig.16) consists of very few fibers at most (completely missing in some specimens). Snodgrass (1937) finds this muscle well-developed in *Tenodera sinensis* (Mantidae; muscle **13** in Snodgrass' fig.10D). Hence, **l8** of *Sphodromantis* represents either a vestige or an early evolutionary stage of this muscle. Since **l8** is missing in *Mantoida* and all Blattaria it is not assumed to be a muscle of the Mantodean ground-plan.

6.2.4. Homology relations and character states of the elements in Blattaria

Polyphaga, Ergaula, Tryonicus, Archiblatta, and *Eurycotis*

These species have been sufficiently discussed in 6.2.1..

Lamproblatta

The pouch and the ventral lobe labelled **lve** and **vla** in fig.180 resemble in many respects the **lve** and **vla** of the previous species: The **lve**-pouch lies ventral to the **pne**-pouch. Its dorsal wall is largely sclerotised (**L2A, L2B**). Its ventral wall is mostly membranous, is at the same time the dorsal **vla**-wall (fig.180, 181), and contains the genital opening (**D** in fig.180, 181) in its right part. The ventral wall of **vla** is part of the ventral wall of the left complex and is partly sclerotised (**L4R** in fig.174, 181). However, in *Lamproblatta* there are two problems:

- Instead of only one sclerite **L2** as in the former species there are two within the **lve**-pouch (**L2A** and **L2B**), and around articulation **A4** the **lve**-pouch has a deep recess (fig.180). The questions arise if either only the part to the left of the recess (with **L2A**) corresponds to the **lve**-pouch of the other species, or if the part to the right of the recess (with **L2B**) is also a true part of **lve**, and whether **L2B** really is a part of **L2** (or of **L1**:

a split off part of the **L1m**-region like **L1B** of *Sphodromantis*, fig.10?). This equals the question which of the articulations **A2** (fig.178) and **A4** (fig.180) is the true **A2**.

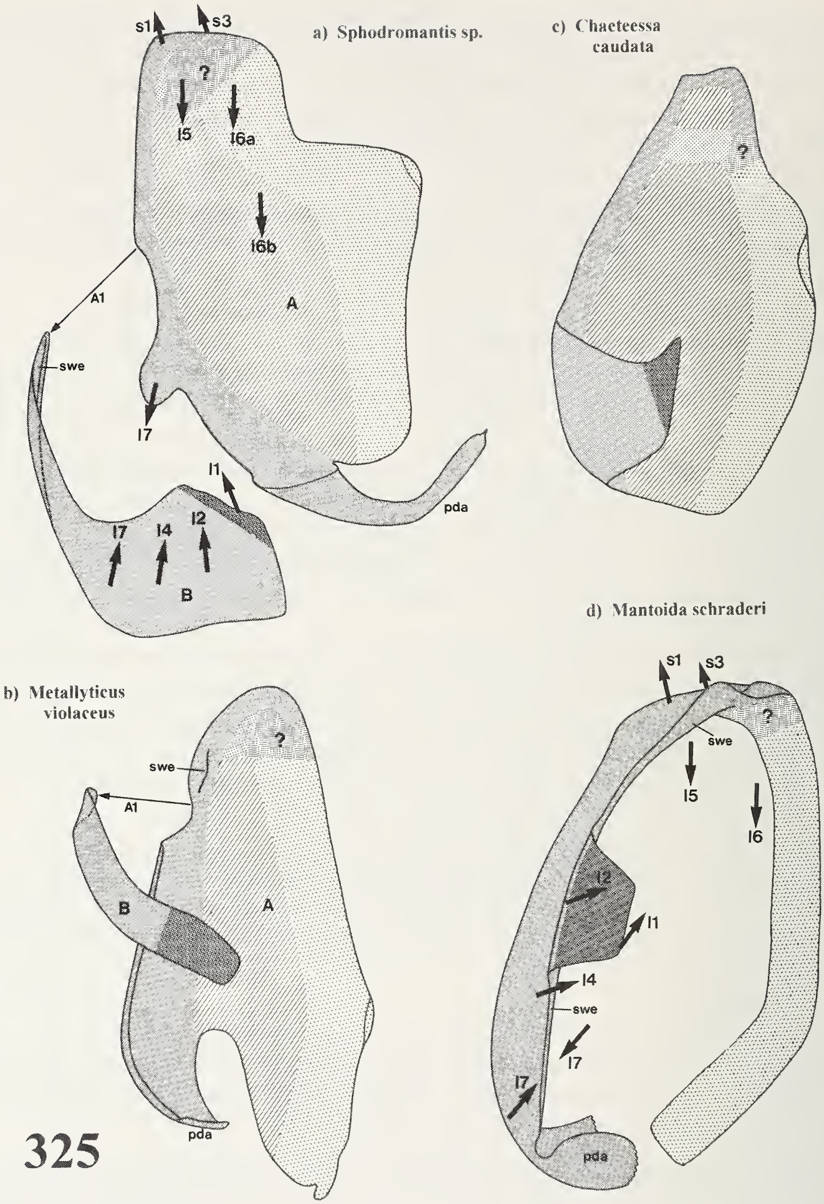
- In *Mantoida, Polyphaga*, and *Tryonicus* the left posterior part of **L2** leaves the pouch and continues into the sclerotisation of the processes **paa** and **pda** (fig.46, 96, 118). In *Lamproblatta*, the left posterior part of **L2A** also has an extension that leaves the pouch (**L4S** in fig.178, 180), and right-anterior to this area there is a sclerotisation with two processes (**paa** and **pda** in fig.178, 179), which, however, is completely separated from **L2A** and **L4S**). The question arises if **paa** and **pda** of *Lamproblatta* are homologous with those of the other species.

These problems can be solved by a comparison of the musculature of *Lamproblatta* and the other species – especially *Polyphaga*.

- *Lamproblatta* also has a stout muscle from **L1** to **lve** (**l3** in fig.187; compare *Polyphaga*, **l3** in fig.128). Its insertion area on **lve** is within the recess and also includes parts of **L2B**.
- *Lamproblatta* and *Polyphaga* have 4 muscles (**l5**, **l6a**, **s3**, **s12**) inserting close to each other in the anteriormost ventral wall of the left complex (fig.133, 188); homology is assumed for all of them (**s3** and **s12** are discussed in 6.9.). In *Polyphaga* the two posterior muscles (**l5** and **l6a**) run to **L2** at the left or right, respectively, anterior edge of the **lve**-pouch. In *Lamproblatta* **l5** runs to **L2A** on the left of the recess, **l6a** runs to **L2B** on the right of the recess.
- The two **l6b**-bundles (fig.189) of *Lamproblatta* are assumed to be homologous with the **l6b** of the other species (*Polyphaga*: fig.132): The ventral insertion is posterior to that of **l6a**. The insertion in the dorsal **vla**-wall is somewhat different in *Polyphaga* and *Lamproblatta* (next to the genital opening or far posterior to it), but the insertions of the two bundles of *Lamproblatta* are similarly situated as the insertion of the one bundle of **l6b** of *Sphodromantis* (fig.18) or *Cryptocercus* (fig.155, 157, see below).
- Muscle **l12** of *Lamproblatta* and *Polyphaga* inserts in the right part of the ventral = outer **lve**-wall – very close to the dorsal insertion of **l6a** (fig.128, 129, 186, 188) – and runs to a small sclerite in the right dorsal wall of the left complex (**L8**, homology discussion in 6.5.). Homology is assumed for these **l12.** In *Lamproblatta* **l12** inserts to the right of the recess, on **L2B**. (**L8** and **l12** are derived features of *Polyphaga, Ergaula*, and *Lamproblatta*.)
- Muscle **l10** of *Polyphaga* (fig.129) runs from **L2** in the left dorsal wall of **lve** to the sclerotisation in between the processes **paa** and **pda**. *Lamproblatta* has a muscle (**l10** in fig.186) from the same area of **lve** to the sclerotisation between **paa** and **pda**. Such a muscle is missing in all species discussed before.

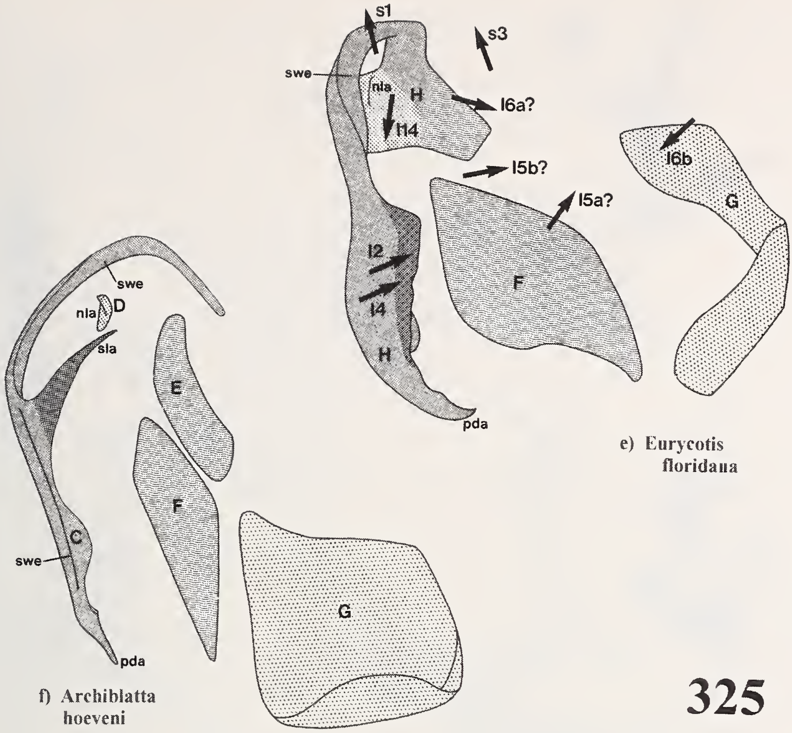
The course of **l10** suggests homology for **paa** and **pda** of *Lamproblatta* and *Polyphaga*. Since the **pda**-sclerotisation is part of **L4**, the discussion of this topic will be continued in 6.3.4..

The insertions of **l3**, **l6a**, and **l12** clearly demonstrate that **L2B** is a true part of **L2** (regioning in fig.324i) and that the respective part of the pouch is a true part of **lve**. That the right part of **L2B** curves dorsad and leftward like the right part of **L2** in other Blattaria and that the genital opening is to the right of the recess (fig.122, 180) supports this



325

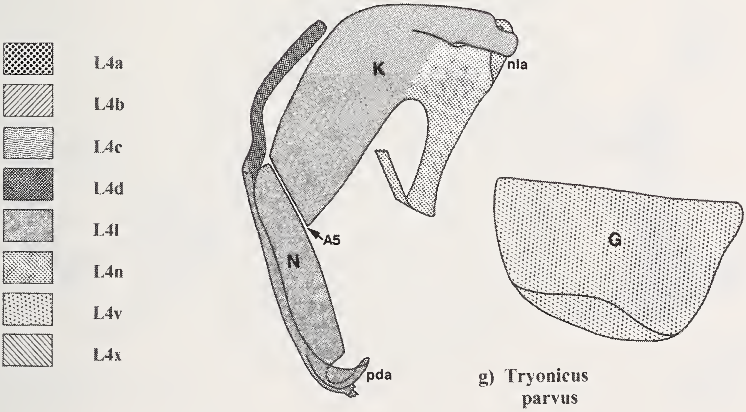
Fig.325: Left complex, homologous regions of main sclerite **L4**. – Only **L4**-sclerotisations are shown. Dorsal views. **L4** is divided into the regions **L4a, L4b, L4c, L4d, L4l, L4n, L4v**, and **L4x** (definition in 6.3.1.). If **L4** is divided into several sclerites, these are labelled with the capital letters used in the text and in fig.1-319 (e.g. **B** = **L4B**). The sclerites are mostly shown as they are arranged in the left



e) Eurycotis floridana

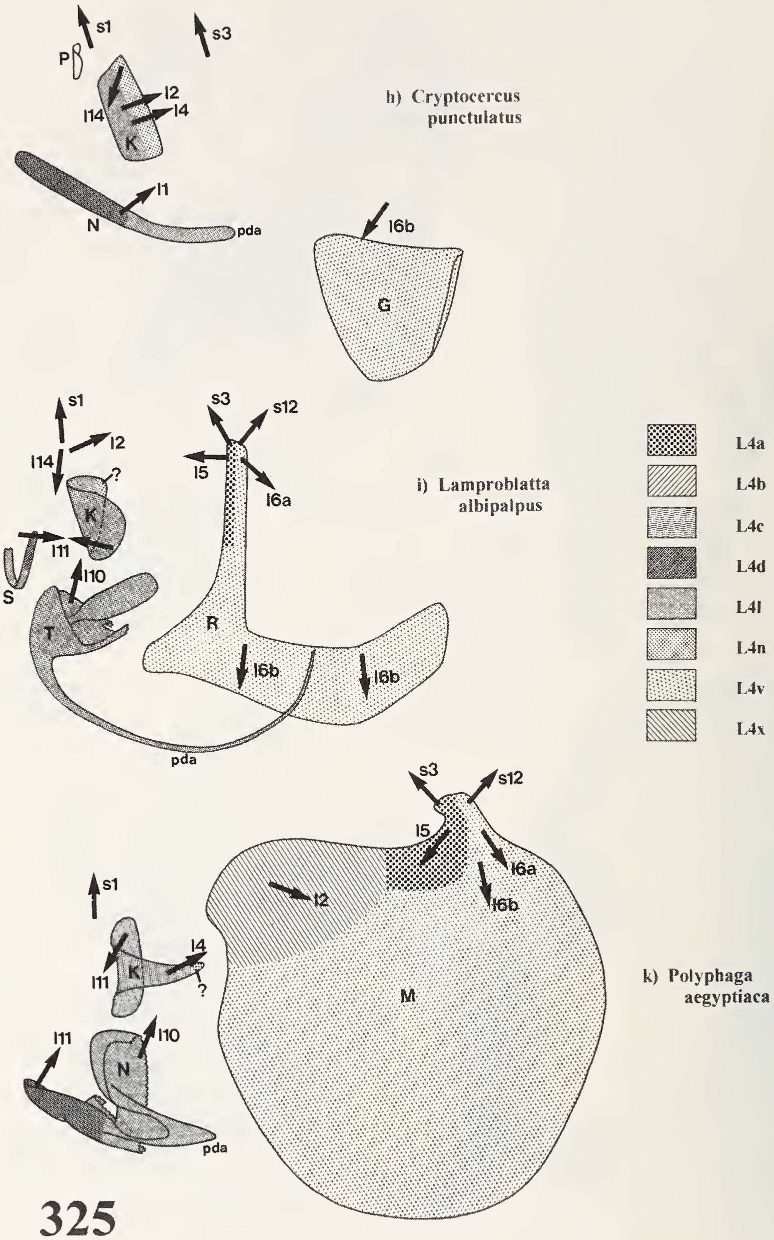
f) Archiblatta hoeveni

325



g) Tryonicus parvus

(contd.): complex; only in *Sphodromantis* (fig.325a) and *Metallyticus* (fig.325b) the dorsal sclerites **L4B** are shifted to the left (thin arrows). Undulate lines are cutting lines through sclerotisations (if **L4** is fused with parts of other main sclerites, e.g. **L2**). **A1** and **A5** are articulations between **L4**-sclerites. **pda, via, nla, sla, vsa, tve**, and **swe** are formative elements occupied at least partly by **L4**-



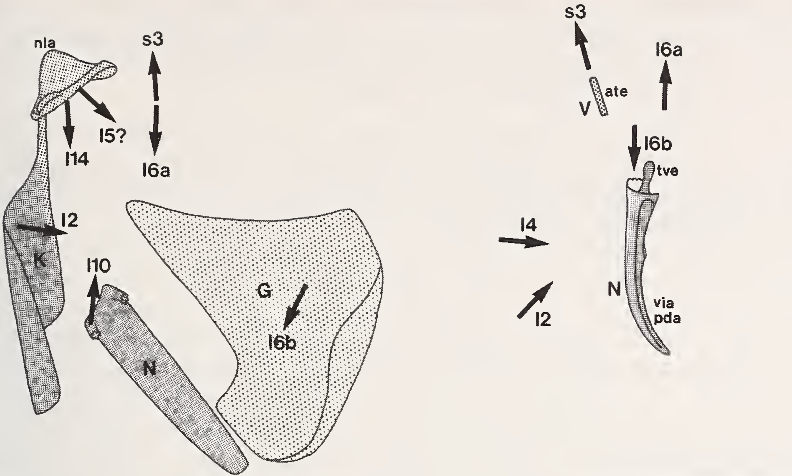
h) Cryptocercus punctulatus

i) Lamproblatta albipalpus

k) Polyphaga aegyptiaca

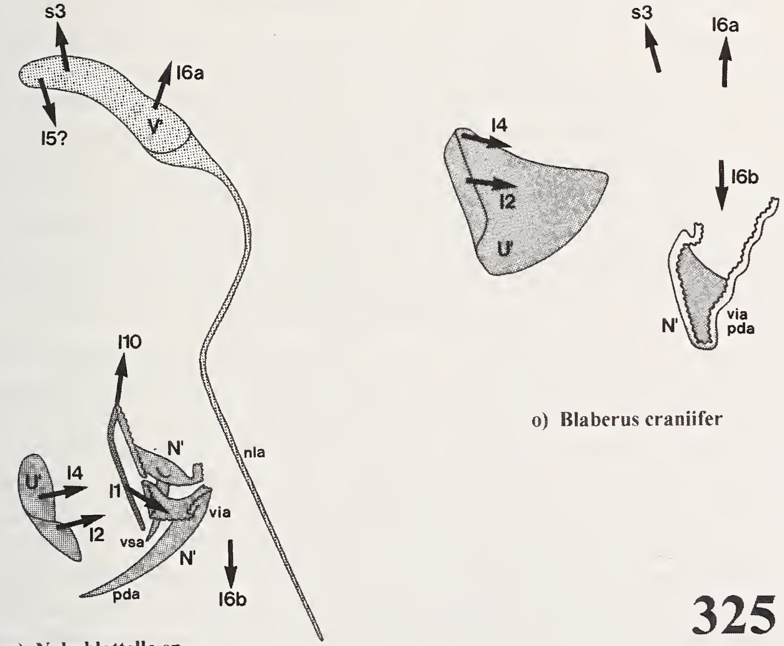
325

(contd.): sclerotisations. Broad arrows represent muscles inserted on or near **L4**-sclerotisations; **l5** is certainly homologous in most species; if homology with these **l5** is questionable, the muscle is labelled **l5?** (in *Anaplecta* and *Nahublattella* **l5?** are homologous). In Mantodea the presence of region **L4c** is questionable (? in fig.325a-d). The sclerite of *Parcoblatta* (fig.325n) and *Blaberus* (fig.325o)



n) Parcoblatta lata

l) Anaplecta sp.



o) Blaberus craniifer

m) Nahublattella sp.

325

(contd.): which is termed **L2** in the text has to be designated correctly **L2D+(L2E+L4N)**, compare in 6.2.4.; only the **L4N**-part is shown in the figures.

interpretation. Thus, the articulation between **L2B** and **L1** (**A2** in fig.178) is homologous with **A2** of the other species. In correlation with the right-anteriad shift of **L1** (compare in 6.1.4.), **A2** of *Lamproblatta* is far anteriorly. The articulation **A4** and the recess within the **lve**-pouch are derived features of *Lamproblatta*.

Another derived feature of *Lamproblatta* is the lack of muscle **l4**. Another derived feature common to *Lamproblatta* and *Polyphaga* (and *Ergaula*) – in addition to **L8** and **l12** – is that the **lve**-pouch and the **vla**-lobe extend nearly to the left edge of the left complex (compare edges **7** in fig.122 and 180).

Cryptocercus

The elements **L2, lve, paa**, and **vla** (fig.151, 152) can be clearly identified by many features corresponding with the other species: **L2** lies ventral to the **pne**-pouch and is connected with it by a stout muscle (**l3** in fig.158, 159). The posterior part of **L2** bends into the dorsal wall of the left complex, and the area of bending forms a bulge-like process (**paa** and **L2d** in fig.151, 152, 324h; compare *Tryonicus*, fig.95, 97, 324g). This dorsal part of **L2** extends anteriad as far as to the opening of the phallomere-gland (**P** in fig.151, 152) – like in *Polyphaga* (fig.118, 120). The right anterior part of **L2** occupies the dorsal wall of a pouch-like invagination (**lve** in fig.150-152), which, however, is restricted to the anteriormost part of the left complex. The ejaculatory duct (**D** in fig.150, 151; compare *Mantoida*, fig.46) opens into this **lve**-pouch. The ventral **lve**-wall is at the same time part of the dorsal **vla**-wall (fig.150-152), and the ventral **vla**-wall is partly sclerotised (**L4G** in fig.148, 152). Muscle **l10** (fig.155) runs from **L2** to the membrane to the left of **paa**. This membranous area is in between the processes **paa** and **pda** (**pda**, fig.150, is discussed in 6.3.4.), and thus the left insertion of this **l10** is like that of the **l10** of *Polyphaga* (fig.129) and *Lamproblatta* (fig.186). However, the right insertion is by far more posteriorly, and the homology of these **l10** is not certain. Muscle **l4** (fig.155, 158) runs from the anterior part of **L2** to **L4K** in the left part of the left complex like **l4** of *Polyphaga* (fig.132; **l4** of *Cryptocercus* is strongly reduced; **L4K** is discussed in 6.3.4.).

Cryptocercus has some features which are, compared with the ground-plan, clearly derived: (1) **L2** is, like in most Mantodea and *Eurycotis*, more plate-like, though the primitive arch is still recognisable (compare **L2**-regions in fig.324h and d,f,k). (2) The right part of **L2** is, like in Mantodea, not upcurved (fig.151, 152). However, since the contact between **L2** and **L1** (articulation **A2**) has been lost, this is not interpreted as a primitive situation – as suggested by the outgroup comparison with Mantodea – but as a reduction of the right part of **L2**. Consequently, the right-dorsal part of the **lve**-pouch, which contains the upcurved part of **L2** in other Blattaria, has been strongly reduced. (3) The **vla**-lobe is separated from the remaining ventral wall of the left complex as far as to the anterior margin of the left complex (edge **61** in fig.148). Accordingly, the invagination of the **lve**-pouch begins very far anteriorly (see left end of edge **7** in fig.150, 151), and the left-ventral part of **lve** has been strongly reduced. This is an extreme modification of the situation in *Tryonicus* (edge **61** in fig.87 and edge **7** in fig.97). (4) Of the muscles from the ventral wall of the left complex to the **lve**-pouch and the ejaculatory duct only one is present (**l6b** in fig.155). According to its insertions (anterior margin of **L4G**, membrane posterior to genital opening), it is likely to be the homologue of **l6b** of *Eurycotis* (fig.71), *Sphodromantis* (fig.18), and the other species. **l5** and **l6a** have been lost; this might be a consequence of the extreme reduction of the **lve**-pouch.

Anaplecta

The homology of the elements designated **L2**, **lve**, **vla**, **paa**, and **pda** in *Anaplecta* with the respective elements of the other species is suggested by the following features: The whole area labelled **lve** (fig.210-213), whose anterior part narrows to form the **lve**-apodeme, is a large invagination to the anterior, which lies beneath the **pne**-"pouch" (fig.209). **lve** and **pne** are connected by a stout muscle (**l3** in fig.201, 222, 50, 128). **L2** is mainly restricted to the dorsal wall of **lve**. Anteriorly, however, **L2** also occupies the margins of the ventral **lve**-wall (fig.211, 225) – similar to *Polyphaga* (fig.123) and *Lamproblatta* (fig.181). That a phallomero-sternal muscle inserts on the **lve**-pouch resembles *Eurycotis* (**s7** in fig.58, 200). That **L2** forks at the base of the **lve**-apodeme is regarded as a vestige of the primitive arch-shape (compare fig.324l and d,k); this is confirmed by the morphology of the two branches of the fork: The right branch is upcurved at its right margin (fig.211-213), like the right part of **L2** in other Blattaria. The cuticular area containing this part of **L2** can therefore be regarded as the right dorsal (= inner) wall of the **lve**-pouch. Anterior to this right **L2**-part there opens, like in the other species (e.g. *Mantoida,* fig.46), the ejaculatory duct (**D** in fig.211). The left branch of **L2** continues into a sclerotisation bearing two processes (**paa** in fig.211, **pda** in fig.214). This is the same situation as at the left end of the **L2**-arch of *Mantoida*, *Polyphaga*, and *Tryonicus*. Muscle **l10** runs, like **l10** of *Polyphaga* and *Lamproblatta* (fig.222, 129, 186), from the sclerotisation of **paa** and **pda** to **L2** in the left-dorsal **lve**-wall. The relative positions of the **vla**-lobe (fig.205, 218-220) and its sclerite **L4G** (fig.205) in the ventral wall of the left complex are especially similar to those of **vla** and **L4G** of *Tryonicus* (fig.87, 205), with **vla** having a left edge (**61** in fig.205) reaching far anteriad (farther than in *Tryonicus*, fig.87, but not as far as in *Cryptocercus*, fig.148).

In contrast to all other species, the edge of the **lve**-pouch is – except in the area of the **lve**-apodeme – not continuous throughout (compare edges **7** in fig.55, 122, 180, 211, 212) but interrupted by some apomorphic membranous foldings (fig.212-219): e.g. outfolding **vfa**, infolding **vpe** (fig.214, 215, 217). For that reason it is difficult to determine the homologies of the muscles of this area with the **l5**- and **l6**-muscles of the other species. **l6b** (fig.224) is probably homologous with **l6b** of e.g. *Sphodromantis*, *Eurycotis*, *Cryptocercus*, and *Lamproblatta* (fig.18, 71, 155, 189): All these **l6b** run from the sclerite plates in the ventral **vla**-wall, or from their vicinity, to the dorsal **vla**-wall. In *Anaplecta*, however, the dorsal insertion is not immediately behind the genital opening but is separated from it by the outfolding **vfa** (compare fig.223 and 224). **vfa** is therefore assumed to be evaginated from the anteriormost dorsal wall of **vla** and the ventral wall of the ejaculatory duct. This assumption is supported by two other muscles: **s10** inserts on the ejaculatory duct in *Nahublattella* (fig.249) and *Parcoblatta* (fig.276) but on the dorsal base of **vla** in *Anaplecta* (fig.222). **l13** of *Polyphaga* (fig.132), *Cryptocercus* (fig.155), and *Eurycotis* (**l13h** in fig.72) runs from the ejaculatory duct to the dorsal **vla**-wall posterior to it. **l13** of *Anaplecta* (fig.222) also inserts on the ejaculatory duct but bridges the **vfa**-outfolding on its way to its insertion on the dorsal base of **vla** (discussion of **l13** in 6.5.). Muscle **l6a** of *Anaplecta* (fig.222) resembles **l6a** of *Polyphaga* and *Lamproblatta* (fig.133, 188) in inserting ventrally behind **s3** and dorsally at the right anterior edge of the **lve**-pouch. Whether muscle **l5** is homologous with **l5** of the other species (fig.133, 188, 223) is questionable: The insertion on **L2** is similar in *Anaplecta* and e.g. *Polyphaga*; the anterior insertion (on **L4**), however, is situated quite differently in these two species. Homology is also unclear for the muscles **l25** and **l26** (fig.224).

As compared with the previous species, *Anaplecta* has some important derived features: (1) The anterior part of the **lve**-pouch is a tube-like **lve**-apodeme. (2) Edge **7** is interrupted by **vfa** and **vpe**. (3) The common sclerotisation of **paa** and **pda** is stout and ring-shaped at its base. (4) Muscle **l4** from **L2** to left parts of **L4** has been lost (like in *Lamproblatta*).

Nahublattella

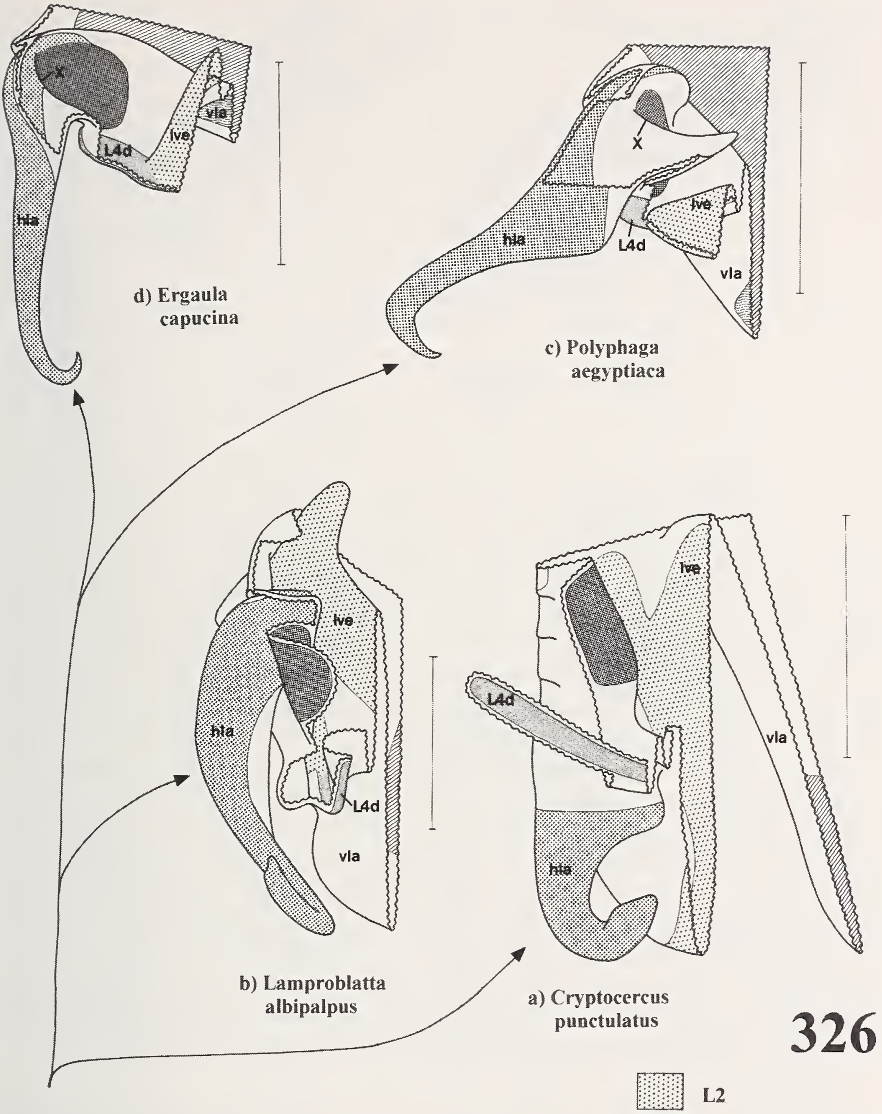
The part of the left complex comprising the large pouch **lve** (fig.242), the opening of the ejaculatory duct (**D** in fig.242), the processes, **via, vsa, paa**, and **pda** (fig.244, 245), and the sclerotisations **L2D', L2E'**, and **L4N'** show a lot of similarities with the elements of *Anaplecta* discussed before:

All these elements lie in the center of the left complex and (antero-)ventral to the **pne**-pouch. The anterior part of the **lve**-pouch (see edges **7** in fig.242) is a tube-like **lve**-apodeme, whose dorsal wall is completely sclerotised, and whose ventral wall contains a membranous stripe (**44** in fig.206, 212, 239a, 245). Muscle **s7** runs from the **lve**-apodeme to the subgenital plate (fig.200, 234).

At the base of the apodeme, **L2D'** is somewhat forked (fig.243, 324m), like **L2** in *Anaplecta* (fig.212, 324l): Extension **36** is the left branch, the posterior main part of **L2D'** is the right one. At the left branch there adjoins a ring-shaped sclerotisation lying at the base of some processes (**paa** and **pda** in *Anaplecta*, fig.211-214; **via** with **vsa**, **paa**, and **pda** in *Nahublattella*, fig.244, 245). A stout muscle **l10** (fig.222, 250) runs from the **lve**-apodeme to the left part of this sclerite-ring. However, in *Nahublattella* the sclerite ring has become separated from the rest of **L2** (**L2D'**) by an articulation (**A10** in fig.244). At the base of the left branch the **L2**-sclerotisation bends into the ventral **lve**-wall and forms a posterior extension (**28** in fig.215, 245). However, in *Anaplecta* the cuticle around extension **28** forms a process (**gta** in fig.215), which is missing in *Nahublattella*.

The right branch of **L2** or **L2D'**, respectively, extends rightward in *Anaplecta* but more posteriad in *Nahublattella*. The relation between this sclerotisation and the dorsal wall of the ejaculatory duct (**D** in fig.245, 246) is the same in the two species (fig.211, 245), but only in *Nahublattella* the right-anterior margin of this **L2**-part folds narrowly back to the left (towards edge **38** in fig.245).

Two further muscles inserting on **L2D'** of *Nahublattella* correspond with muscles of the other species: **l3** running to the **pne**-pouch (fig.250, compare e.g. fig.50, 71, 128, 221), and **l4** running to **L4**-sclerotisations in the left part of the left complex (fig.249, compare e.g. fig.50, 71, 129; missing in *Anaplecta*; homology discussion of **L4** in 6.3.4.).



326

░ L2

▒ L3

▓ L4K

░ L4N, L4S (with L4d)

▨ L4G, L4M, L4R

▤ L5

Fig.326: Left complex of *Lamproblatta*, *Cryptocercus*, *Polyphaga*, and *Ergaula*, homology relations of the sclerotisations in the left part. – Only cuticular elements of the left part of the left complex are shown. Dorsal views. Scale 1mm. The sclerites are patterned differently according to their homology relations. **lve, hla**, and **vla** are formative elements. The position of region **L4d** is given. Undulate lines are cutting lines. The branching black lines represent the assumed phylogeny.

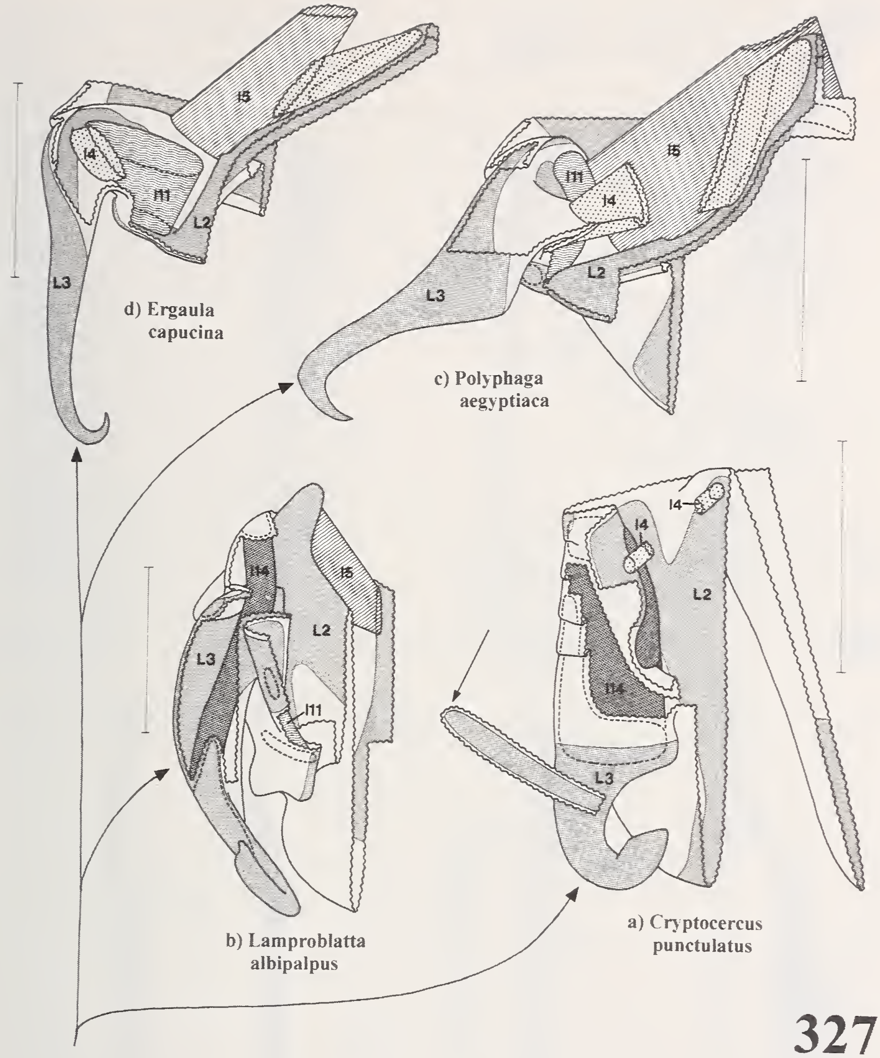
The membranous lobe **vla** (fig.239a, 245-247) has similar features as the **vla**-lobe of e.g. *Sphodromantis* (fig.6,12), *Lamproblatta* (fig.174, 180), *Cryptocercus* (fig.148, 151), and *Eurycotis* (fig.63, 66): Its ventral wall is part of the ventral wall of the left complex. Its dorsal and its ventral walls are connected by a stout muscle **l6b** (fig.251, 252, 18, 71, 155, 188, 189). (These two features are also true of *Anaplecta*, fig.205, 218, 224). Its dorsal wall is at the same time the ventral wall of the **lve**-pouch. (This is not true of *Anaplecta* because of the membrane foldings between **lve** and **vla**, especially **vfa**).

Like the other species (with the exception of *Cryptocercus*), *Nahublattella* has muscles from the anterior ventral wall of the left complex to the **L2**-sclerotisations: **l5** is certainly homologous with **l5** of *Anaplecta* (similar posterior insertion on the left branch of **L2**; the homology of the anterior insertion is discussed in 6.3.4.), but, as in *Anaplecta*, homology with the **l5** of the other species is questionable. Muscle **l6a** (fig.250) could be homologous with **l6a** of *Anaplecta* (and the other species); however, the insertion on the **lve**-apodeme is by far more anteriorly (fig.222, 250), and the insertion in the ventral wall is on sclerotisation. Alternatively, homology with **l26** (fig.224) of *Anaplecta* seems possible.

Nahublattella shows some important derived features as compared with *Anaplecta* and, at least in the case of (2)-(6), all other previously discussed species: (1) The right branch of **L2** (posterior part of **L2D'**) is by far narrower (compare fig.213 and 245). Moreover, the whole right posterior dorsal part of the left complex – that part with the right **L2**-branch in its ventral wall (*Anaplecta*: fig.211-213) – is strongly reduced to form just the bifid **psa**-process (fig.245; compare fig.328a and b). (2) **L2** has divided into **L2D'** and **L2E'** by articulation **A10**. (3) The sclerotisation at the common base of the processes **paa** and **pda**, which is ring-shaped in *Anaplecta* (fig.211-213), has lengthened to form a cylinder (fig.244). Hence, the processes **paa** and **pda** (and **vsa**) are now only the distal branches of a larger evagination, which has been defined as a "new" process **via** (**paa**, **pda**, and **vsa** are subordinate parts of **via**). The homologies of the single processes of *Anaplecta* and *Nahublattella* are hardly determinable, but in my view the relations expressed by the designations are the most probable. In accordance with *Anaplecta*, the sclerotisation of **via** is assumed to comprise a **L2**-part (**L2E'**, roughly the **L2d'**-region; dorsally on **via** and near articulation **A10**; fig.324l,m) and **L4N** (ventrally on **via** and near the insertion of **l10**; fig.325l,m; discussion of **L4N** in 6.3.4.). (4) This sclerotisation of **via** is divided into a basal and a distal sclerite (**39** in fig.241, 244). (5) There is no sclerotisation in the ventral wall of the **vla**-lobe (compare fig.205 and 239a). (6) The main muscle of the **hla**-hook (**l14** in fig.249) has its anterior insertion on the **lve**-apodeme (discussion in 6.4.).

Parcoblatta, Blaberus, and other Blattellidae and Blaberidae

The **L2**-sclerotisations, the pouch **lve**, the processes **via, paa, pda**, and **psa**, the lobe **vla**, and the muscles **s7**, **l4**, and **l10** have been studied not only in *Parcoblatta* and *Blaberus* but also in *Supella, Euphyllodromia, Loboptera, Ectobius* and *Nyctibora* (Blattellidae), *Nauphoeta* and *Blaptica* (Blaberidae) (muscles not studied in *Ectobius*). Morphology and homology of these elements are shown in fig.328. The morphology of all these species is derived from a situation similar to *Nahublattella*.



d) Ergaula capucina

c) Polyphaga aegyptiaca

b) Lamproblatta albipalpus

a) Cryptocercus punctulatus

327

Fig.327: Left complex of *Lamproblatta*, *Cryptocercus*, *Polyphaga*, and *Ergaula*, homology relations of the muscles in the left part. – Cuticular elements are shown as in fig.326, but some parts are removed. Dorsal views. Scale 1mm. All sclerotisations are patterned in the same manner. The muscles **l4, l5, l11**, and **l14**, if present, are shown and patterned differently according to their homology relations. **l4** is always cut through. The ventral insertion of **l5** is shown only in *Lamproblatta*. Undulate lines are cutting lines. The branching black lines represent the assumed phylogeny.

▒ **Sclerotisation**

░ **l4**

▨ **l5**

▤ **l11**

▓ **l14**

328

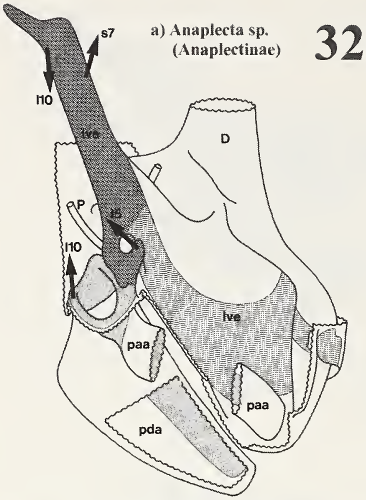


Fig.328: Left complex, evolution of main sclerite **L2** and sclerite **L4N** in Blattellidae and Blaberidae. – The central part of the left complex is shown, with pouch **lve**, terminal parts of ejaculatory duct (**D**) and phallomere-gland (**P**), processes **paa, pda, via**, and **psa**, ventral lobe **vla**, and tendon **tve**. Dorsal views. Patterned areas are sclerotised. Undulate lines are cutting lines through the cuticle. **L2D** and **L2E** are separate **L2**-sclerites, **A10** is the articulation between them. Broad arrows represent the muscles **l4, l5, l10**, and **s7** (not investigated in *Ectobius*, fig.328g). Curved arrows in *Parcoblatta* (fig.328e) and *Blaberus* (fig.328k) show the direction of rotations. **X** and **Y** are special elements of *Loboptera*. (Detailed information in 6.2.4.). Species with "S" behind their names have side-reversed phallomeres, and a mirror-image of the original preparation is shown. The branching black lines represent the assumed phylogeny.

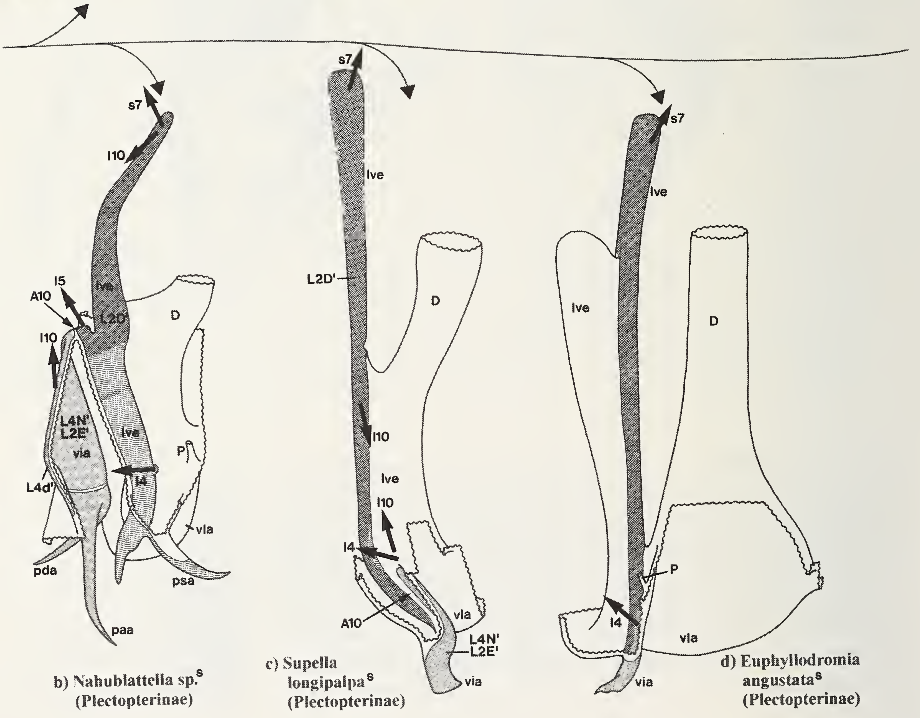
The sclerotisations are patterned as follows:

░ Sclerotisation of processes **pda** (= posterior part of region **L4l** = main part of sclerite **L4N**) and **paa** (= region **L2d** = left posterior part of sclerite **L2** or **L2E**), or of process **via**

▩ Regions **L2p** and **L2a**

▨ Region **L2m**

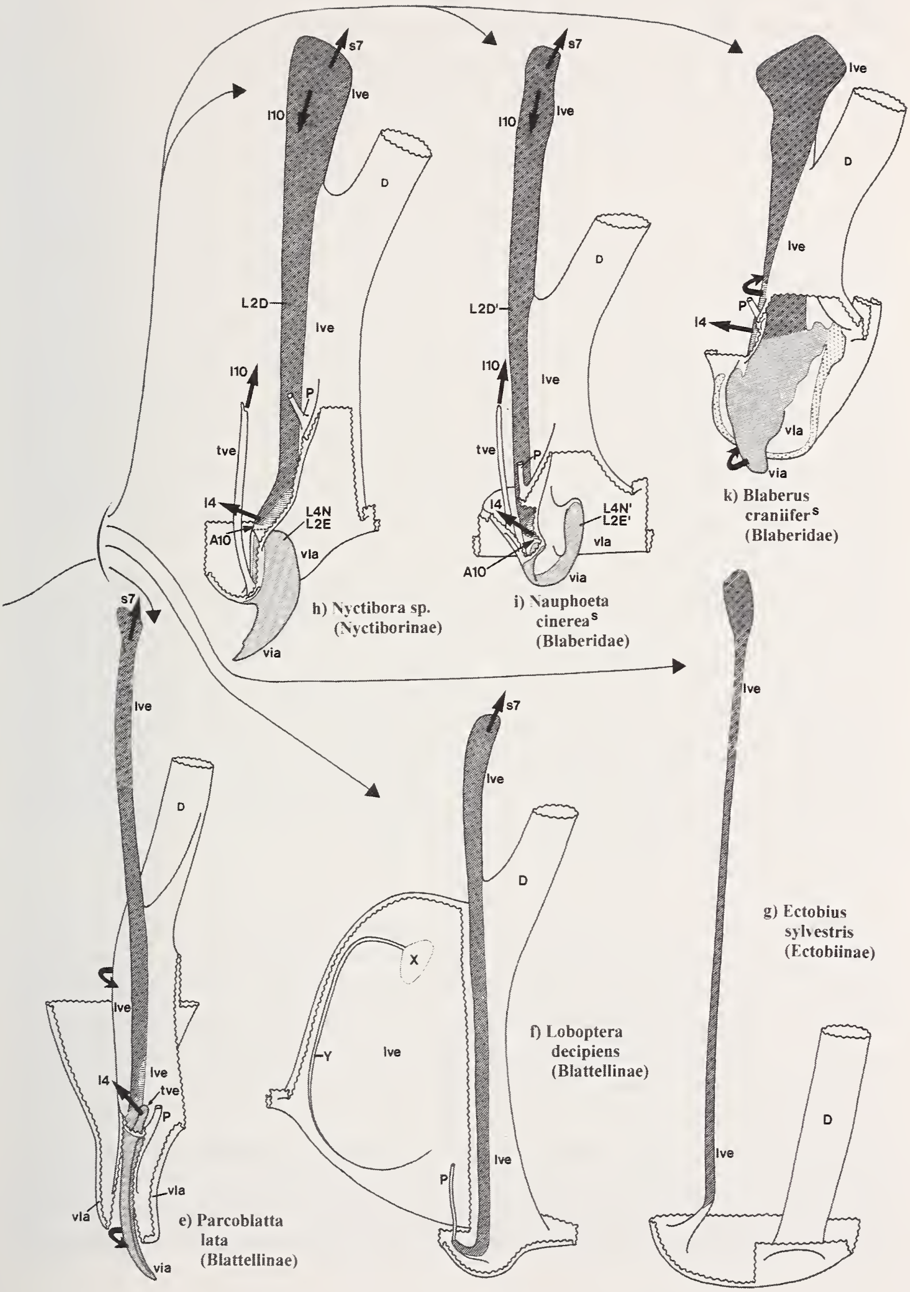
▒ Sclerite **L10** (only in *Blaberus*, fig.328k)



b) **Nahublattella sp.**^{S}
(Plectopterinae)

c) **Supella longipalpa**^{S}
(Plectopterinae)

d) **Euphyllodromia angustata**^{S}
(Plectopterinae)



h) Nyctibora sp. (Nyctiborinae)

i) Nauphoeta cinerea^s (Blaberidae)

k) Blaberus craniifer^s (Blaberidae)

e) Parcoblatta lata (Blattellinae)

f) Loboptera decipiens (Blattellinae)

g) Ectobius sylvestris (Ectobiinae)

Pouch **lve** and its **L2**-sclerotisation The elements designated **lve** and **L2** have a lot of features in common with **lve** and **L2** of *Nahublattella* and/or *Anaplecta*: **lve** is a deep anteriad-directed invagination in the center of the left complex which is partly sclerotised (by **L2**; fig.210, 242, 268, 299, 328). The anterior part of this **lve**-pouch is a tube-like **lve**-apodeme with a membranous stripe in its ventral or right wall (**44** in fig.206, 239a, 245, 266, 297a). A muscle **s7** runs from the **lve**-apodeme to the left half of the subgenital plate (fig.221, 249, 276, 328); in Blaberidae, **s7** is missing in *Blaberus* but present in *Nauphoeta*. A muscle **l10** runs from the **lve**-apodeme to the base of the **lve**-pouch; however, the positions of the **l10**-insertions are not exactly the same in the various species, and in some species **l10** is missing (fig.328d,e,f,k; discussion below). The ejaculatory duct joins the **lve**-pouch from the right side at the base of the **lve**-apodeme (like in *Nahublattella*; **D** in fig.242, 268, 299, 328). The genital opening is to the right of the apodeme – only in *Blaberus* its position is more dorsal (fig.328k), and only in *Parcoblatta* its position is more ventral (fig.328e). Only in *Ectobius* the ejaculatory duct opens far to the right of the apodeme (fig.328g). Where the ejaculatory duct joins the **lve**-pouch, **lve** strongly widens, like in *Nahublattella*, and the right posterior part of **lve** is membranous (fig.328b-k; both is not true of *Ectobius*, fig.328g). The phallomere-gland opens into the posteriormost dorsal **lve**-wall (like in *Nahublattella*, **P** in fig.328; the phallomere-gland has been lost in *Supella*, fig.328c, and *Ectobius*, fig.328g). A muscle **l4** runs from the **L2**-sclerotisation (fig.249, 276, 303, 328) to the left wall of the left complex, where it is attached to **L4**-sclerotisations if present (discussion of **L4** in 6.3.4.). **l4** was not found in *Loboptera*.

The remaining muscles of this area have been investigated only in *Parcoblatta* and *Blaberus*. Two further muscles having homologues in *Nahublattella* insert anteriorly on the **lve**-apodeme: **l14** or **l14a,b** (fig.249, 276, 303) run to the **hla**-hook (discussion of **l14** in 6.4.3.). **l6a** (fig.250, 277, 304) runs posteroventrad. In *Blaberus* and *Nahublattella* the posterior **l6a**-insertion is still in the anteriormost ventral wall of the left complex, but in *Parcoblatta* it has shifted far posteriad to the ventral wall of the genital pouch (fig.267). In *Blaberus* and *Parcoblatta* **l6a** has strongly enlarged. **l15** is restricted to *Nahublattella* (fig.249); **l42** is restricted to *Blaberus* (fig.304). *Parcoblatta* and *Blaberus* have lost muscle **l3** (from **lve** to **pne**, compare *Nahublattella*, fig.250).

Process **via** and its **L2**- and **L4**-sclerotisations All species except *Loboptera* (fig.328f) and *Ectobius* (fig.328g) have a sclerotised process behind the **lve**-pouch (**via** in fig.328), whose shape and size varies, and whose sclerotisation can be connected with (fig.328d,e,k) or separated from (fig.328c,h,i) the **L2**-sclerotisation in the **lve**-pouch. The question arises whether these processes are homologous with the **via**-process (fig.244) or with the **psa**-process (fig.245) of *Nahublattella*, and whether this homology relation is the same in all species.

Some similarities strongly suggest that **via** of *Nyctibora* is homologous with **via** of *Nahublattella*: The sclerotisation at the right base of **via** articulates (**A10** in fig.328b,h) with the left posterior end of the **L2**-sclerite occupying the **lve**-apodeme. The basal sclerotisation of **via** forms a complete cylinder. A stout muscle runs from the **lve**-apodeme to the left base of **via** (**l10** in fig.250, 328b,h). Thus, the bipartition of **L2** (by **A10**: **L2D** and **L2E**) is assumed to be homologous in *Nyctibora* and *Nahublattella*, and for **via** of *Nyctibora* the same composition of **L2E** and **L4N** is assumed as for **via** of *Nahublattella* (further details on **L4N** in 6.3.4.). In some features *Nyctibora* is more derived than *Nahublattella*: (1) The right posterior branch of **L2D** (fig.244, 245; compare fig.328b and h) is reduced to a vestige, and the process **psa** is completely missing. (In *Nyctibora* the vestige can be identified by the insertion of **l4**, which is much closer to articulation **A10** than in *Nahublattella*: fig.328b,h). (2) The posterior insertion of **l10** is upon a long cuticular tendon (**tve** in fig.328h). (3) The **via**-process is no longer forked, and **paa** and **pda** (and **vsa**?) must be fused or partly reduced.

Nauphoeta (fig.328i) strongly resembles *Nyctibora*: The **via**-process, the articulation **A10**, the insertions of **l4** and **l10**, the **tve**-tendon, and the phallomere-gland are arranged in the same way (compare fig.328h and i). However, the basal sclerotisation of **via** is no longer a complete cylinder and does not reach the base of the **tve**-tendon.

Supella (fig.328c) is similar to *Nauphoeta*, but some features are different: The phallomere-gland and the **tve**-tendon are missing. The sclerotisation of **via** has expanded anteriad along the right margin of **L2D'**, and articulation **A10** is therefore long and hinge-like. The right insertion of **l4** is in the usual position but has shifted from **L2D'** to the adjacent membrane. The posterior insertion of **l10** has shifted to the right; its position can be explained by a clockwise (as seen from behind) rotation of the **via**-process along its longitudinal axis (similar to *Parcoblatta*, see below). The anterior **l10**-insertion on **L2D'** is by far more posteriorly than in the other Blattellidae and Blaberidae having a **l10**; however, in *Anaplecta*, fig.222, and *Nahublattella*, fig.250, the **l10**-insertion also extends far posteriad.

Alternatively, one could assume that in *Supella* the process is not **via** but **psa** (compare fig.328b and c) and that **via** is missing. However, no muscle in any of the Dictyopteran species studied here would then have the same course as **l10** of *Supella* (from the anterior part of **L2** to its right part), and articulation **A10** of *Supella* would likewise have no homologue at least in Blattellidae and Blaberidae. Therefore, and since the respective area is quite similar in *Supella* and *Nauphoeta*, the process is more likely to be **via**.

Euphyllodromia (fig.328d), *Parcoblatta* (fig.328e), and *Blaberus* (fig.328k) have, in contrast to *Nahublattella, Nyctibora, Nauphoeta*, and *Supella*, the sclerotisation of **via** firmly connected with the **L2**-sclerotisation of the **lve**-pouch (like in *Anaplecta* and in the ground-plan), and muscle **l10** is missing (however, **l42** of *Blaberus*, fig.304, might possibly be a **l10** with its posterior insertion shifted far to the left). The basal sclerotisation of **via** is a complete cylinder (fig.328d, 273, 274, 300, 302). Muscle **l4** is present (fig.328d,e,k).

In *Parcoblatta* the **via**-process and the surrounding area have undergone a rotation (clockwise as seen from behind; lower curved arrow in fig.328e). This can be recognised by the following features: (1) The contact between the lumina of the **via**-process and of the rest of the left complex (fig.328e, 273, 274) is dorsal to the connection of the sclerotisations of **via** and **lve**, not to the left of this connection as e.g. in *Nyctibora* (fig.328h) and *Nahublattella* (fig.328b). (2) The right part of the **lve**-pouch, including the distal part of the ejaculatory duct, has partly wrapped around the **L2**-sclerite (again, clockwise as seen from behind; upper curved arrow in fig.328e). (3) Posteriorly the sclerotisation on the left edge of the **lve**-pouch bends more and more into the dorsal **lve**-wall (compare fig.271 and 272). (4) The genital opening has been rotated in the same way and is now in the right ventral wall of the left complex (in between the lobes **47**, **48**, **49** in fig.266, 271).

In contrast, the area of **via** has been rotated counterclockwise in *Blaberus* (as seen from behind; curved arrows in fig.328k): The contact between the lumina of the **via**-process and of the rest of the left complex is situated ventral to the connection of the sclerotisations of **via** and **lve** (fig.328k, 300, 302). Posteriorly the sclerotisation on the left edge of the **lve**-pouch bends more and more into the ventral **lve**-wall (compare fig.299 and 300). In contrast to the other species (fig.328b,c,d,h,i), the genital opening is not exactly on the right side of the **lve**-pouch but more in its dorsal wall.

The **tve**-tendon is missing in *Euphyllodromia* and *Blaberus*. In *Parcoblatta* the invagination anteriorly on the **vge**-groove (**vge, tve** in fig.273) has exactly the same position as the **tve**-tendon in *Nyctibora* (fig.328e,h): At the base of **via**, opposite to where the sclerotisations of **via** and **lve** are connected. In *Parcoblatta* the right insertion of **l4** has shifted to **tve**, and this might be the reason for the retention of **tve** despite the loss of muscle **l10**.

The **via** of *Nyctibora* and *Nauphoeta* are clearly homologous with **via** of *Nahublattella*; the **via**-morphology of *Supella* and the remaining species can be derived from that of *Nyctibora* and *Nauphoeta*. Therefore, for all species shown in fig.328 it is assumed that the processes designated **via** are homologous. The presence of two sclerites **L2D** (in **lve**) and **L2E+L4N** (on **via**) is probably plesiomorphic. (Exact argumentation in 7.5.; the interpretation results from the situation in *Nahublattella*). In the species having these two sclerites fused, the resulting sclerite would have to be named correctly **L2D+(L2E+L4N)**. I will simply designate it **L2**.

In most of the species shown in fig.328b-k, **L2** or **L2D** occupy the entire left edge of the **lve**-pouch and the adjacent margins of the dorsal and ventral **lve**-walls (cross-section like in fig.270 or 301). This groove shape of **L2** or **L2D** extends posteriad as far as to the base of **via** (articulation **A10**, if present). This is the case in *Nahublattella*, where, however, **A10** is far anteriorly (fig.328b), and close to **A10** there is a kink to the left (edge **7** at **36** in fig.242). Between **A10** and the kink, **L2D'** bears the extension **28** (fig.245) into the ventral **lve**-wall, which has a homologue in *Anaplecta* (**28** in fig.216). In *Supella, Parcoblatta, Nyctibora, Nauphoeta*, and *Blaberus* (fig.328c,e,h,i,k) **L2** is also groove-shaped, but **A10** or the **via**-base are by far more posteriorly, and there is no kink (except for a hint of one in *Nyctibora*) and no extension **28**.

In *Euphyllodromia* (fig.328d) and *Loboptera* (fig.328f) the sclerotisation of the **lve**-pouch is – except for the anteriormost part – restricted to the dorsal wall (and not groove-shaped), and the membranous left edge of the **lve**-pouch is extensively invaginated. For a correct interpretation of these invaginations (origin, homology in *Euphyllodromia* and *Loboptera*?) further investigations are necessary. Only *Loboptera* has a bulge (**X** in fig.328f; thickened cuticle?) in the ventral wall of this invagination, which bears a sclerotised whip-like process (**Y** in fig.328f). (Since there is no **via**-process at the posterior end of **L2**, these

X- and **Y**-structures could possibly be **via**, which then would be in a rather primitive position; compare *Nahublattella*, fig.328b).

Ventral lobe **vla** *Parcoblatta* and *Blaberus* have retained a distinct **vla**-lobe. Like in *Nahublattella*, however, the **L4**-plate in the ventral **vla**-wall has been lost (compare e.g. **L4G** in *Anaplecta*, fig.205).

The **vla**-lobe of *Blaberus* (fig.297a, 299: beneath the **via**-process) can be identified as the true **vla** by some of its features in common with *Nahublattella* and other species: The dorsal **vla**-wall continues anteriad into the ventral **lve**-wall (fig.12, 181, 246, 300). The ventral **vla**-wall is part of the ventral wall of the left complex (fig.6, 174, 239a, 297a). The dorsal and ventral **vla**-walls are connected by a very stout muscle (**l6b** in fig.18, 188, 189, 251, 252, 305, 306). In contrast to all other species, however, *Blaberus* has the dorsal insertion of **l6b** on the **L2**-sclerotisation. This is a consequence of the rotation of **via** and of the posterior parts of **L2** described above, by which extensive parts of **L2** must have shifted into the insertion area of **l6b**.

Parcoblatta has a similar **vla**-lobe (fig.268-270), which, however, lies to the left and dorsal to the **via**-process. This location corresponds to the rotation of **via** and of the genital opening described above, in which **vla** has been involved, too. Muscle **l6b** (fig.278, 279) is in the same position as in *Blaberus*; its dorsal insertion, however, is on the membranous parts of the **lve**-pouch wrapped around the **L2**-sclerite; this situation is, again, an effect of the rotation.

In the other species (fig.328c,d,f,g,h,i; **l6b** not investigated) there is no distinct lobe **vla**. By comparing the relative positions of the phallomere elements adjacent to the **vla**-lobe in *Blaberus* and *Parcoblatta*, however, a membranous area that is assumed to be the last vestige of **vla** (fig.328c,d,h,i) can be determined. Only in *Loboptera* (fig.328f) and *Ectobius* (fig.328g) this is not possible because of extensive reductions in this part of the left complex.

A sclerotisation **L10** on **vla** is only present in *Blaberus* (fig.299) and some other Blaberidae (e.g. *Blaptica*, fig.291). **L10** is discussed in 6.3.4..

The muscles of this area have been investigated only in *Parcoblatta* and *Blaberus*. Muscle **l5** of *Anaplecta* (fig.223) and *Nahublattella* (fig.251) is probably missing in *Parcoblatta* and *Blaberus* or might possibly be incorporated into muscle **l6b**. *Nahublattella* (fig.251, 252), *Parcoblatta* (fig.277-279), and *Blaberus* (fig.305, 307) have some muscles in the ventral wall of the left complex (**l30**, **l31**, **l32**, **l37**, **l38**, **l40**, **l44**, **l45**), most of which are rather diffuse. These can be homologised only in part, and the most probable homologies are expressed by the designations.

6.3. Left complex III: Main sclerites L4 and L10 and associated elements

6.3.1. Comparison between Blattaria and Mantodea

The homology relations between Blattaria and Mantodea and the common ground-plan can be best deduced from a comparison between *Mantoida, Archiblatta, Eurycotis*, and

Tryonicus. Features of *Periplaneta* will also be discussed (no figures). In *Mantoida* **L4** is one large sclerite, in the Blattarian species **L4** is a group of sclerites.

L4 of *Archiblatta* (fig.53-57) and **L4** of *Periplaneta* are very similar: 5 sclerites **L4C, L4D, L4E, L4F**, and **L4G** in the same arrangement. *Eurycotis* (fig.65-69) has three sclerites **L4H, L4F**, and **L4G**.

That both **L4F** and **L4G** are homologous in the three species is evident from the identical positions and similar outlines of the sclerites and from the fact that in *Eurycotis* as well as in *Periplaneta* the muscles **l5** (fig.72) and **l6b** (fig.70, 71) insert on them. A special feature of *Eurycotis* is the **mla**-lobe (fig.63, 68, 69).

L4H of *Eurycotis* (fig.65-68, 325e) is composed of three parts which are homologous with **L4C**, **L4D**, and **L4E** of *Archiblatta* (fig.53, 57, 325f) and *Periplaneta*: (1) The left, crescent-shaped part of **L4H** corresponds to **L4C**. It lies in the left edge and in the anteriormost ventral wall, an apodeme **swe** runs along it, and its posteriormost part occupies a process **pda**. In *Eurycotis* and *Periplaneta* the muscles **l2** and **l4** (fig.70, 71) insert on the posterior part of **swe** and run to the pouches **pne** and **lve**. (2) The left part of the **L4H**-plate in the anterior ventral wall is homologous with **L4D**. It takes a position left-posterior to the right-anterior end of **swe** and bears a node-like process **nla**. *Eurycotis* and *Periplaneta* have a stout muscle from this sclerotisation to the **hla**-hook (**l14c** in fig.72). (3) The right part of the **L4H**-plate in the anterior ventral wall is homologous with **L4E**. It takes a position in between the right-anterior end of **swe** and **L4F**. *Eurycotis* and *Periplaneta* have a muscle from this sclerotisation to the anterior part of the **lve**-pouch (**l6a** in fig.73).

The definition of the regions of main sclerite **L4** is mainly based on the condition of **L4** – as several isolated sclerites – in *Archiblatta* (compare fig.53-57 and fig.325f). The choice of *Archiblatta* as the type of reference is made for practical reasons and has nothing to do with an assumption of a primitive state. The positions of muscle insertions on the various **L4**-regions (not studied in *Archiblatta*) are taken from *Periplaneta* and *Eurycotis* – in accordance with the homology relations to *Archiblatta* discussed above. For *Archiblatta* and *Eurycotis* the regioning is shown in fig.325e,f.

- **L4l** (lateral): The sclerotisation homologous with sclerite **L4C** of *Archiblatta*, minus its dorsal extension to the right (**L4d**, see below). **L4l** bears the **swe**-apodeme and sclerotises the **pda**-process posteriorly. On **L4l** there are the left insertions of the muscles **l2** and **l4**, which run to the pouches **pne** and **lve**.
- **L4d** (dorsal): The sclerotisation homologous with the dorsal, rightward directed extension of sclerite **L4C** of *Archiblatta*.
- **L4n** (node): The sclerotisation homologous with sclerite **L4D** of *Archiblatta*. **L4n** bears the evagination **nla**. On **L4n** there is the anterior insertion of muscle **l14**, which runs to the **hla**-hook.
- **L4c** (central): The sclerotisation homologous with the sclerites **L4E** and **L4F** of *Archiblatta*.
- **L4v** (ventral): The sclerotisation homologous with sclerite **L4G** in the ventral wall of the **vla**-lobe of *Archiblatta*. On **L4v** there is the ventral insertion of muscle **l6b**, which runs to the **lve**-pouch.

Eurycotis has no distinct **L4d**-region; the demarcation of **L4d** in fig.325e is tentative. In *Archiblatta* (fig.325f) and *Periplaneta* **L4d** is very distinct.

Three other **L4**-regions are not present in *Archiblatta* but are apomorphic sclerotisations of certain subgroups:

- **L4a** (anterior), **L4x**: Sclerotisations of *Lamproblatta* and *Polyphaga* (and *Ergaula*) which have developed by an expansion of the sclerites in the ventral wall of the **vla**-lobe (definition in 6.3.4.).
- **L4b** (between): A new sclerotisation in the ventral wall of the left complex of *Chaeteessa*, *Sphodromantis*, and *Metallyticus* (definition in 6.3.3.).

The left part of **L4** of *Mantoida* (fig.44, 45) and the muscles inserting on it are very similar to the regions **L4l** and **L4d** of *Archiblatta*, *Periplaneta*, and *Eurycotis*; homology is assumed for the following similarities and elements (fig.325d,e,f):

1. Both the left part of **L4** (*Mantoida*) and **L4C** (*Archiblatta*) occupy the whole left edge of the left complex and the anteriormost ventral wall (fig.44, 45, 53, 54).
2. An apodeme **swe** extends along most of this sclerotisation (fig.44, 45, 53, 54); anteriorly **swe** is massive and beam-like, posteriorly it is groove-like.
3. The posteriormost part of both **L4** and **L4C** occupies a process (**pda** in fig.44, 53). However, only in *Mantoida* the sclerotisation of **pda** is connected with the **L2**-sclerotisation of the **paa**-process (compare in 6.2.1.).
4. Both **L4** and **L4C** have a distinct dorsal extension to the right (**L4d** in fig.44, 53).
5. Muscle **l2** inserts on the **swe**-apodeme in the posterior half of **L4** (*Mantoida*), or **L4C** (*Periplaneta*), or **L4H** (*Eurycotis*) (fig.49, 70). **l2** runs to the **pne**-pouch and inserts on **L1** (*Mantoida* and *Periplaneta*) or in the membrane to the left of **L1** (*Eurycotis*).
6. Muscle **l4** inserts on **swe** ventral to **l2** (fig.50, 71) and runs to the **lve**-pouch.
7. Muscle **s1** (fig.48, 70), which comes from the left apophysis of the subgenital plate (fig.37, 59), inserts on that part of **L4**, **L4C**, or **L4H** in the anteriormost ventral wall.

The right part of **L4** of *Mantoida* has some features in common with the regions **L4v** and **L4c** of *Archiblatta*, *Periplaneta*, and *Eurycotis* (fig.325d,e,f):

8. The posterior right part of **L4** (fig.41, 47) has the same position in the ventral wall of the **vla**-lobe as the **L4G**-sclerites (= **L4v**-region) have in *Eurycotis* (fig.63, 66) and *Archiblatta* (fig.54).
9. The anterior right part of **L4** is, like the anterior **L4c**-region in *Archiblatta* (**L4E** in fig.57) and *Eurycotis*, situated between the right anterior end of the **L4l**-region and the anterior end of the **L4v**-region.
10. A muscle running to the ventral wall of the ejaculatory duct inserts on or near the right part of **L4** or on **L4G**, respectively: the posteroventral part of **l6** in *Mantoida* (fig.52), **l6b** in *Eurycotis* (fig.70, 71) (compare in 6.2.1.).

These features 1.-10. suggest the homology relations shown in fig.325d,e,f. In *Mantoida*, the regions **L4l**, **L4d**, and **L4v** can be unambiguously identified, and the similarities 1.-8. and 10. can be regarded as features of the common ground-plan of Blattaria and Mantodea. **L4c** might be contained in the anterior right part of **L4** (feature 9.), but this is not certain since in *Mantoida* the extension of the **L4v**-region to the anterior cannot be determined and the **L4c**-region is only indicated by its relative position in between **L4v** and **L4l** (**?** in fig.325d). Hence, 9. is an uncertain ground-plan feature. In *Mantoida* there is no indication for the presence of a **L4n**-region, and a **nla**-process is missing.

Evidence from *Chaeteessa* (complete discussion in 6.3.3.) suggests that the **L4n**-region is also an element of the common ground-plan of Blattaria and Mantodea and that the lack of **L4n** in *Mantoida* is derived:

11. The heavier sclerotised transverse bridge in the anterior ventral wall of the left complex of *Chaeteessa* might, according to its very similar position, well be homologous with the **L4n**-region of *Eurycotis* (compare fig.31 and 65, 69; fig.325c,e).

Tryonicus has some features in common with *Archiblatta* and *Mantoida* which suggest the homology relations shown in fig.325d,f,g. The two sclerites **L4K** and **L4N** (fig.85, 97) together form a broad ribbon in the left wall of the left complex, which takes, like **L4C** in *Archiblatta* (fig.54), a position left-dorsal to the base of the **hla**-hook. Most of **L4K** and **L4N** is therefore assumed to represent the **L4l**-region. The **nla**-process (fig.97) on **L4K** corresponds to the **nla** of *Archiblatta* (fig.56) and *Eurycotis* (fig.68) in its shape, in its location in the anterior ventral wall, and in its position relative to the other **L4**-sclerotisations and to the **hla**-base. Thus, the part of **L4K** on **nla** is regarded as the **L4n**-region. That part of **L4K** which anterior to **nla** extends to the right (fig.95) has the same relative position as the right-anterior part of the **L4C**-crescent of *Archiblatta* (fig.53, 55) and is hence assumed to belong to the **L4l**-region. The ribbon-like extension of **L4N** (**L4d** in fig.88-95) corresponds in its shape and relative position with the **L4d**-region of *Mantoida* (fig.45) and especially *Archiblatta* (fig.53). The posteriormost part of **L4N** occupies a process (**pda** in fig.91) like in *Mantoida* and *Archiblatta* (**pda** in fig.44, 53) and can be regarded as part of the **L4l**-region. Like in *Mantoida* but in contrast to

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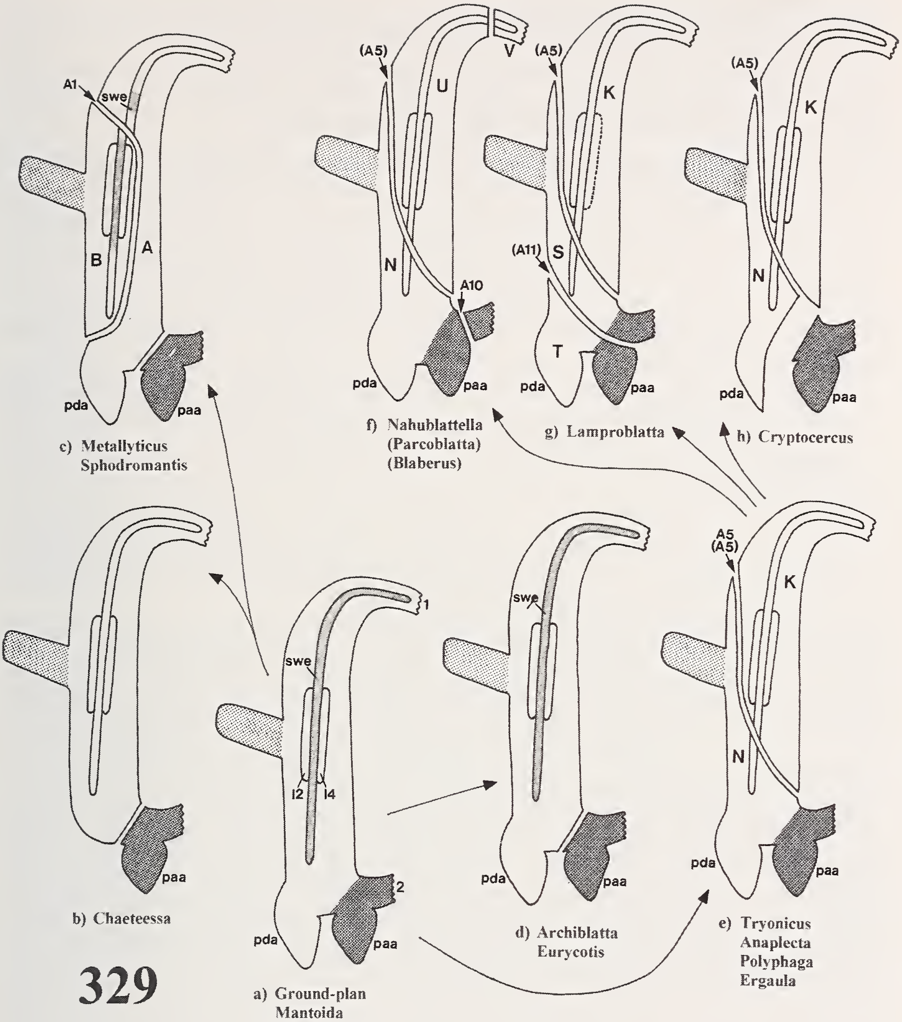
Fig.329: Left complex, subdivisions of regions **L4l** and **L4d** into individual sclerites in Blattaria and Mantodea. – Region **L4l** (discussion in 6.3.) is in its primitive condition undivided and connected with region **L2d** posteriorly (between processes **paa** and **pda**). In many species **L4l** is connected with region **L4n** anteriorly (ground-plan condition unclear). The various subdivisions of **L4l** in the subgroups of Blattaria and Mantodea and the hypothetic directions of evolutionary transformation are shown. The various types – or further derivations of them – are present in the species listed. It is intended to emphasise principal similarities and differences in the subdivision of **L4l**. For comparability, all elements are left in their most primitive condition (like in fig.329a) – except for the subdivisions of **L4l** and of the included parts of **L2**. Inner views from the right side; dorsal←, ventral→, anterior↑, posterior↓.

The following structures are shown:

- The sclerite regions **L4l** (white) and **L4d** (light pattern) and parts of **L2** (dark pattern; mainly region **L2d** on process **paa**). The right-anterior undulate line (**1** in fig.329a) represents the removal of region **L4n**. The right-posterior undulate line (**2** in fig.329a) represents the removal of the remainder of **L2**. **L4d** is always shown in its most primitive position, orientation, and shape, even if these have changed or if **L4d** has been lost.
- The dividing lines which cause a division of these sclerotisations into individual sclerites. Dividing lines along which the respective sclerites are still in close contact are labelled **A**+Number (articulation, e.g. **A5**; like in the text); if the respective sclerites are farther away from each other the name of the respective articulation is put in brackets (e.g. **(A5)**).



c) Metallyticus Sphodromantis

f) Nahublattella (Parcoblatta) (Blaberus)

g) Lamproblatta

h) Cryptocercus

b) Chaeteessa

a) Ground-plan Mantoida

d) Archiblatta Eurycotis

e) Tryonicus Anaplecta Polyphaga Ergaula

329

- The individual **L4**-sclerites produced by the division of **L4l** and **L4d**. These are labelled with the capital letters used in the text and in fig.1-319 (e.g. **B** = **L4B**).
- The apodeme **swe**. **swe** is always shown in its most primitive condition and position (like in fig.329a), but only the parts of **swe** retained in the respective species are patterned and labelled.
- The insertion areas of the muscles **l2** and **l4**, which are also always shown in their most primitive condition and position (like in fig.329a).
- The processes **pda** (with its **L4l**-sclerotisation) and **paa** (with its **L2d**-sclerotisation).

The various types can be derived from each other in the way indicated by the arrows. *Mantoida* (fig.329a) conforms completely with the ground-plan. *Parcoblatta* and *Blaberus* can be derived from *Nahublattella* but differ in some respects (e.g. secondary fusion at **A10**).

Archiblatta, **paa** is bulge-shaped and its sclerotisation is connected with that of the **paa**-process (fig.96). Sclerite **L4G** (fig.92, 325g) resembles **L4G** of *Archiblatta* (fig.325f) in its outline and its position in the ventral wall of the **vla**-lobe and probably represents the **L4v**-region; however, it cannot be excluded that, additionally, sclerotisations of the **L4c**-region are contained in this **L4G** (in its left and anterior parts).

As compared with *Archiblatta*, *Eurycotis*, and *Mantoida*, some features of *Tryonicus* can be regarded as derived: The **L4l**-sclerotisation of *Tryonicus* is (1) broader and (2) divided into two sclerites (**L4K, L4N**; fig.325d,f,g) by the articulation **A5** (fig.88, 97; compare fig.329a,d,e). (3) The **swe**-apodeme is completely missing. (4) **L4d** is directed more anteriad.

On the other hand, some features of *Tryonicus* can contribute to the common ground-plan of Blattaria and Mantodea:

12. As already stated in 6.2.1., feature 4., the connection of the sclerotisations of **pda** (**L4l**) and **paa** (**L2d**) present in *Tryonicus* and *Mantoida* is a ground-plan state. The separation of these sclerotisations in *Archiblatta* and *Eurycotis* is derived (compare feature 3.).
13. In *Tryonicus* and in *Mantoida* no sclerotisations can be unambiguously assigned to the **L4c**-region, and a sclerite corresponding to **L4F** of *Archiblatta* and *Eurycotis* is definitely missing. Thus, **L4F**, and possibly the whole **L4c**-region, can be regarded as a derived element of *Archiblatta* and *Eurycotis*.

Concerning the common ground-plan of Blattaria and Mantodea, four questions remain open: (1) It cannot be decided if there is a **L4c**-region. (No sclerotisations undoubtedly homologous with the sclerotisations defined as **L4c** in *Archiblatta*, *Eurycotis*, and *Periplaneta* have been identified in any other species). (2) It cannot be determined whether the **L4l**-region is connected with or separated from the **L4v**-region (or **L4c**-region, if present) in the anterior ventral wall of the left complex (**?** in fig.321e), since there is always a connection in Mantodea but never in Blattaria. (3) It cannot be decided if a **nla**-process is present (but compare in 7.5. (**M**), (**N**)). (4) In *Tryonicus*, *Eurycotis*, and, if the assumption in 11. is true, in *Chaeteessa* the regions **L4l** and **L4n** are firmly connected. Hence, the separation of **L4l** and **L4n** in *Archiblatta* (sclerites **L4C** and **L4D**) might be regarded as apomorphic. However, the position of the connection between **L4n** and **L4l** is rather different in *Tryonicus* (to the left of **nla**, fig.96, 97) and *Eurycotis* (to the right of **nla**, fig.67, 68), and these connections might be non-homologous. Thus, it seems better to regard the respective ground-plan state of **L4n** (connected with **L4l** or not) as unresolved.

6.3.2. The elements in the common ground-plan of Blattaria and Mantodea

The features 1.-13. in 6.3.1. permit the reconstruction of many ground-plan features of **L4, pda, vla**, and some adjacent elements: (fig.321e,g,i): **L4** is composed of sclerotisations in the left edge and in the anterior and right ventral wall of the left complex. The **L4l**-region is located in the left edge and in the anteriormost ventral wall. The **swe**-apodeme runs along most of **L4l**. **swe** is massive and beam-like anteriorly and groove-like posteriorly. There is a distinct dorsal extension **L4d** directed to the right and possibly slightly anteriad. The posteriormost part of **L4l** completely sclerotises a bulge-like process **pda**. The sclerotisation of **pda** is connected with the sclerotisation of **paa** (region **L2d**). The right posterior part of **L4** (region **L4v**) lies in the ventral **vla**-wall. The presence of the **L4c**-region is questionable, but a sclerite **L4F** is certainly missing. The **L4n**-region is present. The presence of the **nla**-process is unclear. The muscles **l2, l4**, and **l6b** are present. **l2** and **l4** have their **L4**-insertions close together on the **swe**-apodeme in the left edge of the left complex.

6.3.3. Homology relations and character states of the elements in Mantodea

In *Chaeteessa* (fig.28), *Metallyticus* (fig.20), and *Sphodromantis* (fig.6), the ventral wall of the left complex is completely sclerotised, not only along its margins as in *Mantoida* (fig.41). In *Chaeteessa*, however, the marginal ventral sclerotisation is distinctly heavier and is assumed to correspond to **L4** of *Mantoida* (fig.325a- d) – composed of the ground-plan regions **L4l** and **L4v** (and possibly **L4c**). The anterior transverse bridge of heavier sclerotisation present in *Chaeteessa* is probably also a ground-plan element (**L4n**-region). The weaker sclerotisation of the remaining ventral wall is new and is defined as a further region of **L4** (fig.325a-c):

- **L4b** (between): The sclerotisation of the ventral wall of the left complex between the ground-plan regions **L4l, L4n**, and **L4v** (and possibly **L4c**).

In *Metallyticus* and *Sphodromantis* this **L4b**-sclerotisation is further derived in being as heavy as the ground-plan regions of **L4.** The presence of **L4n** is not assessable for this uniformity of the ventral sclerotisation (in fig.325a,b the interpretation is done in accordance with *Chaeteessa*). The presence of a region **L4c** is in *Chaeteessa, Metallyticus*, and *Sphodromantis* as uncertain as in *Mantoida* (**?** in fig.325a-d).

As compared with *Mantoida* (fig.44) or *Archiblatta* (fig.53), in *Chaeteessa* (fig.31), *Metallyticus* (fig.21), and *Sphodromantis* (fig.9) the **L4**-sclerotisation in the dorsal wall of the left complex has expanded to the right: In *Chaeteessa* and *Sphodromantis* **L4** occupies most of the dorsal wall, in *Metallyticus* it is restricted to the anterior part. By this expansion **L4** now covers the external opening of the **pne**-pouch from dorsally. Possibly in correlation with this expansion the **pne**-pouch has rotated to the right (clockwise as seen from behind; compare in 6.1.3.). These shifts are very obvious in *Chaeteessa* and *Sphodromantis* but less distinct in *Metallyticus.*

The muscle insertions on the **L4l**-region of *Mantoida* (fig.48-52, 325d) and on the dorsal part of **L4** (**L4B**) of *Sphodromantis* (fig.15-17, 325a) also demonstrate these shifts: The muscles **l1** (to **L1** anteriorly in the **pne**-pouch), **l2** (to **L1** more posteriorly in the **pne**-pouch), **l4** (to **L2**), and **l7** (to the left posterior ventral wall of the left complex) are certainly homologous in the two species, but in *Sphodromantis* all insertions on **L4** have shifted far to the right. These insertions also show that the extensive dorsal **L4**-sclerotisations of *Sphodromantis* (**L4B**) have not been produced by an expansion of the **L4d**-region (*Mantoida*: fig.44) but of the **L4l**-region (fig.325a): **l2, l4**, and **l7** of *Mantoida* are not inserted on **L4d** but on **L4l**. At the most a small right-anterior part of **L4B** of *Sphodromantis* (posterior to the **l1**-insertion, fig.17) might be regarded as representing **L4d** (fig.325a). Whether this distribution of **L4l** and **L4d** in the dorsal wall is also true of

Chaeteessa and *Metallyticus* is unclear (no data for the musculature); in fig.325b,c **L4l** and **L4d** are demarcated in accordance with the situation in *Sphodromantis*. In any case, in *Chaeteessa, Metallyticus*, and *Sphodromantis* the **L4d**-region is no longer distinct from the **L4l**-region.

The **pda**-process of *Metallyticus* (fig.20, 23-26) is in its shape and in its position relative to the **paa**-process similar to **pda** of *Mantoida* (fig.44-46) and is likewise sclerotised by **L4**. Homology is assumed for the **pda** of the two species. However, in *Metallyticus* the sclerotisations of **pda** and **paa** are separated, and the processes themselves are more distinct from each other and by far longer. These two features also apply to *Sphodromantis* and *Mantis*: In *Mantis* (no figure) **pda** is shovel-shaped and far on the left side as in *Metallyticus*. In *Sphodromantis* (fig.9-12), certainly a close relative of *Mantis*, **pda** is long and slender and has shifted to the right. Thus, despite the different morphology of **pda** in *Mantoida* and *Sphodromantis*, these evolutionary stages suggest homology. In *Chaeteessa* the **pda**-process has been completely lost. (The one posterior process of *Chaeteessa*, fig.28, has proved to be **paa**; compare in 6.2.3.).

Only in *Sphodromantis* and *Metallyticus* (and *Mantis*, which will not be further considered) the dorsal and ventral parts of **L4** have become separated by an articulation (**A1** in fig.6, 10, 20, 24; sclerites **L4A**, **L4B**). The dividing line runs within the **L4l**-region (fig.325a,b). This is evident from the positions of the involved sclerotisations (compare fig.325a,b and c,d) and from the muscle insertions: In *Sphodromantis* (fig.325a) **s1** inserts on **L4A**, but **l2**, **l4**, and **l7** insert on **L4B**, and all these insertions belong to **L4l** (compare *Mantoida*, fig.325d). This division of **L4l** reminds one of the **L4l**-division in *Tryonicus* (by **A5** in fig.88, 97, 325g). However, the courses of the dividing lines are different: The **pda**-sclerotisation, for example, is part of the posterodorsal plate (**L4N**) in *Tryonicus* but part of the ventral plate (**L4A**) in *Metallyticus* and *Sphodromantis* (compare fig.329c and e). Thus, the articulations **A1** and **A5** are certainly not homologous, and the division of **L4l** is a case of parallel evolution.

The **swe**-apodeme is well-developed in *Mantoida* and *Archiblatta* (fig.45, 53). In *Chaeteessa* **swe** has been completely lost. *Metallyticus* has retained a vestige of **swe** on the left margin of the ventral **L4A** (fig.24). *Sphodromantis* has a vestige on the left margin of the dorsal **L4B** (fig.10,11). This suggests that **swe** has been cut through by the division into **L4A** and **L4B** and confirms that the **L4l**-region participates in both **L4A** and **L4B**.

6.3.4. Homology relations and character states of the elements in Blattaria

Archiblatta, Eurycotis, and *Tryonicus*

These species have been sufficiently discussed in 6.3.1.

Cryptocercus, Lamproblatta, Polyphaga, Ergaula, and *Anaplecta*

In *Tryonicus* (fig.325g) the **L4l**-region is divided by articulation **A5**: The anterior parts of **L4l** form, together with **L4n**, the **L4K**-sclerite; the posterior parts of **L4l** (with the **pda**-sclerotisation) form, together with **L4d**, the **L4N**-sclerite. The connection of the sclerotisations of **pda** (**L4l**) and **paa** (**L2d**, fig.324g) is retained. The **swe**-apodeme has been lost. The **nla**-process is well-developed. The **L4v**-region is a plate in the ventral wall of the **vla**-lobe, the **L4G**-sclerite.

From this situation the morphology of the five species in the heading and the remaining Blattellidae and Blaberidae can be derived. In all these species, however, **L4K** and **L4N** are no longer articulated but far away from each other. In some species **L4K** or **L4N** undergo further divisions. In *Cryptocercus*, *Polyphaga, Ergaula*, and *Lamproblatta* the anterior sclerite **L4K** has been strongly reduced (fig.150, 124, 177). The sclerotisations of **paa** and **pda** remain in most species connected, and this connection often becomes very close. The **L4v**-region may retain its shape and position, or it becomes enlarged *(Lamproblatta, Polyphaga, Ergaula)* or lost *(Nahublattella, Parcoblatta, Blaberus).*

As a first point, the evolution of the **L4N**-sclerite and the processes **pda** and **paa** of the species in the heading will be discussed; then the **L4K**-sclerite with the **nla**-process and, at last, the sclerite in the ventral **vla**-wall will be considered. **paa**, **pda**, and **vla** have in part already been discussed in 6.2.4, but a discussion of these elements is only complete by considering them in context with the other **L4**-sclerotisations. This will be done in this section.

L4N-sclerite, processes pda and paa The homology of **L4N** of *Tryonicus* (fig.94-97), *Polyphaga* (fig.117, 118), *Ergaula, Cryptocercus* (fig.150, 151), and *Anaplecta* (fig.210-215) – and of its derivatives **L4S** and **L4T** in *Lamproblatta* (fig.177-180) – can best be deduced from a comparison of the prominent substructures. In *Tryonicus* these are: (1) The **pda**-sclerotisation (posteriormost **L4l**-region), including its close vicinity to and connection with the **paa**-sclerotisation (**L2d**-region). (2) The dorsal extension to the anterior (**L4d**-region).

Further evidence comes from the musculature, which, however, has not been studied in *Tryonicus*. The homology relations and the resulting regioning of these sclerotisations into **L4l** and **L4d** are shown in fig.325g,h,i,k,l.

The **pda** and **paa** of *Tryonicus, Lamproblatta, Polyphaga, Ergaula*, and *Anaplecta* have some features in common, none of which, however, is realised in all these species. But the whole of the similarities is sufficient to regard the **pda** and **paa** of all species as homologous.

- **pda** and **paa** are two processes with their sclerotisations firmly connected. (The sclerotisation of **pda** is designated as **L4N** or **L4T**, that of **paa** as **L2** or **L2C**). *Ergaula*, however, has lost the right process **paa**.
- The position of **pda** and **paa** on the left complex is dorsal, far posterior, and far to the left – near the left end of the **lve**-pouch. In *Lamproblatta*, however, their position relative to **lve** is more to the right (fig.179, 180).
- The common sclerotisation of **paa** and **pda** is, to the right (*Anaplecta*, fig.211) or to the ventral side (*Polyphaga*, fig.118, 122; *Ergaula*; *Tryonicus*, fig.97), firmly connected with the left end of the **L2**-sclerotisation in the **lve**-pouch. *Lamproblatta*, however, has lost this connection (fig.178, 179).
- On the common sclerotisation of **paa** and **pda** there inserts a muscle coming from the left part of the **lve**-pouch (**l10** in fig.129, 186, 222; compare in 6.2.4.; not analysed in *Tryonicus*).

- In *Polyphaga* and *Lamproblatta* the left process **pda** is long and pointed, the right process **paa** is somewhat saucer- or cup-shaped.
- In *Polyphaga* and *Ergaula* the **pda**-processes are nearly identical.

Polyphaga, Ergaula, and *Lamproblatta* (but not *Anaplecta*) have sclerotisations probably homologous with the **L4d**-region of *Tryonicus*:

- In *Tryonicus* the one end of **L4N** (to the right of **pda**) is connected with **L2** occupying **paa** and the **lve**-pouch, and its other end has the extension **L4d** (fig.96), which is directed anteriad.
- In *Polyphaga* and *Ergaula* **L4N** is also connected with **L2**, and its opposite end has an extension, which, however, is directed to the left (**L4d** in fig.118).
- In *Lamproblatta* the sclerotisation **L4S** (fig.178, 180) is connected with **L2** at the left end of the **lve**-pouch. The distal part of **L4S** resembles **L4d** of *Polyphaga* – with the difference that it is not connected with the sclerotisation of **pda** and **paa** (compare fig.325i and k). I assume that in *Lamproblatta* a dividing line has formed which has separated the following sclerotisations from each other (fig.329e,g): Posterior to the line is the common sclerotisation of **pda** and **paa** (composed of **L4T**, a part of the former **L4N**-sclerite, and **L2C**, a part of the former **L2**-sclerite). Anterior to the line are (1) the part of the **L2**-sclerotisation at the left posterior end of the **lve**-pouch and (2) the other part of the former **L4N**-sclerite (**L4S**) which maintains the connection with **L2** at its one end and has the extension **L4d** at its other end (fig.178).
- The homology of the extensions **L4d** in *Lamproblatta*, *Polyphaga*, and *Ergaula* is confirmed by muscle **l11**, which inserts on or near **L4d** and runs to sclerite **L4K** (fig.128, 188, 327).
- *Nahublattella* (complete discussion below) also has an extension similar to **L4d** of *Tryonicus* or *Polyphaga* (**L4d'** in fig.242); it extends, like **L4d** of *Polyphaga*, from the common sclerotisation of **paa** and **pda** to the left. In *Anaplecta* **L4d** has been lost.

L4d is directed to the right in *Mantoida* (fig.44), right-anteriad in *Archiblatta* (fig.53), and anteriad in *Tryonicus* (fig.94). In *Polyphaga* and *Ergaula* (and *Nahublattella*) **L4d** has even further rotated (counterclockwise as seen from above) and is directed to the left. From such a position, **L4d** of *Lamproblatta* has additionally rotated 90° (clockwise as seen from behind) and shows a dorsoventral orientation (fig.178).

L4N of *Cryptocercus* (fig.150) is assumed to be homologous with the **L4N** of the other species and to have the same orientation as in *Polyphaga* and *Ergaula* (compare fig.117 and 150, 325h and k): Its left part is **L4d**, its right part is the **pda**-sclerotisation (fig.325h). This is suggested by the following features:

- **L4N** lies, like in the previous species, in the left dorsal wall of the left complex (fig.150).
- The right part of **L4N** lies, like the right part of **L4N** of *Polyphaga* and the right-posterior part of **L4N** of *Tryonicus*, on a process (**pda** in fig.150, 118, 96).
- **pda** is, like in *Tryonicus*, *Mantoida*, and *Polyphaga*, situated to the left of (and somewhat dorsal to) the **paa**-process (fig.150, 96, 44, 117).
- Within the angle formed by the sclerites **L4N** and **L2** (fig.150) there is the base of the **hla**-hook. *Tryonicus* shows the same relations (fig.97).
- In *Cryptocercus* and *Mantoida*, the muscles **l1** (fig.48, 155) and **l2** (fig.49, 156) run

from the **pne**-pouch to the left and dorsad (homology discussion in 6.1.1.). The insertion of **l1** is in *Cryptocercus* on **L4N** (including **L4d**), in *Mantoida* on and to the right of **L4d**.

- In *Cryptocercus* and *Mantoida*, muscle **l9** (fig.49, 155) runs transversely within the dorsal wall of the left complex (homology discussion in 6.5.). Its left insertion is in *Cryptocercus* anterior to the left end of the assumed **L4d**-part of **L4N**, in *Mantoida* near the right end of **L4d**; regarding the orientation of **L4N** assumed for *Cryptocercus*, these ends of the sclerites would be homologous. In *Cryptocercus*, however, **l9** does not extend as far to the right as in *Mantoida*.

Some features of *Cryptocercus* are derived: (1) The sclerotisation of **pda** is largely reduced (fig.150, 329h), and, possibly as a consequence of this, (2) the sclerotisations of **pda** (**L4**) and **paa** (**L2**) have separated (like in *Chaeteessa*, *Metallyticus*, *Sphodromantis*, *Archiblatta*, and *Eurycotis*).

L4K-sclerite, process **nla L4K** of *Anaplecta* (fig.209, 212) is probably homologous with **L4K** of *Tryonicus* (fig.98); similarities are:

- The position in the left and left-ventral walls of the left complex.
- The anterior part is on a bulge-like evagination (**nla** in fig.97, 212). Like in *Tryonicus*, this sclerotisation is regarded as the **L4n**-region (fig.325g,l).
- The posterior part is plate-like, with a broadly truncate posterior margin, and this part partially encloses the retracted **hla**-hook from the left side (fig.85, 202). Like in *Tryonicus*, this sclerotisation is regarded as an anterior part of the **L4l**-region (fig.325g,l).

A comparison of the muscles of *Anaplecta* and *Eurycotis* confirms these assignments to **L4n** and **L4l**:

- That in both species the anterior insertion of the main muscle of the **hla**-hook (**l14c** or **l14**; fig.73, 222) is on or near the sclerotisation of the **nla**-bulge shows the homology of these **nla**. The **nla**-sclerotisation of *Eurycotis* is, by definition, the **L4n**-region (fig.325e,l).
- In *Eurycotis* and *Mantoida* the muscles **l2** (fig.49, 70) and **l4** (fig.50, 71) insert close to each other on the **L4l**-region and run to the pouches **pne** and **lve**, respectively. *Anaplecta* also has a muscle **l2** from the posterior part of **L4K** to the **pne**-"pouch" (fig.221, compare in 6.1.4.); muscle **l4** is missing. *Nahublattella* (complete discussion below), however, has both **l2** and **l4** (to the pouches **pne** and **lve**), and their left insertions are on a sclerotisation homologous with the posterior part of **L4K** of *Anaplecta* (**L4U'** in fig.249).

The narrow sclerotisation which extends in *Tryonicus* from the anteriormost part of **L4K** to the right (anterior to **nla**, fig.96, 97, 325g) is missing in *Anaplecta* (fig.325l). Since this sclerotisation probably corresponds to the anteriormost **L4l**-region of *Archiblatta* and *Mantoida* (bearing the anterior part of the **swe**-apodeme; fig.44, 53, 325d,f), this feature of *Anaplecta* is regarded as derived.

The course of the dividing line through the **L4l**-region of *Anaplecta* (separating **L4K** and **L4N**) can be deduced from the positions of the **l2**- and **l4**-insertions in *Eurycotis*, *Mantoida*, *Anaplecta*, and *Nahublattella* and from the distribution of the other substructures: Anterior to the line (on **L4K**) there are the insertion of **l2** (and **l4** in *Nahublattella*) – and hence parts of the **L4l**-region – the **L4n**-region, the **nla**-process, and the **l14**-insertion. Posterior to the line (on **L4N**) are the **pda**-process – and hence posterior parts of the **L4l**-region – and the **l10**-insertion (and the **L4d'**-extension in *Nahublattella*). The course of the line is shown in fig.329e. The distribution of all cuticular elements present is the same as in **L4K** and **L4N** of *Tryonicus*, and the dividing lines of *Anaplecta* and *Tryonicus* (and *Nahublattella*) are strongly suggested to be homologous.

L4K of *Cryptocercus* (fig.150, 151) is homologous with **L4K** of *Tryonicus* and *Anaplecta* and is likewise composed of the anterior **L4l**-region and of the **L4n**-region. Both **L4l** and **L4n**, however, are strongly reduced. These relations are, firstly, suggested by similarities in the cuticular elements of *Tryonicus* and *Cryptocercus*:

- **L4K** of *Cryptocercus* has the same position like the left-dorsal half of **L4K** of *Tryonicus*: left-dorsal to the base of the **hla**-hook (compare fig.85, 97 and 145, 151). In *Tryonicus* this sclerotisation has been regarded as an anterior part of the **L4l**-region (fig.325g,h). Sclerite **L4P** of *Cryptocercus* (fig.151) probably corresponds to that part of **L4K** of *Tryonicus* immediately anterior to the **hla**-base. The right-ventral half of **L4K** of *Tryonicus* (fig.325g) with the anteriormost **L4l**-region (the anterior extension to the right) and the **L4n**-region (**nla**-sclerotisation) has been, like the **nla**-process itself, lost in *Cryptocercus*.

Secondly, the same relations result from a comparison of the muscle insertions of *Cryptocercus* and other species:

- The **l2** and **l4** of *Cryptocercus* (fig.155, 156), *Mantoida* (fig.49, 50), and *Eurycotis* (fig.70, 71) run from the pouches **pne** and **lve** to the leftmost part of the left complex, where their insertions are close to each other. Homology can be assumed. The left insertions are on the **L4l**-region in *Eurycotis* and *Mantoida* (fig.325d,e), and on **L4K** in *Cryptocercus*. The contribution of the **L4l**-region to **L4K** of *Cryptocercus* is thus confirmed (fig.325h). This can be only an anterior part of **L4l** since the posterior part (with the **pda**-sclerotisation) is included in sclerite **L4N**. In *Anaplecta* **L4K** also bears the left **l2**-insertion (fig.221), and in *Nahublattella* the homologue of the posterior part of **L4K** (**L4U'**) bears the left **l2**- and **l4**-insertions (fig.249).
- The **l14** of *Cryptocercus* (fig.157), *Eurycotis* (fig.72), and *Anaplecta* (fig.222) run from the anterior left wall of the left complex to a large hook (**hla**) and are certainly homologous (discussion in 6.4.). *Cryptocercus* (fig.157) and *Eurycotis* (fig.70) have phallomero-sternal muscles **s1+3** or **s1** inserting immediately anterior to **l14**; the left part of **s1+3** (= **s1**) is probably homologous with **s1** of *Eurycotis* (**s1** is missing in *Anaplecta*; discussion in 6.9.).
- In *Eurycotis* and *Anaplecta* **l14** inserts on the **L4n**-region (on the **nla**-process, fig.72, 73, 222), and in *Eurycotis* **s1** inserts at the border between **L4n** and the anterior **L4l** (fig.73, 325e). In *Cryptocercus* part of **l14** inserts on **L4K**; this suggests that the **L4n**-region also contributes to **L4K**. The larger part of the **l14**-insertion and the entire **s1+3**-insertion, however, are on membrane (ventral and anterior to **L4K**); this suggests that the **L4n**-region as well as the anteroventral part of the **L4l**-region (corresponding to the

anterior extension to the right on **L4K** of *Tryonicus*) are strongly reduced. Probably as a consequence, the **nla**-process is missing.

Thus, **L4K** of *Cryptocercus* is composed of anterior parts of **L4l** (with the insertions of **l2** and **l4**) and a highly reduced **L4n** (with part of the insertion area of **l14**). **L4N** of *Cryptocercus* is made of the posterior part of the **L4l**-region (with the reduced **pda**-sclerotisation) and of **L4d**. The distribution of all elements present is the same as in **L4K** and **L4N** of *Anaplecta* and *Tryonicus*, and homology can be assumed for **L4K**, for **L4N**, and for the dividing line between them (through **L4l**). The reduction of the **L4n**-region and the loss of the **nla**-process are derived features of *Cryptocercus*. The anteroventral part of **L4l** has also been lost in *Anaplecta*.

L4K of *Lamproblatta* (fig.177, 178) resembles **L4K** of *Cryptocercus* (fig.150, 151):

- The sclerites take the same position dorsal to the base of the **hla**-hook.
- A process **nla** on or near **L4K** is missing.

Anterior to **L4K** in *Lamproblatta* or on and anterior to **L4K** in *Cryptocercus* there insert some muscles having the same course, and the insertions on or near **L4K** show the same positions relative to each other:

- A muscle to the subgenital plate (**s1** in fig.185; left part of **s1+3** in fig.157).
- A muscle to sclerite **L3** on the **hla**-hook (**l14** in fig.184, 157). The **l14**-insertion is partly on **L4K** in *Cryptocercus* but completely on membrane in *Lamproblatta*.
- A muscle to the **pne**-pouch (**l2** in fig.184, 156). The **l2**-insertion is on **L4K** in *Cryptocercus* but on the membrane anterior to **L4K** in *Lamproblatta*.

Therefore, **L4K** of *Lamproblatta* and *Cryptocercus* are assumed to be homologous and to have the same composition: anterior part of **L4l**, vestiges of **L4n**. However, since in *Lamproblatta* the insertions of **l2**, **l14**, and **s1** are exclusively on membrane and muscle **l4** has been lost (compare fig.155), the muscles do not yield any direct evidence for the presence of the regions **L4l** and **L4n** and for the distribution of **L4l** and **L4n** within sclerite **L4K**. The distribution can only be deduced from a comparison with *Cryptocercus*, as it is done in fig.325h,i. That the **l14**-insertion is completely on membrane could be interpreted as a further reduction of the **L4n**-region as compared with *Cryptocercus*. That the **l2**-insertion is anterior to **L4K** (not on **L4K** as in *Cryptocercus*) is interpreted as a shift of this insertion to the anterior, not as a reduction of the respective **L4l**-sclerotisation (comparison with *Polyphaga*, see below).

L4K of *Polyphaga* is situated not in the dorsal but in the posteroventral part of the **hla**-base (fig.122-124; compare fig.151, 178). It is assumed to be homologous with **L4K** of *Lamproblatta* and *Cryptocercus* and to have shifted and rotated (clockwise as seen from the left) ventrad around the posterior part of the **hla**-base. This is suggested by the following features:

- In *Polyphaga* and *Lamproblatta* **L4K** is broadly horseshoe-shaped and curves into the base of the **hla**-hook. (According to the assumed shift and rotation in *Polyphaga* – the latter is almost 180° – the orientation of the sclerite is in *Lamproblatta* and *Polyphaga* opposite). In *Cryptocercus* this curvature of **L4K** is missing.
- In *Polyphaga* and *Cryptocercus* **L4K** bears the insertion of a muscle coming from the left-anterior part of **L2** (**l4** in fig.132, 155). **l4** is missing in *Lamproblatta*.

- In *Polyphaga* and *Lamproblatta* **L4K** bears the insertion of a muscle coming from the sclerotisation **L4d** (or from the adjacent membrane; **l11** in fig.128, 184). Taking the assumed rotation of **L4K** in *Polyphaga* into account, the insertion on **L4K** is in exactly the same position. **l11** is missing in *Cryptocercus* and all other species and is a derived feature of *Polyphaga*, *Ergaula*, and *Lamproblatta*.

The insertion of muscle **s1** (fig.127) has retained the same position as in *Lamproblatta* (fig.185) and *Cryptocercus* (left part of **s1+3** in fig.158, 159): on the basal line anterior to the **hla**-base. The **hla**-muscle **l14**, present in all other Blattaria studied (discussion in 6.4.), is missing in *Polyphaga*, and the **hla**-hook and its sclerite **L3** are bare of muscles. The function of **l14** has probably been taken over by the very stout **l4**, which does not insert on **L3** but on the dorsal part of **L4K** situated within the **hla**-base.

The muscles **l2** are certainly homologous in *Polyphaga*, *Lamproblatta*, *Cryptocercus* (fig.128, 184, 156), *Mantoida*, *Eurycotis*, and *Anaplecta* (fig.49, 70, 221; discussion in 6.1.). The ground-plan positions of the **l2**-insertions are shown by the three latter species: right insertion in the left wall of the **pne**-pouch; left insertion roughly in the middle of the left edge of the left complex. In *Cryptocercus*, *Lamproblatta*, and *Polyphaga*, as a first point, the right **l2**-insertion has shifted anteriad to the top of the **pne**-pouch (compare in 6.1.). As a second point, the left insertion also shows a gradual shift to the anterior and takes a position (1) more anteriorly than in the ground-plan but still on the **L4l**-sclerotisation (**L4K**) in *Cryptocercus*, (2) even more anteriorly and anterior to the **L4l**-sclerotisation (**L4K**) in *Lamproblatta*, and (3) still more anteriorly, and ventrally, but again on sclerotisation (**L4M**) in *Polyphaga*. The various stages of this **l2**-shift are regarded as synapomorphies of the species concerned. The **l2**-insertion is assumed to have shifted away from the **L4l**-region (*Lamproblatta*, *Polyphaga*) and to have later reached a position on another sclerotisation formed by an enlargement of the ventral sclerotisation of the **vla**-lobe (*Polyphaga*; this aspect is discussed below). Hence, contrary to the definition of **L4l** in 6.3.1., the sclerotisation bearing the **l2**-insertion in *Polyphaga* is not assigned to **L4l** since the fact that the shifted **l2** inserts on sclerotisation is not the result of a concomitant shift or expansion of **L4l**.

In *Polyphaga* the contribution of the **L4l**-region to **L4K** can be directly deduced from the **l4**-insertion on **L4K**. For the presence of **L4n**, however, there is, like in *Lamproblatta*, no direct evidence (the **nla**-process and muscle **l14** are missing). **L4K** is hence assumed to be mainly made of anterior parts of **L4l**, with little (like in *Cryptocercus*) or no contribution from **L4n**.

The situation in *Ergaula capucina* (fig.326d, 327d) can be derived from that in *Polyphaga* (fig.326c, 327c): **L4K** is likewise ventral to the **hla**-base but has shifted even further anteriad. The dorsal part of **L4K**, which bends into the **hla**-base, is distinctly shorter (compare edges **X** in fig.326c and d) and fused to the ventral anterior margin of sclerite **L3** (along edge **X** and more anteriorly). A muscle coming from the same part of **L2** as **l4** in *Polyphaga*, which is certainly homologous with this **l4**, inserts on this compound sclerite (mainly along edge **X**: **l4** in fig.327d). Muscle **l11** has the same insertions as in *Polyphaga* and *Lamproblatta* (fig.327b,c,d) but is much stouter. The muscles **l2** and **s1** insert like in *Polyphaga*.

The morphology of **L4K** and **l4** of *Ergaula* could easily be mistaken as corresponding with the situation in Blattellidae (*Anaplecta* excluded) and Blaberidae: In the latter groups the main muscle of the **hla**-hook (**l14** in fig.249, 276, 303) runs from the anteriormost part of **L2** to sclerite **L3**. The situation in *Anaplecta* (fig.222) suggests that this **hla**-muscle is a true **l14** whose anterior insertion has been translocated from the **L4n**-region (with **nla**) to **L2** (discussion in 6.4.3.). Looking at *Ergaula* only, the "**hla**-muscle" (**l4**) with its course from **L2** anteriorly in the **lve**-pouch to the "base of **L3**" (= **L4K**) could easily be misinterpreted as the "**l14**", with the "translocation" of its anterior insertion to **L2** being a synapomorphy of *Ergaula* and the respective Blattellidae and Blaberidae. However, the situations in *Polyphaga* and *Lamproblatta* clearly show that in *Ergaula* the muscle is **l4** (not **l14**), the sclerite is **L4K** (not the basal part of **L3**), and the similarity with Blattellidae is a case of convergence.

Ventral sclerite plate Sclerite **L4G** in the ventral wall of the **vla**-lobe of *Eurycotis* and *Archiblatta* is, by definition, the region **L4v** (fig.325e,f). **L4G** of *Tryonicus* (fig.325g) probably also corresponds exactly to the **L4v**-region, but it cannot be excluded that parts of the **L4c**-region are contained in the sclerite (compare in 6.3.1.). In the latter case, **L4G** of *Tryonicus* and **L4G** of *Eurycotis* and *Archiblatta* would be only partly homologous. The ventral plate of *Anaplecta* (**L4G** in fig.205) lies similarly in the ventral wall of the **vla**-lobe like **L4G** of *Tryonicus* (fig.87), and in both species **L4G** is, apart from the ventral parts of sclerite **L4K**, the only sclerotisation in the ventral wall of the left complex. This indicates that **L4G** of *Tryonicus* and *Anaplecta* are strictly homologous. The ventral plates of *Cryptocercus* (**L4G** in fig.148), *Lamproblatta* (**L4R** in fig.174), and *Polyphaga* (**L4M** in fig.115) also lie in the ventral **vla**-wall and can be assumed to be at least in part homologous with each other and with the **L4G**-plates of the other species. These plates, however, are rather different in their relative sizes, and the homology relations should be analysed in detail.

Some evidence for the exact homology relations comes from the muscles **l2**, **l5**, **l6a**, **l6b** (homology discussion in 6.1. and 6.2.), and **s3** (homology discussion in 6.9.). In *Sphodromantis*, *Mantoida*, *Polyphaga*, and *Lamproblatta* **s3**, **l2**, **l5**, **l6a**, and **l6b** can be homologised one by one (with the exception that in *Mantoida* **l6a** and **l6b** have fused). In *Cryptocercus* homology is clear for **s3** (right part of **s1+3**), **l2**, and **l6b**; **l5** and **l6a** have been lost. In *Eurycotis* and *Anaplecta* homology is also clear for **s3**, **l2**, and **l6b**; as regards **l5** and **l6a**, homology with the **l5** and **l6a** of the other species is questionable. The relations between the ventral plates and the insertions of **l6b**, **s3**, and **l2** are different in the various species:

- In *Eurycotis*, *Cryptocercus*, and *Anaplecta* only **l6b** (fig.70, 157, 224) inserts, at least in part, on the ventral plate (**L4G** in fig.63, 148, 205). **s3** (fig.70, 157, 222) inserts in the membrane left-anterior to **L4G**. The positions of these insertions may suggest (but do not prove) that the **L4G** of *Anaplecta* and *Cryptocercus* are strictly homologous with **L4G** of *Eurycotis* (i.e. only **L4v** but no parts of **L4c** or of other sclerotisations are included; fig.325e,h,l). The same might be assumed for *Tryonicus* since its **L4G** is similar to **L4G** of *Anaplecta* (fig.325g).

- *Lamproblatta* and *Polyphaga* (and *Ergaula*) differ from the previous species (fig.132, 133, 188, 189): (1) Not only **l6b** but also **s3** inserts on the ventral plate (**L4R** in fig.174; **L4M** in fig.115). This is certainly a derived feature. (2) **l5** and **l6a** also insert on the ventral plate, but since the homology relations with the respective muscles of the previous species are uncertain, this feature is not interpretable (no **L4c**-region is included in fig.325i,k, but its absence is questionable). (3) A special muscle **s12** from the right half of the subgenital plate runs to the ventral plate and inserts immediately to the right of **s3**. The presence of **s12** is also a derived feature.
- *Polyphaga* (and *Ergaula*) shows an additional derived feature already mentioned above: Muscle **l2** inserts on the ventral plate **L4M** (fig.128).

The derived condition that, in *Lamproblatta* and *Polyphaga* (and *Ergaula*), the insertions of some muscles are now on the sclerotisation of the ventral plate (at least **s3** in *Lamproblatta* and **s3** and **l2** in *Polyphaga*) is interpreted as an expansion of this plate, and the sclerotisations bearing these insertions are defined as new regions of **L4**:

- **L4a** (anterior): The sclerotisation of the insertion area of **s3**. (The **s3**-insertion has not changed its position.)
- **L4x** : The sclerotisation of the insertion area of **l2**. (The **l2**-insertion has shifted ventrad.)

According to this interpretation, **L4M** and **L4R** are not strictly homologous with each other and with the **L4G** of the other species: **L4R** evolved from **L4G** by expansion (new region **L4a**), and **L4M** evolved from **L4R** by an additional expansion (new region **L4x**). In *Ergaula* a small anterior part of **L4M** (with the insertions of **s3** and **s12**) has split off to form a sclerite of its own (compare fig.322l and m).

Nahublattella

The homologue of sclerite **L4K** of *Anaplecta* (fig.209) has divided into two sclerites **L4U'** and **L4V'** (fig.242). **L4U'** resembles the posterior part of **L4K**: It has the same position on the left edge of the left complex, the same position relative to the **hla**-hook, and a similar shape (curved plate). **L4V'** resembles the anterior part of **L4K**: It lies in the anteriormost ventral wall of the left complex and forms a process (**nla** in fig.242, 248). The homology of the **nla**-processes of the two species is, regarding their different shape, debatable.

These relations are supported by the muscles: **L4U'** bears the insertions of **l2** and **l4** (fig.249). **l2** runs to the basalmost part of the **hla**-hook (membrane **30**). **l2** of *Anaplecta* (fig.221) runs to the **pne**-pouch next to the **hla**-base (**30** in fig.210, 211). I assume homology for the **l2** of the two species and a slight shift of the right insertion in *Nahublattella*. **l4** of *Nahublattella* inserts immediately ventral to **l2** and runs to the **lve**-pouch, exactly like **l4** of e.g. *Eurycotis* (fig.70, 71) and *Cryptocercus* (fig.155, 156). As mentioned above, **l4** has been lost in *Anaplecta*. **L4V'** bears the insertions of **l5**, **l6a**, and **s3** (fig.250, 251). **l5** has its posterior insertion like **l5** of *Anaplecta* (fig.223) at the left base of the **lve**-apodeme, and homology is highly probable for these **l5**; that the anterior insertion is on the anterior part of **L4K** in *Anaplecta* confirms the homology between this part of **L4K** and **L4V'** (and, maybe, the homology of the **nla**-processes, too). The insertions of **s3** and **l6a** in *Anaplecta*, however, are on the **ate**-tendon to the right of the sclerotisation (fig.222). (Homology is quite certain for **s3** but not for **l6a**; discussion in 6.9. and 6.2.4.). That the dorsal insertion of **s3** is on a sclerotisation is not comparable with the situation in *Lamproblatta* and *Polyphaga*: In the latter species the sclerotisation concerned is an expansion of the ventral plate (**L4a**-region); in *Nahublattella* the sclerotisation with the **s3**-insertion is an expansion of the former **L4K**-sclerite. (The respective area of the sclerite could be defined as a new sclerite region, but this is omitted).

Thus, **L4U'** is assumed to consist of the same parts of the **L4l**-region as the posterior part of **L4K** in *Anaplecta*. **L4V'** roughly corresponds to the **L4n**-region (fig.325m, compare fig.325l); however, the line dividing the two sclerites does certainly not exactly correspond to the border between **L4l** and **L4n**; this is only the case – by definition – in *Archiblatta*.

The homology relations of the processes **paa** and **pda** of *Anaplecta* and **via, paa, pda**, and **vsa** of *Nahublattella* (fig.241, 244) and of their sclerotisations have been discussed in 6.2.4.. **L4N'** of *Nahublattella* is probably the left-ventral sclerotisation of the **via**-process (including **pda** and **vsa**; fig.325m). The ribbon-like extension **L4d'** at the left base of **via** (fig.244, 250) closely resembles **L4d** of *Polyphaga* and *Tryonicus* (fig.94, 97, 118, 129) in its position relative to **paa** and **pda** and their sclerotisation and to the **l10**-insertion. Like in *Polyphaga* and *Cryptocercus*, **L4d'** is directed to the left. Like in *Mantoida* and *Cryptocercus*, **L4d'** has a muscle running to the **pne**-pouch (**l1** in fig.48, 155, 249). Homology is assumed for the **L4d** and **l1** of all species. In *Nahublattella* the whole area containing **via, pda, paa**, and **L4d'** is sunken anteriad into the left complex and has become the left part of an expanded **lve**-pouch, and **L4d'** lies in the left edge of this enlarged **lve**-pouch and runs posteriad (**L4d'** is, so to speak, invaginated). This is in contrast to all other species; only *Anaplecta* shows a slight anteriad invagination of the **paa+pda**-sclerotisation (but **L4d** has been lost). The separation of the **paa+pda**-sclerotisation from the **L2**-sclerotisations in the **lve**-pouch reminds of *Lamproblatta* (fig.177-179), but the division of the sclerotisations is different and non-homologous: **L4d** is connected with the **paa+pda**-sclerotisation in *Nahublattella* but with the sclerotisation of the **lve**-pouch in *Lamproblatta* (compare fig.329f and g).

The identification of the **vla**-lobe (fig.245-247) was done in in 6.2.4.. That there is no sclerite plate in its ventral wall (**L4v**-region; compare **L4G** of *Anaplecta*, fig.224) is a derived feature.

Parcoblatta, Blaberus, and other Blattelidae and Blaberidae

Sclerite **L4U'** of *Blaberus* has the same shape, relative position, and muscle insertions as **L4U'** of *Nahublattella* (fig.242, 249, 299, 303). In both species **l4** runs to sclerite **L2**, and **l2** runs to the **hla**-base (**30** in fig.249, 303). In *Parcoblatta*, the morphology of the left part of the left complex (compare fig.268-270 and 299-301) and the arrangement of **l2** and **l4** (compare fig.276 and 303) are nearly the same as in *Blaberus*; however, sclerite **L4U** has been lost. In *Nyctibora* **L4U** is present and very similar to **L4U'** of *Blaberus*.

Blaberus and *Parcoblatta* both have a tendon-like invagination (**ate** in fig.268, 271, 302) near the ventral basal line of the left complex. **ate** is also present, and in the same position, in other Blattellidae and Blaberidae (investigated species: those listed in 5.15.; *Blaptica*: fig.291). The homology of these **ate**-tendons is confirmed by the insertion of a phallomero-sternal muscle (**s3b**, studied in *Parcoblatta*, *Blaberus*, and *Blaptica*; fig.277, 304; homology discussion of **s3b** in 6.9.) and by the presence of a sclerite in the dorsal wall of the tendon (**L4V** or **L4V'**, which, however, is present only in *Parcoblatta*, *Nyctibora*, and *Blaptica*, fig.289, 291).

The evolutionary origin of tendon **ate** and sclerite **L4V** of these species is unclear. The terms used express the possible homologies with structures being in similar positions in *Anaplecta* (**ate** in fig.212) and *Nahublattella* (**L4V'** in fig.244):

– **ate** and, if present, **L4V** resemble both **ate** of *Anaplecta* and **L4V'** of *Nahublattella* in bearing the insertion of at least part of (1) muscle **s3** (**s3b** of *Parcoblatta* and *Blaberus*, fig.277, 304) and (2) muscle **l6a** (only *Blaberus*, fig.304). However, it is impossible that both homologies – of **ate** and **L4V** – are true in a strict sense since in *Anaplecta* the **ate**-tendon and the sclerotisation homologous with **L4V'** of *Nahublattella* (anterior **L4K**) are located side by side.

– As a combined hypothesis accepting a partial homology of the **ate**-tendons and a strict homology of the **L4V**-sclerites, it might be assumed that in the more derived Blattellidae and Blaberidae, as compared with *Anaplecta*, the cuticular area forming the **ate**-tendon has expanded basad and that by this process **L4V** has become integrated into the tendon. *Nahublattella* could be an intermediate, with the anteriormost ventral part of the left complex being a very broad **ate**-"tendon", and with **L4V'** integrated into this "tendon". In the other Blattellidae and Blaberidae this anterior part with **L4V'** must then be assumed to have become very narrow, and **L4V'** has become smaller. If this is true, the **ate**-tendon of *Anaplecta* would be homologous with the distalmost part of the **ate**-tendon (anterior to **L4V**, if present) of e.g. *Supella, Euphyllodromia, Parcoblatta, Nyctibora, Blaptica*, and *Blaberus*.

– However, the lack of a sclerotisation within the **ate** of *Supella*, *Euphyllodromia*, and other species might suggest that **L4V** of *Parcoblatta*, *Nyctibora*, and *Blaptica* is a new element not homologous with **L4V'** of *Nahublattella*. If this is true, **ate** of *Anaplecta* could be strictly homologous with **ate** of the more derived Blattellidae and Blaberidae.

These questions concerning **ate** and **L4V** cannot be settled here.

The sclerotisation of the **via**-process has been assumed, in accordance with the situation in *Nahublattella*, to be composed of **L4N** and **L2E** (posterior **L4l**-region and **L2d**-region: fig.325m,n,o and 324m,n,o; discussion in 6.2.4.). Since the primary processes **paa** and **pda** are no longer distinguishable in these **via**-processes (fig.328c-k), the exact arrangement of **L4N** and **L2E** is less clear than in *Nahublattella*. In determining the position of the **L4N**- and **L2E**-sclerotisations on **via** of *Parcoblatta* and *Blaberus* one must consider the rotation of the **via**-process. An extension corresponding to **L4d'** of *Nahublattella* is missing in all species (compare fig.328b and c-k), and the **L4d**-region is assumed to have been lost like in *Anaplecta* (fig.325l,m,n,o and 324l,m,n,o).

At least *Parcoblatta, Nyctibora, Blaptica, Nauphoeta*, and *Blaberus* (the other species not investigated) lack, like *Nahublattella*, a sclerite plate in the ventral wall of the **vla**-lobe (fig.266, 268, 297): The **L4v**-region has been lost. Sclerite **L10'** of *Blaberus* (fig.299) and the small sclerites **L10'** of *Blaptica* (fig.291) are not assumed to be descendants of **L4v** but new sclerotisations having evolved within Blaberidae. In the blaberid *Nauphoeta* **L10'** is missing.

6.4. Left complex IV: Main sclerite L3 and associated elements

6.4.1. Comparison between Blattaria and Mantodea

In *Archiblatta* (fig.53-55) the **hla**-hook is an evagination of the anterior left ventral wall of the left complex, and its base is immediately beneath the arched anterior part of the **L4C**-sclerite = **L4l**-region. *Mantoida* has no process in the corresponding part of the ventral wall (fig.45, 46), and the neighboring processes **paa** and **pda** have proved to be homologous with **paa** and **pda** of *Archiblatta* and other Blattaria. The elements of the left complexes of *Chaeteessa, Metallyticus*, and *Sphodromantis* – including the processes **paa** and **pda** – have all been homologised with elements of *Mantoida*. Thus, none of the Mantodean species studied has a homologue of the **hla**-hook; **hla**, and also its sclerite **L3** and its main muscle **l14**, are restricted to Blattaria.

6.4.2. The elements in the common ground-plan of Blattaria and Mantodea

Since **hla** is present in all Blattaria (discussion in 6.4.3.) but absent in all Mantodea, its presence in the common ground-plan cannot be reliably decided. However, a comparison of the copulation habits of Blattaria and Mantodea might indicate that the lack of **hla** and **L3** in Mantodea is a derived feature.

In Blattaria copulation has several successive phases (data from Scudder 1971, who refers to Gupta 1947): In *Periplaneta*, in phase (1), the male places itself in front of the female, with its rear end facing the female. Then the female climbs upon the back of the male, both animals facing the same direction. In this phase the **hla**-hook of the male makes the first contact of the genital regions: It seizes the terminal lobes of the female subgenital plate (Scudder: "initial seizing"). (2) This connection being established, the male rotates ca. 180° in the horizontal plane (clockwise as seen from above). (3) After this rotation the animals are again in a line, with their rear ends still in contact. Now other phallomere elements establish a firmer contact – mainly the seizing apparatus formed by the posterior part of the male's right phallomere (Scudder: "final holding"). Scudder describes a several-phase process with similar positions for some subgroups of Ensifera. But, of course, the connection of male and female genitalia is established by completely different structures. Nevertheless, it seems plausible that a copulation procedure with a sequence of these positions might be plesiomorphic for a higher taxon including at least Orthoptera and Dictyoptera.

Mantodea have a different copulation procedure, which Scudder regards as apomorphic: The male mounts the female (often by jumping) and then clings to the female thorax with its grasping legs. Holding this position, the male curves its terminal abdomen to the right and pushes it into the female genital pouch from laterally (e.g. Kumar 1973). Together with the modified fore legs, the very special feeding habits of Mantodea (lurking predators) are certainly derived. It might be plausible that changes in behaviour correlated with these new feeding habits might have caused changes in the copulation procedure. (So to speak, it is no longer advisable for the male to place itself in front of the female in the way Blattaria do).

Thus, the outgroup comparison with Ensifera as well as biological properties of Mantodea suggest that the copulation procedure of Blattaria is plesiomorphic and that of Mantodea apomorphic: Phase (1), in which Blattaria make use of their **hla**-hook, can be regarded as secondarily lost in Mantodea. Additionally, since the phallomeres of Mantodea and e.g. *Periplaneta* are rather similar in their morphology (and completely different from those of Ensifera), it might be assumed that the way the Mantodean phallomeres functioned before the copulation procedure has changed was similar to that of the Blattarian phallomeres, and that a **hla**-hook was present for initial seizing. Though these ideas are highly speculative, it is at least plausible that **hla** and the associated elements **L3** and **l14** were present in the common ground-plan of Blattaria and Mantodea and have been lost in Mantodea. The same might also be true of the **nla**-process, which is present in many Blattaria (fig.69, 98, 212) but never in Mantodea. **nla** probably has the function to stiffen the sclerotisation at and near the **l14**-insertion, and if **hla** and **l14** are lost an additional loss of **nla** could be expected.

6.4.3. Homology relations and character states of the elements in Blattaria

The **hla**-hook is present in all Blattaria. The homology of all these **hla** is suggested by their position in the leftmost part of the left complex, by their similar shape, and by the presence of a special sclerite **L3** occupying the distal part of **hla** (**L3**, however, can be very different in its extension). Apart from these superficial features, additional similarities between certain species confirm this homology assumption. The most important question in this context is whether the main muscles of the **hla**-hooks (called **l14** in most species) are homologous.

Archiblatta, *Periplaneta*, and *Eurycotis*

The homology of **L3**, **hla**, and **l14** of these species is quite evident. (1) The **hla**-base takes the same relative position: right-ventral to the **L4l**-region, left-posterior to the **L4n**-region with the **nla**-process, and left-anterior to sclerite **L4F** (fig.54, 56, 66, 67). (2) **L3** occupies the entire **hla** except for the basalmost part (**30** in fig.65-67). (3) The tip of **hla** is two-pointed (fig.53, 65). (4) In *Periplaneta* and *Eurycotis* the main muscle of **hla** (**l14c** in fig.72) comes from the **L4n**-region on and near the **nla**-process and inserts immediately behind **s1** (fig.70). However, only *Eurycotis* has one accessory **hla**-muscle **l14d** (fig.73) – possibly a subdivision of **l14c**.

Cryptocercus and *Lamproblatta*

The **hla**-base has a similar position relative to the insertions of **l2** and **s1** (fig.156, 157, 184, 185) as in *Eurycotis* (fig.70), and the anterior insertion of the main muscle of **hla** (**l14** in fig.157, 184, 185) is likewise immediately behind the **s1**-insertion (fig.157, 158, 184, 185). Thus, homology can be assumed for the **hla, L3**, and **l14** of these three species (homology discussion of **s1** in 6.9.). *Cryptocercus* has one accessory **hla**-muscle **l19** (fig.156); *Lamproblatta* has two, **l22** and **l23** (fig.184-186). These accessory muscles and **l14d** of *Eurycotis* all have different insertions, and homology relations are not assumed. In *Cryptocercus* – as compared with the previous species, *Polyphaga*, and *Ergaula* (see below) – the base of **hla** is more posteriorly, and **hla** is shorter (fig.151).

Polyphaga and *Ergaula*

The homology of **hla** with **hla** of *Lamproblatta* and *Cryptocercus* is suggested mainly by the similar position of the **hla**-base posterior to the **s1**-insertion (fig.127, 157, 185) and by the similar relations between the **hla**-base and sclerite **L4K** (discussion in 6.3.4.). A muscle inserting directly on **hla** or **L3** (**l14**) is missing; the very stout **l4** has probably taken over the function of **l14** (discussion in 6.3.4.).

Tryonicus

The **hla**-base has the same relative position as in *Eurycotis*: right-ventral to the **L4l**-region and left-posterior to the **nla**-process (sclerites **L4K** and **L4N** in fig.97). **hla** and **L3** of the two species are certainly homologous. *Tryonicus*, however, shows three special features as compared with the species discussed so far: (1) The **hla**-base is distinctly more posteriorly (compare fig.87, 97 and 63, 67). However, this is also true of *Cryptocercus*. (2) The introversible membranous basal part of **hla** (**30** in fig.97) is by far more extensive, and, consequently, **hla** can be retracted more deeply into the left complex. (3) The basal margin of **L3** is connected with **L4** (**L4K**) by the sclerite ribbon **L3a** (fig.89,98). This last feature is restricted to *Tryonicus*.

Anaplecta, Nahublattella, Parcoblatta, and *Blaberus*

The two first-mentioned peculiarities of *Tryonicus* are more pronounced: The **hla**-base is at the posterior edge of the left complex, and the membranous basal part of **hla** (**30** in fig.210, 242, 269, 300) is so extensive that **hla** can be retracted into the left complex except for its distalmost part only (fig.210, 242, 269) or even completely (fig.295a). (These two features have also been investigated and found in all other Blattellidae and Blaberidae listed in 5.15.). Another feature common to these 4 species is the membranous infolding **fpe** separating the left part of the left complex (with the **hla**-base) from the right part (fig.210, 243, 268, 299). These similarities clearly suggest the homology of **hla** and **L3** in the 4 species. With *Tryonicus* as an intermediate, homology can also be assumed with **hla** and **L3** of the previous species.

Additionally, the homology of **hla** and **L3** in *Anaplecta* and *Eurycotis* is more directly suggested by the anterior insertion of the **hla**-muscle **l14** or **l14c,d**, which is, in both species, on and near the **nla**-process (fig.72, 73, 222). In *Nahublattella*, *Parcoblatta*, and *Blaberus*, however, the anterior insertion of the main muscle of **hla** (**l14** or **l14a,b** in fig.249, 276, 303) is on **L2D'** or **L2**, on top of the **lve**-apodeme (**L2a**-region). In *Anaplecta*, interestingly enough, the top of the **lve**-apodeme and the **nla**-process are firmly connected with each other (fig.222). This might suggest that all Blattellidae and Blaberidae have gone through an evolutionary stage showing this connection, and that, at that time, muscle **l14** has shifted from **L4n** to **L2a**. Homology is assumed for all **hla**-muscles **l14**. (The shift of **l14** will be disscussed in a functional context in 7.5.).

Of these 4 species only *Parcoblatta* and *Blaberus* show the following features: (1) **l14** is divided into two bundles (**l14a** and **l14b** in fig.276, 303; the division in *Eurycotis* mentioned above is clearly not homologous with this division). (2) There is a muscle within the membranous basal part **30** of **hla** (**l36** in fig.276, 303). (3) The distal part of

hla has a groove **hge** with a notch **45** in its ventral wall (fig.266, 297a). In the species studied only in part (listed in 5.15.), the **hge**-groove and the notch **45** are distinctly present in *Supella, Euphyllodromia, Loboptera, Byrsotria*, and *Blaptica*; *Nyctibora* has only **hge** but no notch **45**; in *Ectobius* and *Nauphoeta* the **hge**-groove is quite indistinct, and the notch **45** is missing. (**l14** and **l36** have not been investigated in these species). Muscle **l46** is peculiar to *Blaberus* (fig.304, left part).

6.5. Left complex V: Further main sclerites and muscles

Some Blattaria and Mantodea have small sclerites in the dorsal wall of the **vla**-lobe, which I have designated **L5**. **L5** of *Metallyticus* (fig.26, 27) and *Cryptocercus* (fig.151, 155) is posterior to the genital opening. **L5** of *Periplaneta* (no figure) lies more anteriorly, within the terminal part of the ejaculatory duct. **L5** of *Polyphaga* (fig.123, 124) is far to the left of the genital opening. **L5** of *Ergaula* is situated like in *Polyphaga* but is tranversely orientated and approaches the genital opening more closely (fig.322m). In *Anaplecta* and *Nahublattella*, the extension **28** of the **L2**- or **L2D'**-sclerite (fig.214, 215, 245) takes a very similar position relative to the other parts of **L2** and to the genital opening as **L5** of *Polyphaga* (fig.123) and might be homologous with it. The sclerites **L10'** of *Blaberus* and *Blaptica* (fig.291, 300) lie either in the dorsal **vla**-wall (*Blaptica*) or along the posterior edge of the **vla**-lobe (*Blaberus*); whether they show any kind of homology relation with the **L5** of the other species is unclear, and improbable in my view. Sclerites in the dorsal **vla**-wall are missing in *Mantoida, Chaeteessa, Sphodromantis, Archiblatta, Eurycotis, Tryonicus, Lamproblatta*, and *Parcoblatta*. It cannot be decided whether **L5** is a ground-plan element of Blattaria and Mantodea and has been lost several times, or whether such sclerites have developed several times independently.

Sclerite **L7** is present only in *Polyphaga, Ergaula*, and *Lamproblatta*. These **L7** (fig.115, 174) take the same relative position between the sclerite plate of the **vla**-lobe (**L4M**, **L4R**) and the right phallomere and are therefore assumed to be homologous. **L7** is regarded as an element of the left complex since in a specimen of *Polyphaga* with its external genitalia consisting of two right phallomeres only there was no trace of **L7** (compare in 3.1.). Only in *Polyphaga* and *Ergaula* the area containing **L7** is elaborated as a special lobe-like evagination (**lba** in fig.115; in *Ergaula* the morphology is the same, but **L7** and **lba** are larger). The **lba**-lobe is assumedly homologous with the rightmost part of the **vla**-lobe of the other species. (If this is true, not the **vla**-lobe of *Polyphaga* and *Ergaula* alone but the **vla**- and **lba**-lobes together are the strict homologue of the **vla**-lobe of the other species. That **lba** is not alone the homologue of the **vla** of the other species and that **L7** is not the homologue of the **L4G**-plates is clearly shown by the muscles **l5**, **l6a**, and **l6b**, compare in 6.2.1.. **L7** and **lba** are bare of muscles).

Sclerite **L8** is likewise restricted to *Polyphaga, Ergaula*, and *Lamproblatta* (**L8** = neoformation **N** of Grandcolas & Deleporte 1992). These **L8** take the same position in the right dorsal wall of the left complex, but they differ somewhat in their position relative to the **pne**-pouch (fig.117, in *Ergaula* similar; fig.177). However, it must be considered that in *Lamproblatta*, as compared with *Polyphaga*, the **pne**-pouch has shifted right-anteriad (compare in 6.1.4.). The homology of the **L8**-sclerites is also strongly supported by the insertions of three muscles (**l12**, **b2**, **l9**) in their immediate vicinity: **l12** (fig.128, 129, 186, 188; discussion in 6.2.4.) runs to the right ventral (or outer) wall of the **lve**-pouch, with its insertion close to that of **l6a** (fig.133, 188). **b2** (fig.127, 184; discussion in 6.8.) runs to the ventral part of the right phallomere, where the insertion, however, has a slightly different position in *Polyphaga* and *Ergaula* on the one hand (**R3**, fig.141) and *Lamproblatta* on the other (membrane next to **R2**, fig.198). **l9** (fig.127, 184, 170; discussion below) runs to the left dorsal wall of the left complex. **L8** and the three muscles are assumed to be homologous, and **L8** and **l12** are regarded as derived features of these species.

Ergaula and *Eurycotis* have sclerites in the dorsal wall of the **pne**-pouch (**L9** in fig.322m; **L6A** and **L6B** in fig.66), but **L9** and **L6** are probably not homologous. Sclerite **L11** (fig.91) is peculiar to *Tryonicus*.

Many species have transverse muscles within the dorsal wall of the left complex, which have been termed **l9**: *Mantoida* (fig.49), *Eurycotis* (fig.70), *Polyphaga* (fig.127, 129), *Cryptocercus* (fig.155), *Lamproblatta* (fig.170, 185), *Anaplecta* (fig.221), *Nahublattella* (**l9a** and **l9b** in fig.249), *Sphodromantis* (fig.17; "**b4**, **l9?**" might be the homologue of either **l9** or **b4a** and **b4b** of *Mantoida*: compare in 6.7.3.). However, the exact position and the extension of these **l9** can be rather different. The homology of **l9** of *Lamproblatta* and *Polyphaga* (and *Ergaula*) is highly probable since the right insertion is on or near sclerite **L8** and close to the insertions of **l12** and **b2**. In *Polyphaga* (and *Ergaula*) as well as in *Anaplecta* and *Nahublattella* **l9** has its left insertion, at least in part, on the right wall of the **pne**-pouch. This relation between **pne** and **l9** is assumed to have been lost in *Lamproblatta* by the right-anteriad shift of **pne** and **L1** (compare in 6.1.4.). **l9** of *Eurycotis* has a similar position like the dorsal part of **l9** of *Polyphaga*. In *Cryptocercus* **l9** is far on the left; that its left insertion is next to the **L4d**-region (left part of sclerite **L4N** in fig.155) and close to the **l1**-insertion resembles the situation in *Mantoida* (fig.48, 49; compare in 6.3.4.), but this close relation between **l9** and **L4d** is in contrast to *Polyphaga* (fig.127, 128). On the other hand, **l9** of *Mantoida* is farther to the right than **l9** of *Cryptocercus*, and its overall position is similar to that of **l9** of *Eurycotis* and the dorsal part of **l9** of *Polyphaga*. In my view, these similarities are sufficient to assume homology for all these **l9**-muscles and to regard **l9** as an element of the common ground-plan of Blattaria and Mantodea. In the evolution of **l9**, some shifts might have occurred, or different parts of **l9** might have been reduced or enlarged in the various species.

Some Blattaria have muscles from the ejaculatory duct **D** to that part of the dorsal wall of the **vla**-lobe posterior to the genital opening; these have been termed **l13**: *Polyphaga* (fig.132), *Cryptocercus* (fig.155), *Lamproblatta* (fig.188), *Anaplecta* (fig.222), *Eurycotis* (**l13h** in fig.72). Homology is tentatively assumed for them though their positions are somewhat different. In *Anaplecta* **l13** bridges the base of the **vfa**-outfolding (an outfolding from the anteriormost dorsal wall of **vla**, compare in 6.2.4.). In *Eurycotis* some other diffuse muscles within the **vla**-lobe have been assigned to **l13** (**l13a,b,c,d,e,f,g,i** in fig.71-73); these could be new muscles, or some of them might be split off parts of the true **l13** (*Archiblatta, Blatta, Periplaneta*, and *Deropeltis* not investigated). In Mantodea no **l13**-

muscles have been found; however, muscle **b3** of *Sphodromantis* (fig.15) has its right insertion not far from the dorsal **vla**-wall and might be a shifted **l13**. Hence, it is not clear if **l13** is present in the common ground-plan of Blattaria and Mantodea.

Mantoida and *Cryptocercus* have a longitudinal muscle in the posterior left ventral wall of the left complex (**l7** in fig.52, 158). Since the position is very similar these **l7** could well be homologous. However, the respective part of the left complex is very different in the two species (presence or absence of the **hla**-hook, highly modified **L4**-sclerotisations in *Cryptocercus*), and it is not possible to compare the relative position of **l7** in the two species. Therefore, the homology of these muscles must be regarded as highly questionable. **l7** of *Sphodromantis* (fig.15) is certainly homologous with **l7** of *Mantoida* but has undergone a shift (compare in 6.3.3.). *Nahublattella, Parcoblatta*, and *Blaberus* also have longitudinal muscles in the ventral wall of the left complex (**l30** in fig.251, 307; **l30a**,**b** in fig.278, 279); these **l30** are assumed to be homologous, but since they take a rather different position homology with **l7** of *Cryptocercus* is not assumed.

6.6. Left complex VI: The position of the phallomere-gland opening

The opening of the phallomere-gland **P** certainly has its primitive position within the membranous part of the **pne**-wall (discussion in 6.1.1.). It opens far anteriorly into this membrane in *Mantoida* (fig.45), *Chaeteessa* (fig.32), and *Sphodromantis* (fig.10), and far posteriorly and on the left side in *Cryptocercus* (fig.153, 154), *Polyphaga* (fig.120, 121), *Tryonicus angustus* (fig.107, 108), and – considering the rotation of the **pne**-pouch – *Tryonicus parvus* (fig.95, 96).

In *Ergaula capensis* the opening has, as compared with *Polyphaga*, shifted only a short distance; by this shift, however, it has reached a position left-ventral to the **dca**-processes and outside the **pne**-wall (compare fig.106 and 121). In *Eurycotis* (fig.67, 68) and *Archiblatta* (fig.54-56) the opening is likewise ventral to the **dca**-processes and is assumed to have undergone a similar shift. In *Lamproblatta* the opening has the same position relative to the posterior margin of **L1** (fig.177, 178) as in the previous three species but is farther away from **L1**, and the processes **paa** and **pda** take their position between the opening and the posterior margin of **L1** (fig.178). **paa** and **pda** have, as compared with e.g. *Polyphaga* (fig.118), shifted to the right (relative to the left posterior end of the **lve**-pouch; compare in 6.3.4.) and are assumed to have intruded into the interspace between **L1** and the phallomere-gland opening.

In *Nahublattella* the opening has a similar position relative to sclerite **L1** and the **dca**-process as in e.g. *Ergaula* (fig.243, 244, 328b) but has shifted far anteriad within the membrane ventral to **dca** and lies in the posterior right dorsal wall of the **lve**-pouch – posterior to the dorsal wall of the ejaculatory duct **D**. The muscles **l27** and **l29** (fig.249) are derived features of *Nahublattella*. In *Parcoblatta* (fig.270, 328e), *Blaberus* (fig.300, 328k), *Euphyllodromia* (fig.328d), *Nyctibora* (fig.328h), and *Nauphoeta* (fig.328i) the opening has a similar position as in *Nahublattella* but is slightly more to the left and close to sclerite **L2** or **L2D**.

The situation in *Anaplecta* is difficult to interpret. This concerns the presence of two outlet ducts with their openings close to each other (**P** in fig.216), the position of these two openings, and the presence of a muscle **l25** (fig.224) inserting between them. Taking a situation like in *Nahublattella* as a starting point, the position of the openings could be explained by the assumption of a further shift to the left within the dorsal wall of the ejaculatory duct, and then ventrad to beneath the **lve**-apodeme. However, the preceding shift assumed for *Nahublattella* would have hardly been possible in *Anaplecta* since between the membrane posteroventral to the **pne**-pouch (fig.209) and the posterior dorsal wall of the ejaculatory duct there are still extensive right parts of **L2** (fig.211) "blocking" this shift. The openings of *Anaplecta* are in one respect similarly situated as in *Lamproblatta*: more or less ventral to the processes **paa** and **pda** (compare fig.210 and 178). The position relative to the **lve**-pouch, however, is completely different: dorsal to **lve** in *Lamproblatta*, ventral to **lve** in *Anaplecta*. Possibly, the outlet ducts of *Anaplecta* are new organs. In this case, for the remaining Blattellidae and for Blaberidae the possibility has to be considered that their glands and outlet ducts are homologous with those of *Anaplecta* (or one of them) and not with those of the other species. As a point possibly interesting in this context, the spermathecae of the female genitalia have also been replaced by completely new organs in Blattellidae and Blaberidae (McKittrick 1964).

6.7. The elements of the right phallomere

6.7.1. Comparison between Blattaria and Mantodea

The homology relations and the ground-plan of the elements of the right phallomere can best be deduced from a comparison of *Eurycotis, Chaeteessa*, and *Mantoida*.

The cuticular elements of the right phallomeres of *Eurycotis* and *Chaeteessa* show the following similarities:

1. A sclerite **R3** occupies the anteriormost ventral wall of the right phallomere (fig.28, 77).
2. At least the right and the right anterior margins of **R3** form a groove-like apodeme **age** (fig.28, 77).
3. The right posterior end of **R3** articulates (**A3** in fig.28, 77) with more posterior sclerites (*Eurycotis*: **R1F** in fig.77; *Chaeteessa*: **R1B** in fig.28).
4. The anterior part of both **R1F** and **R1B** extends to the left and reaches an edge (**16** in fig.28, 77) along which it bends sharply dorsad.
5. Then this sclerotisation arches dorsad and then to the left. The arching in a dorsal direction is extensive in *Eurycotis*; in *Chaeteessa* it is less pronounced and the sclerotisation extends mainly to the left.
6. The posterior margin of this sclerotisation forms a posteriad-directed ridge (**pva** in fig.28, 78).
7. To the left of (*Chaeteessa*) or left-ventral to (*Eurycotis*) this **pva**-ridge the right phallomere has a large central invagination (**cbe** in fig.29a, 31, 77, 78; the whole of **cbe** is a part of the ventral wall of the right phallomere).

8. The posterior part of the right phallomere is composed of a dorsal lobe (**fda** in fig.31, 74) and a ventral tooth or ridge (**pia** in fig.28, 29a, 77, 78). **fda** and **pia** are connected along the right edge of the right phallomere, and they diverge to the left like the two halves of an opened book. In *Eurycotis* **pia** is as large as **fda** (and two-pointed); in *Chaeteessa* **pia** is much smaller than **fda**.
9. The dorsal wall of the **fda**-lobe is sclerotised (*Eurycotis*: **R1H** in fig.74; *Chaeteessa*: **R1A** in fig.31).
10. The posteroventral part of both **R1F** and **R1B** (fig.28, 77; posterior to edge **16**) extends onto the **pia**-tooth. However, the sclerotisations of the anterior and of the posterior parts of **pia** are connected in *Chaeteessa* (**R1B**) but separated in *Eurycotis* (**R1F** anteriorly and **R1G** posteriorly, which articulate in **A9**).
11. A large membranous area (**17** in fig.28, 77) is present at the posterior right edge of the right phallomere, between the right margins of the sclerotisations of **fda** and **pia**.

Homology is assumed for all these similarities, for all elements given the same name, and for the compared sclerotisations taking the same relative positions. 1.-11. are assumed to be features of the common ground-plan of Blattaria and Mantodea.

A further similarity between *Chaeteessa* and *Eurycotis* is that the sclerotisation adjoining articulation **A3** posteriorly (**R1B** in fig.28; **R1F** in fig.74, 77) is separated from the dorsal sclerotisation of the **fda**-lobe (**R1A** in fig.28, 31, 32, **R1H** in fig.74, 77) by membrane (**4** in fig.28, 32, **A8** in fig.74). The dividing lines **4** and **A8**, however, are probably non-homologous (discussion below).

There are also some essential differences between *Eurycotis* and *Chaeteessa*: (1) The separation or connection of the anterior and posterior sclerotisations of **pia** (compare feature 10.). (2) Only *Eurycotis* has a sclerite **R2** (fig.77), which articulates with **R3** (**A7** in fig.75, 77) and **R1F** (**A6** in fig.75). (3) In *Eurycotis* the **cbe**-invagination has a summit in the center of the right phallomere and becomes shallower to the left of this summit (where **R2** adjoins; fig.75, 78); in *Chaeteessa* the **cbe**-invagination becomes continuously deeper to the left (fig.29a, 31). (4) Only *Eurycotis* has a **tre**-tendon in the anteriormost dorsal wall of the **fda**-lobe (fig.74). (5) Only *Eurycotis* has the sclerotisations of **pia** (**R1G**) and **fda** (**R1H**) connected with each other posterior to the membranous area **17** (by a narrow sclerite bridge; fig.77, 78).

As regards the right phallomeres of *Mantoida* and *Chaeteessa*, homology is quite evident for most elements: Sclerite **R3** has the same shape and position and a similar **age**-apodeme (compare fig.28, 29a and 41, 43). The right posterior end of **R3** articulates (**A3** in fig.28, 41) with the sclerotisation adjoining posteriorly (**R1E** or **R1B**). However, only in *Mantoida* the groove-shape of the sclerotisation extends from **R3** (**age**) far beyond **A3** onto the posterior sclerite **R1E** (fig.41, 43). The posterior part of the right phallomere is, like in *Chaeteessa*, composed of a large dorsal lobe (**fda** in fig.44) with a sclerotised dorsal wall (**R1E** in fig.44) and a ventral tooth (**pia** in fig.41, 43) with dorsal and ventral sclerotisations (**R1E** in fig.41, 43). However, in *Mantoida* the sclerotisations in the dorsal **fda**-wall and those on **pia** are interconnected anteriorly by a broad sclerite bridge (**R1E** in fig.41, 44; no membranous stripe **4** as in *Chaeteessa*, fig.28). Behind this bridge there is, like in *Chaeteessa*, a large membranous area (**17** in fig.41). In the ventral wall of the right phallomere, to the left of **A3** and anterior to **pia**, *Mantoida* has likewise a tooth-like evagination (**pva** in fig.41, 28). Its sclerotisation, however, is isolated (**R1D** in fig.41); this is in contrast to both *Chaeteessa* and *Eurycotis* (fig.28, 77, 78) and is assumed to be a derived feature. The edge **16** of *Chaeteessa* and *Eurycotis* (fig.28, 77) has also been lost. The large central invagination **cbe** to the left of the **pva**-tooth resembles **cbe** of *Chaeteessa* (fig.43, 29a).

Taking the homology hypotheses assumed so far as a basis, the muscles of the right phallomere are rather similar in *Mantoida* and *Eurycotis*, and the assumed homologies of the cuticular elements (1.-11.) are confirmed:

12. Some phallomero-sternal muscles insert along the anterior margin of **R3** (**s2** and **s4** in fig.42, 82; homology discussion in 6.9.).
13. The **s2**-insertion on **R3** extends to the right as far as to a keel-apodeme on the **age**-apodeme (**3** in fig.41, 42, 44 and 74, 77, 82). (Keel **3** is missing in *Chaeteessa*.)
14. Muscle **r1** (fig.48, 79) inserts on the right part of **R3**, immediately to the right of the **s2**-insertion and the keel **3**, and runs to the dorsal wall of the **fda**-lobe.
15. Muscle **r2** (fig.49, 80) runs from **R3** to the **cbe**-invagination (compare fig.44, 74 and 49, 80). The right part of the posterior **r2**-insertion is on the **R1**-sclerotisation that forms the **pva**-tooth more posteriorly (fig.50, 80).
16. Muscle **r3** (fig.49, 50, 80) runs from the right wall of the right phallomere to the left where it inserts mainly in the dorsal wall of the **pia**-tooth. The rest of the left **r3**-insertion is on the ventral **fda**-wall in *Mantoida* (compare fig.49 and 50) but in the ventral **pia**-wall in *Eurycotis* (compare fig.80 and 82).

These muscles and the keel **3** are assumed to be homologous and to be features of the common ground-plan of Blattaria and Mantodea. Muscle **r4** is only present in *Mantoida* (fig.49), the muscles **r5** (fig.80) and **r6** (fig.79) only in *Eurycotis*.

Furthermore, *Mantoida* and *Eurycotis* have in common that (1) the **age**-apodeme extends as far as to articulation **A3** (fig.41, 44, 74) and that (2) even the sclerotisation posterior to **A3** is groove-shaped (fig.41; **rge** in fig.74, 77). Both is not the case in *Chaeteessa* (fig.28). (1) is assumed to be a feature of the ground-plan of Blattaria and Mantodea:

17. The **age**-apodeme reaches articulation **A3**.

As regards (2), however, the grooves posterior to **A3** take different positions relative to the right **r3**-insertion (ventral to **r3** in *Mantoida*, dorsal to **r3** in *Eurycotis*) and are regarded as non-homologous.

Main sclerite **R1** is differently divided in the species discussed so far; the questions arise (1) which of these divisions are homologous and (2) when have these divisions evolved. The separation of the **pva**-sclerotisation (sclerite **R1D**, fig.41) in *Mantoida* is certainly apomorphic (compare above).

Chaeteessa and *Eurycotis* have the dividing lines **4** (fig.28, 32) and **A8** (fig.74) in a similar position. *Sphodromantis* has a dividing line (**4** in fig.6, 14) in the same position as **4** of *Chaeteessa*, which is not membranous but only weaker sclerotised than the sclerites **R1A** and **R1B**. This weak stripe **4** of *Sphodromantis* and the membranous stripe **4** of *Chaeteessa* are assumed to be homologous. Muscle **r3** of *Sphodromantis* (fig.16, 19) has the same course as **r3** of *Mantoida* (fig.49, 50). The right insertion of **r3** is posterodorsal to stripe **4** (compare fig.14 and 16, 19). In *Eurycotis*, however, the right insertion of **r3** is anteroventral to articulation **A8** (compare fig.74 and 80). Thus, homology is highly improbable for the dividing lines **4** and **A8**. The dividing line **4** is thus missing not only in *Mantoida* but also in *Eurycotis*, and it is not a feature of the common ground-plan of Blattaria and Mantodea but a derived feature of a Mantodean subgroup containing at least *Chaeteessa* and *Sphodromantis*.

The question remains whether the articulations **A8** and **A9**, both missing in Mantodea, could be elements of the common ground-plan of Blattaria and Mantodea. In *Eurycotis*, **A8**, **A9**, and the sclerite bridge between **R1G** and **R1H** (behind membrane **17** in fig.77, 78) are assumed to be functionally correlated: The posterior part of the right phallomere – composed of **fda** and **pia** – can perform a swinging or flapping movement, with **A8** and **A9** defining the axis. During this movement the membrane **17** is folded and stretched again, and the sclerite bridge may have the function to stabilise **R1G** and **R1H** against each other. Muscle **r3** (fig.80) moves the flap posterolaterad; **r1** and **r6** (and possibly **s8** on the **tre**-tendon; fig.79) pull it anteromediad. In *Mantoida* and *Chaeteessa* nothing suggests that such a flap-mechanism has ever been present. Thus, from this functional point of view, **A8**, **A9**, and the posterior bridge are probably derived features of *Eurycotis* (and other Blattaria, see in 6.7.6.). However, this view is debatable: In the copulation of *Periplaneta* the **hla**-hook has its function in the “initial seizing” and the flap-mechanism in the “final holding”. Since the copulation habits of Mantodea are derived, the flap-mechanism could be in the same way completely obliterated as the **hla**-hook and some correlated elements possibly are on the left side (compare in 6.4.2.). On the other hand, the right phallomeres of *Mantoida* and *Chaeteessa* (fig.28, 41) also seem to have the ability to grasp (mainly by the **pia**- and **pva**-teeth), and the final holding could well have been performed by other structures different from the flap-mechanism in the common ground-plan of Blattaria and Mantodea. Thus, it is improbable but cannot be completely excluded that **A8, A9**, and the posterior bridge are elements of the common ground-plan of Blattaria and Mantodea.

As a result, the articulations **A8** and **A9** separating the sclerites **R1F, R1G**, and **R1H** are probably derived elements of Blattaria. The dividing line between **R1E** and **R1D** (*Mantoida*) as well as the dividing line **4** between **R1A** and **R1B** (*Chaeteessa* and *Sphodromantis*) are certainly derived features of Mantodean subgroups. If these hypotheses are true,

18. **R1** is an undivided sclerite in the common ground-plan of Blattaria and Mantodea.

However, if **A8** and **A9** should prove to be elements of this ground-plan, **R1** would have to be regarded as tripartite – composed of **R1F, R1G**, and **R1H** like in *Eurycotis*. (When **R1** will subsequently be assumed to be undivided in this ground-plan, this must be seen with these reservations in terms of **A8** and **A9**).

A further difference between *Eurycotis* (and some other Blattaria) and all Mantodea studied is the presence or absence of the **tre**-tendon and muscle **s8** and the different condition of the muscles **b4**.

Muscles connecting dorsal parts of the left complex and of the right phallomere have been termed **b4**. *Mantoida*, *Eurycotis*, and *Polyphaga* have two such muscles, **b4a** and **b4b** (fig.36, 48, 58, 109); *Cryptocercus* has three, **b4a, b4b**, and **b4c** (fig.143a). The Blattarian species have the right insertions of all **b4**-muscles on the **tre**-tendon, deeply immersed in the body, and the homology of the **b4**-group as a whole is rather certain. *Mantoida* has the right insertions of both **b4a** and **b4b** on the left dorsal anterior margin of the **fda**-lobe (fig.48; the **b4b**-insertion is not shown; it is immediately posterior to the **b4a**-insertion). Since the external origin of **tre** is at the dorsal anterior margin of **fda**, the right insertions of the **b4**-muscles take the same relative position in Blattaria and *Mantoida*. The left insertions, however, take rather different positions, and some shifts must have taken place: The left **b4a**-insertion is in *Eurycotis* and *Polyphaga* on the utmost right part of the **lve**-pouch (fig.70, 129, 130), in *Mantoida* on an infolding to the right of the **lve**-pouch (fig.48, compare fig.46). These positions are quite similar. The left **b4b**-insertion is in *Polyphaga* (fig.127) in the anterior right dorsal wall of the left complex, far right-dorsal to the **pne**-pouch; in *Eurycotis* (fig.70) it is on the top of the **pne**-pouch; in *Mantoida* the position is intermediate – dorsal to the **pne**-pouch, but next to its base (fig.48).

On the basis of these relations, it is in my view acceptable to regard the **b4a** and **b4b** of *Mantoida*, *Eurycotis*, and *Polyphaga* as strictly homologous and to assume homology between these **b4**-muscles as a whole and the **b4**-group of *Cryptocercus*. The immersion of the right insertions (by **tre**) can possibly be regarded as the derived condition and as an autapomorphy of Blattaria or of a Blattarian subgroup. The same might be assumed for the cooperating **s8**-muscle (homology discussion in 6.9.).

19. Muscles **b4a** and **b4b** are present.
20. Muscle **s8** and the **tre**-tendon are probably absent.

For the simple sclerites **R2** and **R3** there is no necessity for defining regions. The complicated main sclerite **R1** will be divided into regions, which mainly (and arbitrarily) correspond to the division into individual sclerites in *Eurycotis*, and which are defined as follows (fig.331e, 332e):

- **R1d** (dorsal): The sclerotisation homologous with sclerite **R1H** of *Eurycotis* (fig.74) on the **fda**-lobe. On **R1d** there are the posterior insertions of the muscles **r1** and **r6** (fig.80).
- **R1v** (ventral): The sclerotisation homologous with sclerite **R1G** of *Eurycotis* (fig.77, 78) on the posterior part of the **pia**-tooth. On **R1v** there is the left insertion of muscle **r3** (fig.80, 82).
- **R1t** (tooth): The sclerotisation homologous with that part of sclerite **R1F** of *Eurycotis* which extends dorsad from the edge **16** (fig.77, 78) and lies in the right-dorsal wall of the **cbe**-invagination. Along its posterior margin **R1t** forms the ridge or tooth **pva**. On **R1t** there is the insertion of the right-dorsal part of muscle **r2** (fig.80, 81).
- **R1c** (central): The sclerotisation homologous with the remainder of sclerite **R1F** of *Eurycotis*, which adjoins sclerite **R3** posteriorly and articulates with it (**A3**), which extends onto the anterior part of the **pia**-tooth, and which forms the groove **rge** along its dorsal margin. **R1c** is situated centrally between the other **R1**-regions: The border to **R1d** is articulation **A8**; the border to **R1v** is articulation **A9**; the border to **R1t** is edge **16**. On **R1c** there is the right insertion of **r3** (fig.80, 82), the anterior insertion of **r6** (fig.79; on **rge**), and the posterior insertion of **r5** (fig.80; on **rge**).

In fig.331c and 332c this regioning of **R1** is transferred to *Chaeteessa* – according to the homology relations assumed above (features 1.-11.). In *Chaeteessa* (and *Sphodromantis*) the **R1c**-region extends far dorsad into the **R1A**-sclerite (fig.331c); this results from the position of the right **r3**-insertion in *Sphodromantis* (compare fig.16 and 331a,c). The regioning of **R1** of *Mantoida* is shown in fig.331d, 332d.

6.7.2. The elements in the common ground-plan of Blattaria and Mantodea

The features 1.-20. in 6.7.1. permit the reconstruction of many ground-plan features of the right phallomere (fig.321f,h): **R3** is a curved plate in the anteriormost ventral wall. The right posterior end of **R3** articulates with the **R1c**-region (**A3**). At least the right and right anterior margins of **R3** form a groove-like **age**-apodeme, which reaches articulation **A3** (but the groove does not exceed **A3**). **R1** is (probably) an undivided sclerite, with all its regions firmly connected. Along edge **16** the regions **R1c** and **R1t** are sharply angled to each other. **R1t** forms a posteriad-directed tooth or ridge **pva** at its posterior margin. A large central invagination **cbe** is situated to the left of or left-ventral to **pva**. The dorsal lobe **fda** and the ventral tooth **pia** are distinct; they are connected along the right edge of the right phallomere and diverge to the left. Their walls are largely sclerotised by **R1** (regions **R1d** and **R1v**). In the posterior right edge of the right phallomere there is a membranous area **17**. The parts of **R1** in the dorsal wall of **fda** and those on **pia** are interconnected anterior to membrane **17**. Posterior to membrane **17** there is no dorsoventral connection (like in Mantodea) or, at most, a very narrow one (like in *Eurycotis*). The muscles **r1, r2, r3, s2**, and **s4** are present. The insertions of **s2** and **r1** are separated by the keel-apodeme **3**. The **tre**-tendon and the articulations **A8** and **A9** are probably missing. It is unclear if **R2**, the articulations **A6** and **A7**, and the muscles **r4, r5**, and **r6** are present or not.

6.7.3. Homology relations and character states of the elements in Mantodea

The **R3**-sclerites of *Chaeteessa* (fig.28), *Mantoida* (fig.41), *Metallyticus* (fig.20), and *Sphodromantis* (fig.6) are very similar. The **age**-apodeme is always deeper in its left part, where it is more or less plate-like (this is least distinct in *Chaeteessa*). In *Metallyticus* and *Sphodromantis* this deepening of **age** is very abrupt. Only in *Sphodromantis* this left part of **age** has developed a curvature to the posterior and back to the right (fig.6, 8). Only in *Chaeteessa* the left marginal part of **R3** bends dorsad into the **cbe**-wall (fig.29a, 32). Two other derived features of *Chaeteessa* are that the utmost right-posterior part of **age** and the keel-apodeme **3** have been lost (fig.28). In the other species the groove-like shape of the sclerotisation even exceeds **A3** (distinct in *Mantoida*, fig.41, 43, and *Sphodromantis*, fig.6, 8; less distinct in *Metallyticus*, fig.20, 21); the keel **3** has been retained (fig.6, 13, 20, 23, 41, 44). At least in *Sphodromantis* and *Mantoida* keel **3** separates the insertion areas of **s2** and **r1** (fig.15, 48). The apodeme **are** (fig.6, 8) is a derived feature of *Sphodromantis*.

The **cbe**-invagination becomes in all four species continuously deeper to the left (fig.6, 8, 20, 21, 28, 29a, 41, 43), and a sclerite **R2** is always missing (compare *Eurycotis*, fig.77, 78; but see below: *Metallyticus*).

The posterior part of the right phallomere is in all species composed of a large dorsal lobe **fda** (fig.13, 23, 31, 44) and a smaller, leftward projecting ventral tooth **pia** (fig.6, 20, 28, 41). In *Sphodromantis* **pia** has become very small by a reduction of its posterior part. Left-anterior to **pia** there is always another tooth-like process **pva** (fig.6, 20, 28, 41).

The **R1**-sclerotisations are very similar in *Chaeteessa* and *Sphodromantis* (fig.6, 28): The sclerotisation posterior to articulation **A3** is connected with the **pva**-sclerotisation and with the **pia**-sclerotisation (sclerites **R1B**) but more or less separated (by **4** in fig.6, 28) from the dorsal **fda**-sclerotisation (sclerites **R1A**). The dividing line **4** is also present in *Metallyticus* (fig.20), but **R1A** has expanded far into the right ventral wall and occupies the ventral wall of **pia** (fig.20, 21). Only *Mantoida* shows the plesiomorphic state with the dividing line **4** missing. In both *Metallyticus* and *Mantoida* the **pva**-sclerotisation has been separated from the **R1**-sclerotisation posterior to **A3** (sclerites **R1D** in fig.20, 41). That in *Mantoida* these elements are really **pva** and parts of **R1** (and not **R2**) is shown by the posterior insertion of **r2**, whose **right** part inserts on that sclerite (fig.49, 50; compare fig.16, 19). (**R2** of *Eurycotis* bears the **left** part of the **r2**-insertion; compare feature 15. in 6.7.1.). In *Metallyticus*, however, **R1D** adjoins the left posterior end of **R3** in a similar way as **R2** in *Eurycotis* (fig.20, 77) and could really be the homologue of **R2**. But regarding the situations in the other Mantodea, it is certainly more probable that the tooth is the true **pva** and **R1D** the respective part of **R1**. A definite decision might come from an investigation of muscle **r2**.

The membranous area **17** has retained its primitive condition only in *Chaeteessa* and *Mantoida* (fig.28, 41). In *Metallyticus* it has been largely reduced by the expansion of **R1A** onto **pia** (fig.20). In *Sphodromantis* it has lost its boundary to the membranous ventral **fda**-wall by the reduction of the posterior part of the **pia**-tooth and its sclerotisation (fig.6).

The regioning of **R1** of *Chaeteessa* (6.7.1.) can be transferred to *Mantoida, Metallyticus*, and *Sphodromantis* (fig.331a-d and 332a-d). One minor problem is the exact course of the boundary between the regions **R1c** and **R1t**, since the edge **16** is distinct only in *Chaeteessa* (fig.28). In *Mantoida* and *Metallyticus* sclerite **R1D** is tentatively equated with the **R1t**-region, but it probably does not exactly correspond to **R1t** as defined in *Eurycotis*.

The muscles of *Sphodromantis* (fig.15, 16, 19) are very similar to those of *Mantoida* (fig.48, 49, 50), but **r4** is much stouter. Of the muscles connecting the right phallomere and the left complex dorsally (**b4a** and **b4b** in *Mantoida*, fig.48) at most one is retained (**b4, l9?** in fig.17), but its homology with **b4** of *Mantoida* is questionable since both its insertions are on the left complex. This muscle of *Sphodromantis* could also be homologous with **l9** of *Mantoida* (fig.49; compare in 6.5.).

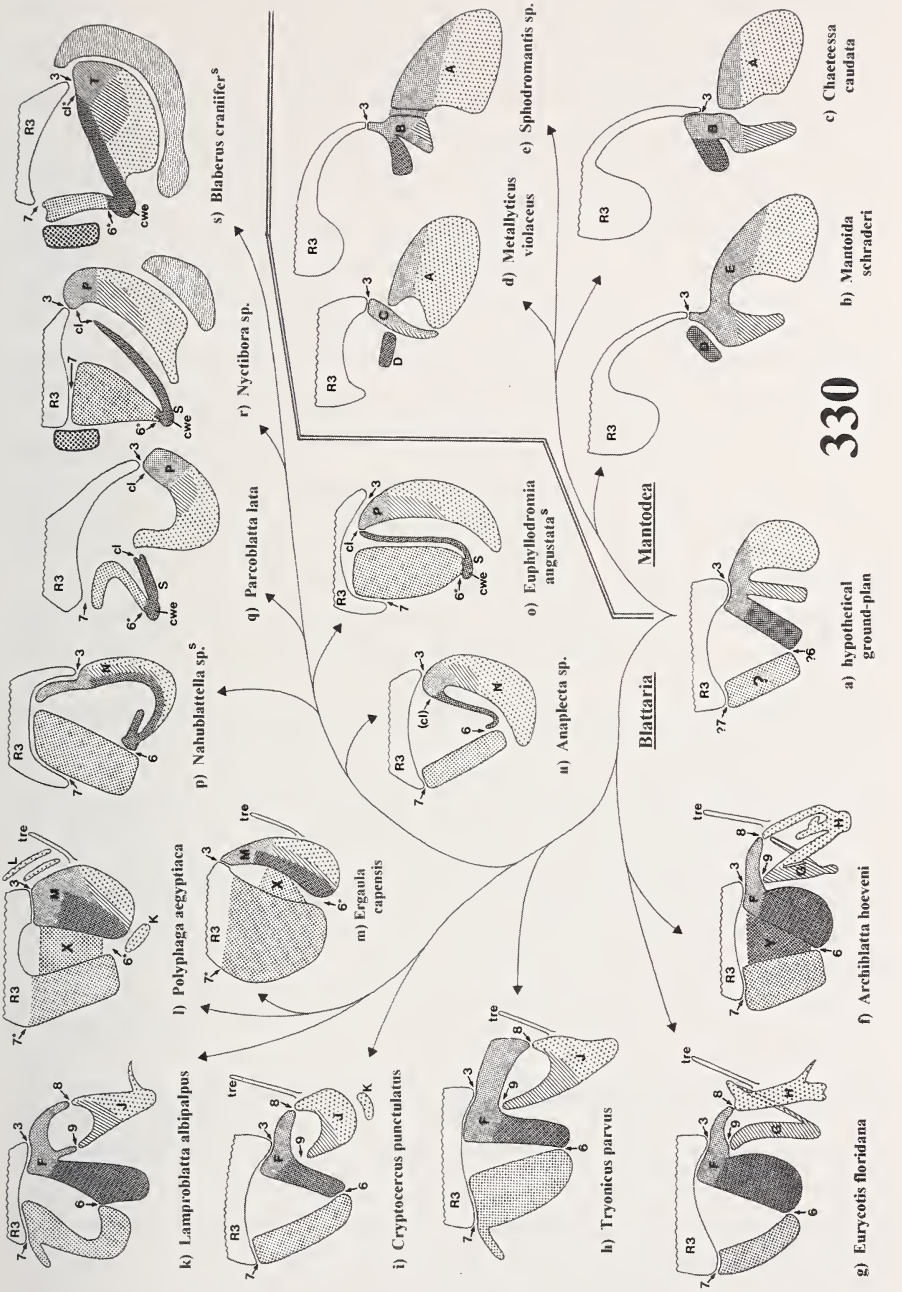
6.7.4. Homology relations and character states of the elements in Blattaria I: The anteroventral elements

In the following discussions in 6.7.4., 6.7.5., and 6.7.6., data of some species are included whose right phallomeres have been studied only in part: *Archiblatta, Ergaula, Euphyllodromia, Nyctibora, Byrsotria* (fig.330f,m,o,r, 318, 319), and *Supella*. *Archiblatta* resembles *Eurycotis* (fig.330g); *Ergaula* resembles *Polyphaga* (fig.330l); *Nyctibora* and *Byrsotria* resemble *Blaberus* (fig.330s). For a discussion of the right phallomeres it is useful to consider first the anteroventral elements (**R2**, **R3**, **cbe**-invagination; 6.7.4.) and the **tre**-tendon (6.7.5.), whose homology relations are quite evident. Then the posterodorsal parts will be discussed (**R1**, **pva**-tooth, **fda**-lobe, **pia**-tooth; 6.7.6.).

The sclerites **R2** and **R3** and the **cbe**-invagination can, as compared with *Eurycotis*, easily be identified in all Blattaria: **R3** (fig.77, 102, 137, 163, 193, 229, 257, 284, 312a) is always a plate in the anteriormost (right-)ventral wall of the right phallomere, and parts of its anterior and lateral margins nearly always form a groove-like **age**-apodeme. The right and left posterior margins of **R3** articulate with more posterior sclerites: **A3** (between **R3** and **R1**) is always distinct. **A7** (between **R3** and **R2**) is in most cases also a true articulation; sometimes, however, **R2** and **R3** are fused in this place (*Polyphaga, Ergaula*: **A7***), or **R2** and **R3** are more distant from each other and no longer articulated (*Parcoblatta, Blaberus*; the term **A7** is still used to designate the homology of the respective areas). Posterior to the central part of **R3** (between **A3** and **A7** or **A7***), the ventral wall of the right phallomere always bends dorsad and (more or less strongly) anteriad to form a central invagination (**cbe** in fig.78, 104, 138, 164, 195, 230, 258, 285, 313). **cbe** is variable in its extension and distinctness and is sclerotised to a varied extent. **cbe** always has its summit in the center of the right phallomere and a descent in the left-ventral direction (missing in Mantodea), at whose base that sclerite adjoins which also approaches **R3** in **A7** or **A7*** (**R2** in fig.75, 100, 135, 161, 191, 227, 255, 282, 310). **R2** has either as a whole the shape of a ridge, often projected into teeth or bulges (fig.75, 76, 135, 136, 161, 162, 191, 192, 227, 228, 281, 285, 287, 310, 311), or **R2** is more plate-like but likewise beset with tooth-like evaginations (fig.99, 100, 102, 254-256). All species with the muscles studied have a stout **r2** from **R3** to the **cbe**-invagination (fig.80, 81, 140, 141, 166, 167, 197, 198, 231, 232, 259, 260, 286, 287, 314, 316), and some phallomero-sternal muscles insert at the anterior margin of **R3** (fig.82, 142, 168, 199, 233, 261, 288, 317; homology discussion in 6.9.). According to these corresponding relative positions and similarities in shape, homology is assumed for the sclerites **R2** and **R3**, the articulations **A3** and **A7** (or **A7***), the **cbe**-invaginations, the **age**-apodemes, and the **r2**-muscles of all species.

Fig.330: Right phallomere, evolution of main sclerites. – The sclerotisations of the right phallomere are shown. The view is roughly cranial but the phallomeres are unfolded. For correct orientation compare fig.1-319.

Of sclerite **R3** (white) only the posterior part is shown (anterior part cut off along undulate line). The other sclerotisations are shown completely and patterned differently. The individual sclerites of **R1** are labelled with the capital letters used in the text and in fig.1-319 (e.g. **F** = **R1F**). **X** (part of sclerite **R2**) and **Y** (part of region **R1t**) are sclerotisations occupying the **cbe**-invagination (compare in 6.7.4.). Articulations between sclerites are labelled with the numbers used in the text and in fig.1-319 (e.g. **6** = **A6**). If an articulation has been lost by fusion of the respective sclerites, the point of fusion is labelled by adding * to the name of the lost articulation (e.g. **6*** = **A6***). **tre** and **cwe** are formative elements. **cl** represents a certain dividing line between **R1**-sclerotisations (compare in 6.7.6.). Species with "S" behind their names have side-reversed phallomeres, and a mirror-image of the original preparation is shown. The branching black lines represent the assumed phylogeny. The ground-plan is in some respects unclear (**?** in fig.330a; discussion in 6.7.1.): Presence of sclerite **R2** and of articulations **A6** and **A7**.



330

a) hypothetical ground-plan

b) Mantoida schraderi

c) Chaeteessa caudata

d) Metallyticus violaceus

e) Sphodromantis sp.

f) Archiblatta hoeveni

g) Eurycotis floridana

h) Tryonicus parvus

i) Cryptocercus punctulatus

k) Lamproblatta albipalpus

l) Polyphaga aegyptiaca

m) Ergaula capensis

n) Anaplecta sp.

o) Euphyllodromia angustata^s

p) Nahublattella sp.^{s}

q) Parcoblatta lata

r) Nyctibora sp.

s) Blaberus craniifer^s

The **age**-apodeme is rather variable in its extension: In *Polyphaga* (fig.137), *Ergaula, Anaplecta* (fig.229), *Archiblatta*, and *Eurycotis* (fig.77), it is restricted to the right and the right anterior margins of **R3**. In *Cryptocercus* (fig.163) and *Nahublattella* (fig.257) it extends along the whole anterior and lateral margins of **R3**. In *Parcoblatta* (fig.284), *Nyctibora*, *Byrsotria*, and *Blaberus* (fig.312a) it is restricted to the anterior marginal areas of **R3**. Only in *Tryonicus* (fig.102) and *Lamproblatta* (fig.193) **age** has been lost.

R2 is an isolated sclerite in *Eurycotis* (fig.75, 76), *Tryonicus* (fig.100, 101), *Cryptocercus* (fig.161, 162), *Lamproblatta* (fig.190, 191), *Anaplecta* (fig.227, 228), *Nahublattella* (fig.254, 255), and *Supella*. In all these species, the right-ventral end of **R2** articulates distinctly with **R3** (**A7**), the left-dorsal end of **R2** articulates distinctly with **R1**-sclerotisations in the dorsal wall of the **cbe**-invagination (**A6**), and **R2** is restricted to the ventral base or, at least, to the ventral wall of the **cbe**-invagination.

In *Euphyllodromia* (fig.330o), *Parcoblatta* (fig.282, 283, 330q), *Nyctibora* (fig.330r), *Blaberus* (fig.310, 311, 330s), and *Byrsotria* **R2** is fused to **R1**-sclerotisations (**R1S** or **R1T**) in the area corresponding to the **A6**-articulation of the other species. The point of fusion is **A6***, with the **cwe**-thickening (fig.282, 310) in its immediate vicinity. This topic will be discussed in 6.7.6.. In *Parcoblatta* and *Blaberus* **R2** is in close vicinity to **R3** in the area corresponding to the **A7**-articulation of the other species (**A7** in fig.284, 312a) but is not articulated with **R3**. In *Euphyllodromia* and *Byrsotria* (fig.318) **A7** is a distinct articulation. In *Nyctibora* **A7** is distinct and hinge-like (fig.319).

In *Polyphaga* (fig.135-137, 330l) and *Ergaula* (fig.330m) **R2** and **R3** are clearly identifiable by their shapes (**R3** is a broad curved plate, **R2** forms a dental ridge) and by their positions relative to each other, to **cbe**, and to the **r2**-insertions (fig.141; compare *Cryptocercus*, fig.161, 167, and *Eurycotis*, fig.75, 81; **r2** not investigated in *Ergaula*). However, in both species **R2** shows two peculiarities: (1) **R2** is fused to **R3**. (2) **R2** has spread over the **cbe**-invagination (sclerotisation **X** in fig.330l,m) and is broadly fused to **R1**-sclerotisations in the dorsal **cbe**-wall; hence, the whole of **cbe** is sclerotised (fig.134, 135). (1): In *Polyphaga* the stripe of weaker sclerotisation **A7*** (fig.135, 137) takes the same position as articulation **A7** in other Blattaria and is assumed to be the line of fusion between **R2** and **R3** (and a vestige of **A7**). In *Ergaula* **R2** and **R3** are fused without any vestige of **A7** (no weak line), and the border is not exactly determinable. Moreover, **R2** of *Ergaula* has become so broad that **R3** is for most of its breadth confluent with **R2** (compare fig.330l and m). (2): In *Polyphaga* the sclerotisation of **cbe** has a weak line (**13** in fig.134, 138) and an adjacent notch within the sclerite margin; these structures are assumed to mark the border between **R2** and **R1**, and the sclerotisation in the ventral wall and on the summit of **cbe** is assumedly part of **R2** (**X** in fig.330l). **R1** is restricted to the posterior dorsal wall of **cbe**. In *Ergaula* **R1** and **R2** are firmly connected (no weak line); the interpretation of the **cbe**-sclerotisation is done in accordance with *Polyphaga* (**X** in fig.330m is part of **R2**).

Archiblatta also has the whole **cbe**-invagination sclerotised (compare fig.74 and 75 of *Eurycotis*; the sclerotisation concerned is **Y** in fig.330f, compare fig.330g), but, in contrast to *Polyphaga*, the **cbe**-sclerotisation is slightly weaker near the ventral base of the **cbe**-invagination; in the corresponding area of *Eurycotis* **R2** has its dorsal margin and the membranous ventral wall of **cbe** adjoins (fig.75, 76). Therefore, in *Archiblatta* the sclerotisation of **cbe** is assumed to have developed by an expansion of **R1** (**R1t**-region, fig.330f). The situation in *Eurycotis*, with **R1** occupying a large part of **cbe** (fig.75; compare e.g. fig.99, 160), can be regarded as a primitive stage of such a development. As a result, homology is assumed for the **cbe**-sclerotisations of *Polyphaga* and *Ergaula* (mainly part of **R2**, **X** in fig.330l,m), but the **cbe**-sclerotisation of *Archiblatta* (mainly part of region **R1t**, **Y** in fig.330f) is not homologous with these. In *Archiblatta* **R2** and the heavier sclerotised dorsal parts of **R1** are still distinctly articulated (**A6**) in the left-dorsal wall of the **cbe**-invagination (like in *Eurycotis*, **A6** in fig.75). In *Polyphaga* and *Ergaula* this articulation is missing (**A6*** in fig.135, 137).

The shape of **R2** is rather variable. Details are shown in the figures. Some peculiar features are: In *Parcoblatta* (fig.285) **R2** is strongly curved. In *Nahublattella* **R2** bears the conspicuous elements **42** and **43** (fig.254). Only in *Tryonicus* and *Lamproblatta* **R2** has an extension posterior to articulation **A7** (**R2m** in fig.102, 91 and 174, 193), which lies in the rightmost part of the **vla**-lobe (left complex), and which has in *Lamproblatta* a close contact with sclerite **L7**.

Only *Blaberus* (fig.311, 312a), *Byrsotria*, and *Nyctibora* (fig.319) have a peculiar sclerite **R5** ventral to **R2** and **A7**. The **R5** of the three species take exactly the same relative position and are certainly homologous.

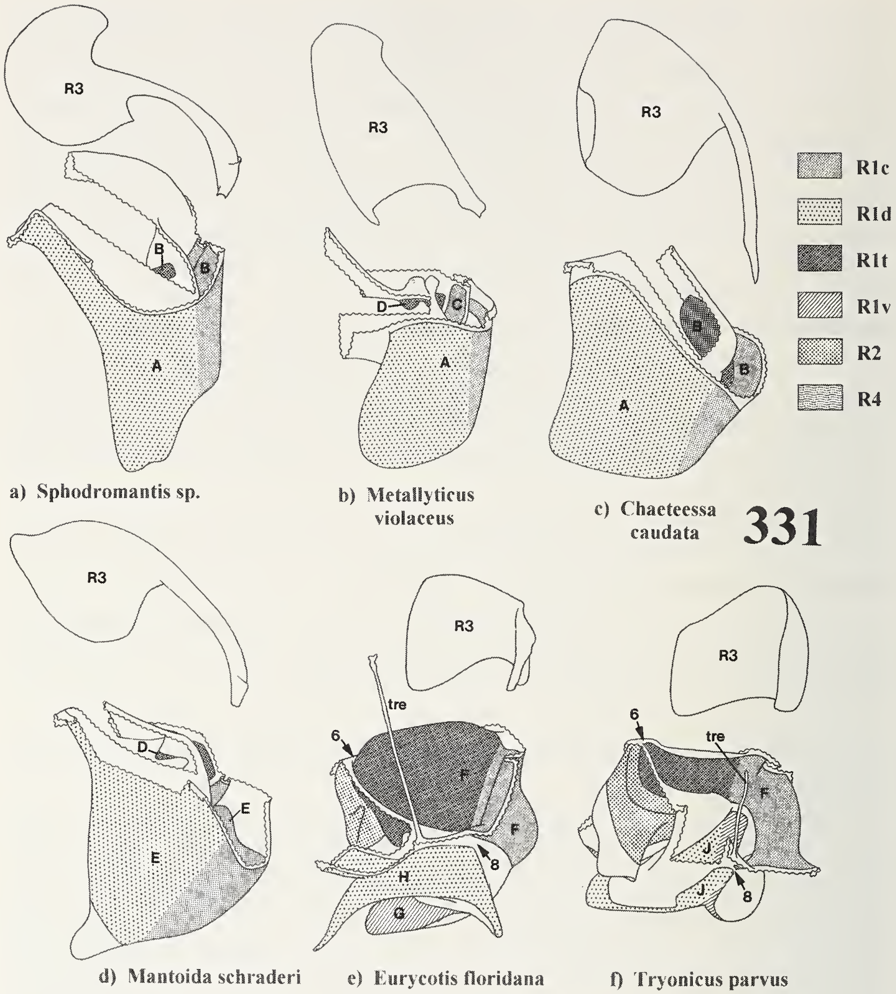
As regards the muscles, **r9** is specific to *Polyphaga* (fig.141; *Ergaula* not studied), and **r8** is specific to *Cryptocercus* (fig.167). Since the posterior insertions take completely different positions, a homology of **r8** and **r9** is most unlikely.

6.7.5. Homology relations and character states of the elements in Blattaria II: The tre-tendon

A **tre**-tendon is present in *Archiblatta* (fig.330f), *Eurycotis* (fig.74, 330g), *Tryonicus* (fig.99, 330h), *Ergaula* (fig.330m), *Polyphaga* (fig.134, 330l), and *Cryptocercus* (fig.160, 330i). Homology is ascertained by the similar position of the **tre**-base in the anterior dorsal wall of the right phallomere, by a muscle from the right half of the sugenital plate (**s8**), and by two or three muscles from the dorsal part of the left complex (**b4**-group; fig.79, 139, 165; muscles not studied in *Tryonicus*). A muscle from **tre** to **R3** is specific to *Cryptocercus* (**r7** in fig.165). In *Lamproblatta* as well as in *Anaplecta, Nahublattella, Parcoblatta, Blaberus*, and all other Blattellidae and Blaberidae studied (fig.330n-s) **tre**, **s8**, and **b4** are missing.

6.7.6. Homology relations and character states of the elements in Blattaria III: The posterodorsal elements

The elements discussed here are those dorsal and posterior to the summit of the **cbe**-invagination and posterior to articulation **A3** (compare fig.321f,h). In *Eurycotis* (fig.74-77), for example, this part of the right phallomere is composed of the dorsal wall of **cbe**, the ridge **pva**, the dorsal lobe **fda**, and the ventral tooth **pia**, and it contains the sclerotisations comprised in **R1**: three sclerites **R1F, R1G**, and **R1H**. This part of the right phallomere has undergone very complicated evolutionary changes.



a) Sphodromantis sp.

b) Metallyticus violaceus

c) Chaeteessa caudata

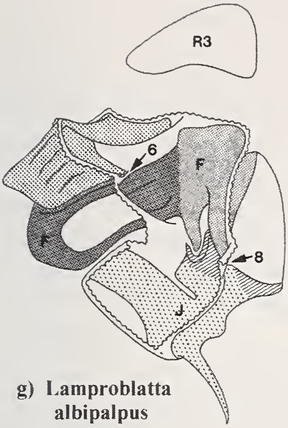
331

d) Mantoida schraderi

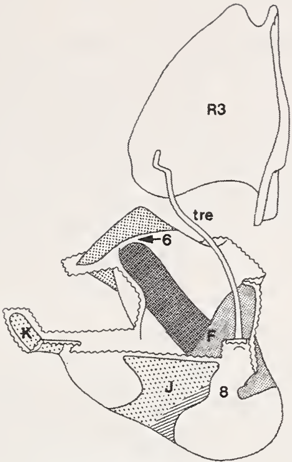
e) Eurycotis floridana

f) Tryonicus parvus

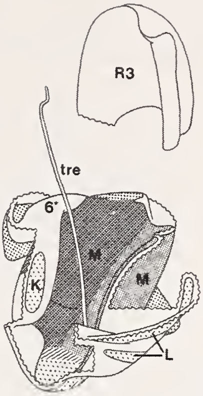
Fig.331: Right phallomere, homology of main sclerites and homologous regions of main sclerite **R1** (dorsal views). – The cuticular elements of the right phallomere are shown, but some membranous parts are removed. Patterned areas are sclerotised, white areas are (except for sclerite **R3**) membranous. Undulate lines are cutting lines. **R3** is separated from the remainder of the right phallomere and shifted anteriad. **R5** of *Blaberus* is not shown. The individual sclerites of **R1** are labelled with the capital letters used in the text and in fig.1-319 (e.g. **F** = **R1F**). Articulations between sclerites are labelled with the numbers used in the text and in fig.1-319 (e.g. **6** = **A6**). Articulations **A3** and **A7** are not labelled (see fig.332). If an articulation has been lost by fusion of the respective sclerites, the point of fusion is labelled by adding * to the name of the lost articulation (e.g. **6*** = **A6***). **tre** and **cwe** are formative elements.



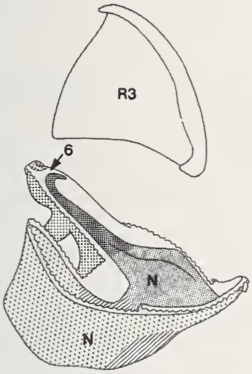
g) Lamproblatta albipalpus



h) Cryptocercus punctulatus

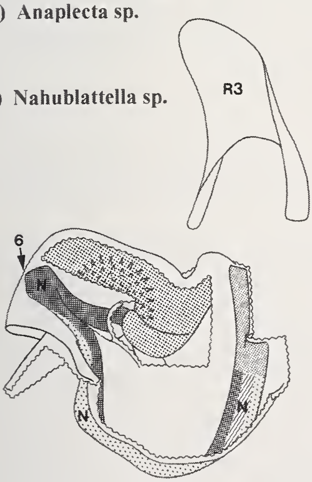


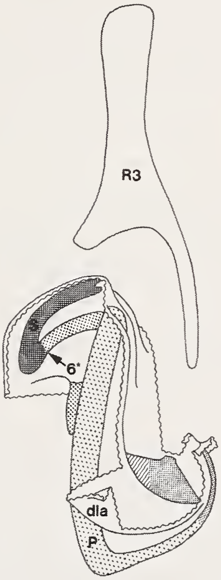
i) Polyphaga aegyptiaca



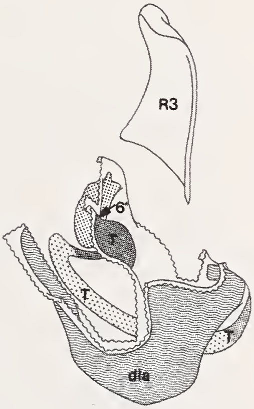
k) Anaplecta sp.

l) Nahublattella sp.





m) Parcoblatta lata



n) Blaberus craniifer

331

Eurycotis and *Archiblatta*

For *Eurycotis* this area has been fully discussed in 6.7.1.. In *Archiblatta*, like in *Eurycotis* and in all Mantodea, the **fda**-lobe and the **pia**-tooth are both very distinct. Sclerite **R1F** (fig.330f, regions **R1c** and **R1t**) closely resembles **R1F** of *Eurycotis*. The sclerotisations of the **R1d**- and **R1v**-regions are more complicated than in *Eurycotis* (compare fig.330f and g) but similarly structured in a dorsal (**R1H** = **R1d**) and a ventral (**R1G** = **R1v**) sclerite. The sclerite bridge connecting **R1H** and **R1G** in *Eurycotis* (behind membrane **17** in fig.77; fig.330g) has a short gap in *Archiblatta*; instead, there is a ribbon-like connection between **R1H** and **R1G** across the ventral wall of the **fda**-lobe (compare fig.330f and g).

Tryonicus, Cryptocercus, and *Lamproblatta*

In these species (fig.99-104, 160-164, 190-195) the posterodorsal part of the right phallomere has only two sclerites **R1F** and **R1J**. **R1F** corresponds to **R1F** of *Eurycotis* (fig.74-78). The area posterior to **R1F** contains **R1J**, which is a fusion product of **R1H** and **R1G** of *Eurycotis*, and is an undivided lobe (**fda**, no ventral tooth **pia** present). The regioning of **R1** is shown in fig.331e,f,g,h and 332e,f,g,h.

R1F (fig.102, 163, 193) is in these species, like in *Eurycotis*, somewhat horseshoe-shaped (open to the left, with a dorsal and a ventral arm), and along **R1F** there are the following structures in common, which are all regarded as homologous:

- The ventromedian end of **R1F** articulates with **R2** (**A6** in fig.75, 100, 160, 164, 190).
- The ventral arm lies in the dorsal wall of the **cbe**-invagination (fig.74, 99, 160, 190). It bears a ridge (**pva** in fig.80, 99, 164, 190, 196), which is formed by cuticular evagination in *Eurycotis*, *Tryonicus*, and *Lamproblatta*, and by cuticular thickening in *Cryptocercus* (cross-section in fig.164).
- At the base of this ventral arm the posterior margin of **R1F** articulates with sclerite **R1J** (**A9** in fig.102, 103, 190, 193), or the sclerites are at least in close vicinity (**A9** in fig.163, 166). This corresponds to the position of articulation **A9** of *Eurycotis* (compare fig.77 and 78). Special features of *Lamproblatta* are the extension **20** of that part of **R1F** bearing **A9** and the immersion of the whole articulation.
- From **A9** **R1F** extends to articulation **A3**; then it curves into the dorsal wall of the right phallomere.
- At its dorsomedian end **R1F** has another articulation with **R1J** (**A8** in fig.99, 190) or, at least, closely approaches **R1J** (**A8** in fig.160). This corresponds to the position of articulation **A8** of *Eurycotis* (fig.74).
- This dorsal arm of **R1F** has, like in *Eurycotis*, a sclerotised groove at its dorsal margin, between the articulations **A3** and **A8** (**rge** in fig.74, 77, 99, 102, 160, 163, 190, 193).

R1J (fig.99, 102-104, 160-164, 166, 190, 192-195, 197) bears both the articulations **A8** (like **R1H** or region **R1d** in *Eurycotis*) and **A9** (like **R1G** or region **R1v** in *Eurycotis*) and is therefore regarded as a compound sclerite **R1d+R1v** (fig.331f,g,h, 332f,g,h). Thus, in contrast to the situation in Mantodea, *Eurycotis*, and *Archiblatta*, there is now a very broad connection between the **R1d**- and **R1v**-regions posterior to membrane **17**, and this is clearly a derived feature. For *Cryptocercus*, *Lamproblatta*, and *Eurycotis* these relations are confirmed by a comparison of the muscles, since **R1J** bears insertions which are in *Eurycotis* either on **R1H** or on **R1G**:

- Muscle **r3** of *Cryptocercus* and *Lamproblatta* (fig.166, 197) runs from that part of **R1F** posterior to articulation **A3** to the right margin of **R1J**. It is assumed to be homologous with **r3** of *Eurycotis* (fig.80), which inserts on **R1G**.
- Muscle **r6** of *Lamproblatta* (fig.196) runs from the **rge**-groove to the dorsal wall of the right phallomere, like **r6** of *Eurycotis* (fig.79). The left insertion is partly on **R1J** in *Lamproblatta* and on **R1H** in *Eurycotis*. Such a muscle is missing in *Cryptocercus*.
- Muscle **r1** of *Cryptocercus* (fig.165) runs from the **age**-apodeme on **R3** to the dorsal wall of the right phallomere, like **r1** of *Eurycotis* (fig.79). The posterior insertion is partly on **R1J** in *Cryptocercus* and on **R1H** in *Eurycotis*. Such a muscle is missing in *Lamproblatta*.

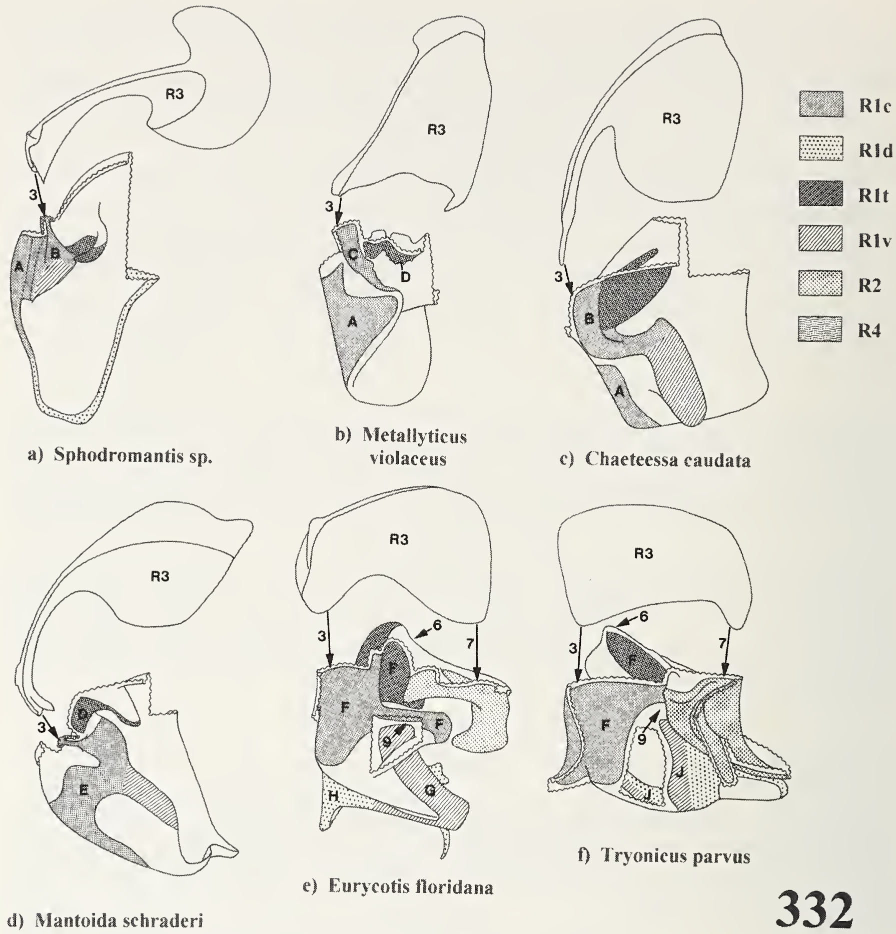
The **fda**-lobe of *Tryonicus* (fig.99, 102-104), *Cryptocercus* (fig.160-164, 166), and *Lamproblatta* (fig.190-195, 197) largely corresponds to **fda** of *Eurycotis*. However, parts of its ventral wall assumedly correspond to the **pia**-walls of *Eurycotis* (after having been leveled). Thus, the **fda**-lobes of these species are not strictly homologous with **fda** of *Eurycotis*. The levelling of **pia** is also a derived feature.

At least *Lamproblatta* has a similar flap-mechanism as *Eurycotis* (with **fda** being the flap and the stout **A8** and **A9** defining the axis of movement). To what extent this is also practised in *Tryonicus* and *Cryptocercus* is questionable since the articulations **A8** and **A9** are by far less distinct.

Polyphaga and *Ergaula*

In *Polyphaga* the posterodorsal part of the right phallomere contains the large sclerite **R1M** and the smaller sclerites **R1K** and **R1L** (fig.134). The regions **R1c**, **R1t**, **R1d**, and **R1v** can be identified and demarcated by their characteristic features (fig.331i, 332i), but some points remain unclear.

- **R1M** articulates with **R3** (**A3** in fig.137) and forms a **rge**-groove on its dorsal margin (from **A3** to the posterior: fig.134, 137, 140), and **rge** bears the insertion of a stout muscle (**r6** in fig.140). These features resemble the **R1c**-region of *Eurycotis* (fig.331e,i, 332e,i) and the other species. In contrast to the other species, the **rge**-groove extends much farther posteriad (compare fig.74, 99, 160, 190).
- To the left of **A3** **R1M** bends around an edge (**16** in fig.137) to occupy the dorsal wall of the **cbe**-invagination. The right part of muscle **r2**, coming from **R3**, inserts at the anterior margin of this part of **R1M** (fig.140). More to the left this part of **R1M** forms a ridge (**pva** in fig.139, 137, 138). These features resemble the **R1t**-region of *Eurycotis* (fig.331e,i, 332e,i) and the other species. In contrast to the other species, the **pva**-ridge is not transversely but longitudinally orientated (compare **pva** in fig.139 and 80, 99, 197). However, the shape of **pva** of *Polyphaga* is not so different from **pva** of *Lamproblatta* (compare fig.139 and 197), if a lengthening of **pva** along the longitudinal axis and a shortening along the transverse axis is assumed for *Polyphaga*.
- Corresponding to the probable lengthening of **pva** and **rge** to the posterior, it is assumed



a) Sphodromantis sp.

b) Metallyticus violaceus

c) Chaeteessa caudata

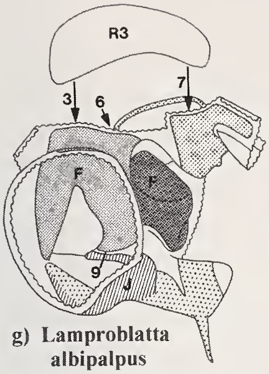
d) Mantoida schraderi

e) Eurycotis floridana

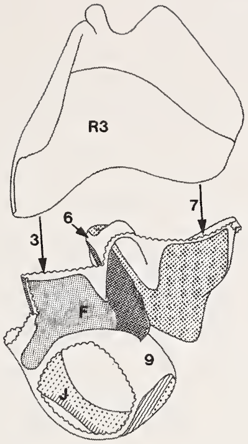
f) Tryonicus parvus

332

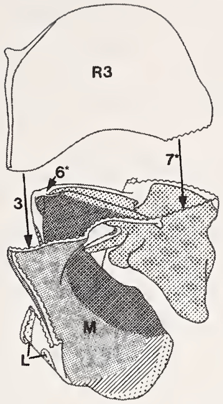
Fig.332: Right phallomere, homology of main sclerites and homologous regions of main sclerite **R1** (ventral views). – The cuticular elements of the right phallomere are shown, but some membranous parts are removed. Patterned areas are sclerotised, white areas are (except for sclerites **R3** and **R5**) membranous. Undulate lines are cutting lines. **R3** and, in *Blaberus*, **R5** are separated from the remainder of the right phallomere and shifted anteriad. The individual sclerites of **R1** are labelled with the capital letters used in the text and in fig.1-319 (e.g. **F** = **R1F**). Articulations between sclerites are labelled with the numbers used in the text and in fig.1-319 (e.g. **6** = **A6**). If an articulation has been lost by fusion of the respective sclerites, the point of fusion is labelled by adding * to the name of the lost articulation (e.g. **6*** = **A6***). The articulation points of **A3** and **A7** are connected by arrows. **cwe** is a formative element.



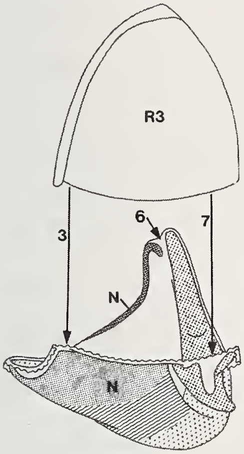
g) **Lamproblatta albipalpus**



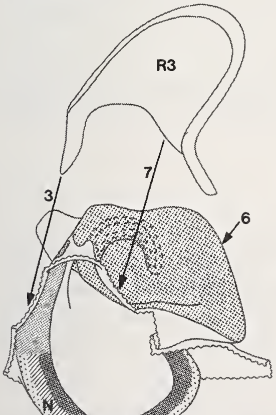
h) **Cryptocercus punctulatus**



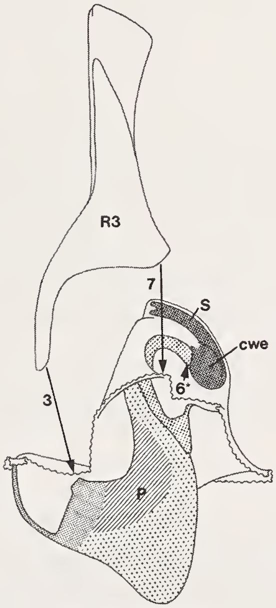
i) **Polyphaga aegyptiaca**



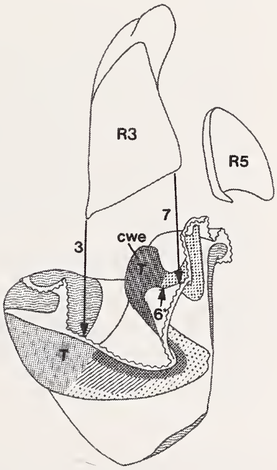
k) **Anaplecta sp.**



l) **Nahublattella sp.**



m) **Parcoblatta lata**



n) **Blaberus craniifer**

332

that in *Polyphaga* the regions **R1t** and **R1c** have considerably expanded posteriad and make up most of **R1M** (fig.331i, 332i).

- Muscle **r1** (fig.139) has its anterior insertion on the right margin of **R3**, like **r1** and **r5** of *Eurycotis*. The dorsal part of **r1** has its posterior insertion in the dorsal wall of the right phallomere (on the **R1L**-sclerites), like **r1** of *Eurycotis* (fig.79). This suggests that the two **R1L**-sclerites are part of the **R1d**-region (fig.331i). The ventral part of **r1** has its posterior insertion on the **rge**-groove (fig.134, 139), similar to **r5** of *Eurycotis* (fig.80) but more posteriorly. Thus, **r1** of *Polyphaga* is certainly homologous with **r1** of *Eurycotis* but possibly also includes the homologue of **r5**. **r1** of *Cryptocercus* closely resembles **r1** of *Polyphaga*, but a contribution of a **r5**-part is less probable since no fibers insert on **rge** or **R1F** (fig.165).
- *Eurycotis* (fig.79) and *Lamproblatta* (fig.196) have the left insertion of **r6** in the dorsal wall of the **fda**-lobe and, by definition, in the **R1d**-region. **r6** of *Polyphaga* has a very similar course; its left insertion is on sclerite **R1K**, which is therefore assumed to belong to the **R1d**-region (fig.331i). Thus, the **R1d**-sclerotisations of *Polyphaga* have become rather fragmented (3 sclerites) and far removed from each other (as the insertions of **r1** and **r6** are). However, **R1K** and **R1L** could also be new elements not homologous with sclerotisations of other Blattaria. **R1K** of *Cryptocercus* (fig.160) could well be homologous with **R1K** of *Polyphaga*. However, since **r6** is missing in *Cryptocercus*, the somewhat similar position of the sclerites is the only indication for homology.
- Further parts of the regions **R1d** and **R1v** might be included in the posterior part of **R1M**. Compared with *Cryptocercus* (fig.160, 163) or *Lamproblatta* (fig.190, 193), this would correspond to a fusion of **R1F** and **R1J** across the membrane **17** and the articulations **A8** and **A9**. This is possibly indicated by the complete loss of muscle **r3**, which in *Cryptocercus* (fig.166) and *Lamproblatta* (fig.196, 197) moves **R1F** and **R1J** upon each other: The loss of **r3** could be the consequence of such a fusion. In fig.330l, 331i, and 332i **R1d** and **R1v** are shown according to this assumption.

The posterior part of the right phallomere is assumed to be composed of the **fda**-lobe and of the **pva**-ridge (fig.136-138). Like in *Lamproblatta, Cryptocercus*, and *Tryonicus*, the ventral tooth **pia** has been lost, and its leveled vestiges are assumed to be contained in the ventral wall of **fda**.

R1M of *Ergaula* is very similar to that of *Polyphaga* but narrower (compare fig.330l and m). **R1L** and **R1K**, however, are missing. The regioning of **R1M** is assumed to be the same as in *Polyphaga*.

Anaplecta

The posterodorsal part of the right phallomere is, like in *Tryonicus, Cryptocercus*, and *Lamproblatta*, an undivided lobe (**fda** in fig.226-230; no **pia**-tooth present). In contrast to these species (with **R1F** and **R1J**), however, there is only one sclerite present (**R1N** in fig.226-230), which somewhat resembles **R1M** of *Polyphaga* (fig.134, 137). The regioning of **R1N** is assumed to be as follows (fig.331k, 332k):

- The part of **R1N** immediately posterior to articulation **A3** (fig.229) is the **R1c**-region. However, the **rge**-groove is missing.

- The extension **34** of **R1N**, which to the left of **A3** bends into the **cbe**-invagination (compare fig.229 and 230; fig.226), exactly corresponds with the **R1t**-region of the other species by its relative position, by its articulation with **R2** (**A6** in fig.226, 227, 230), and by bearing the insertion of the right part of muscle **r2** (fig.231) (compare fig.331k and 331f,h). **R1t** of *Anaplecta* is somewhat thickened to the outside (**pva**) but does not form a true ridge.
- The posterior main part of **R1N** takes the same position as the **R1J**-sclerite in *Tryonicus*, *Cryptocercus*, and *Lamproblatta* and is probably composed of the regions **R1d** and **R1v**.

R1N is assumed to have developed by a fusion of the former **R1F** and **R1J** across the membrane **17** and the articulations **A8** and **A9** (compare fig.160, 163 and 226, 229), as it has also been assumed for **R1M** of *Polyphaga* (compare fig.331i and k, 332i and k). Moreover, like in *Polyphaga*, muscle **r3** has been lost. In contrast to *Polyphaga*, however, the **R1t**-region retains the same degree of independence and the same transverse orientation as it has in e.g. *Eurycotis* and *Tryonicus*, and there are no free sclerites **R1L** and **R1K**. Thus, it is not clear if **R1N** of *Anaplecta* and **R1M** of *Polyphaga* are strictly homologous and if the fusion of the former **R1F** and **R1J** and the loss of **r3** are homologous in the two species. (Therefore the sclerites are given different names).

The muscle connecting **R3** and **R1N** (**r1** in fig.231) could be homologous with **r1** or **r5** or both muscles of *Eurycotis* (fig.79, 80) and with the **r1** of *Polyphaga* (fig.139) and the other species. Like in *Polyphaga*, the muscle will be named **r1** in *Anaplecta* (and in the other Blattellidae and Blaberidae discussed below).

Nahublattella

The posterodorsal part of the right phallomere is, like in *Anaplecta*, an undivided lobe (**fda** in fig.253, 256: no ventral tooth **pia**) with one sclerite (**R1N'**), but the **R1t'**-sclerotisation seems to be missing (compare **34** in fig.226). However, similar to the left end of **34** in *Anaplecta*, the left end of **R1N'** (**34** in fig.253) articulates with **R2'** (**A6** in fig.254, 255, 226) and curves back to the right like a hook. Therefore, the **R1t'**-region is assumed to have fused to the main part of **R1N'** lying posterior to it (fig.331l). Apart from this difference, **R1N'** of *Nahublattella* is regioned in the same way as **R1N** of *Anaplecta* (compare fig.331k and l, 332k and l). A peculiar feature of *Nahublattella* is the hinge-like shape of articulation **A3** (fig.253, 257). Muscle **r1** is certainly homologous with **r1** of *Anaplecta* (fig.231, 259). Muscle **r10** (fig.259) is specific to *Nahublattella*.

Supella

The posterodorsal part of the right phallomere is again an undivided lobe **fda** with one large sclerite **R1N'**, but **R1N'** has expanded over the whole **fda**-lobe and over the whole dorsal wall of the **cbe**-invagination. The **R1t'**-region must have been firmly integrated into this sclerotisation. Articulation **A6**, indicating the left end of the **R1t'**-region, is distinct and, like in *Nahublattella*, on the summit of **cbe** (compare fig.253, 254). A hook-like or curved sclerotisation near **A6**, however, is not present. *Supella* resembles *Nahublattella* in probably having **R1t'** completely integrated into **R1N'**, but because of the large expansion of **R1N'** in *Supella* the situations in the two species are hardly comparable.

Parcoblatta, Blaberus, and other Blattellidae and Blaberidae

The morphology of the posterodorsal part of the right phallomere of *Parcoblatta* and *Blaberus* is in some repects very different from *Anaplecta* and *Nahublattella*. Concerned are two areas, which will be discussed separately: (1) the **R1t**-region and (2) the dorsal lobe **fda**. The essence of the changes having taken place can be understood by considering the morphology of some more blattellid and blaberid species included in this investigation.

The **R1t**-region Within Blattellidae and Blaberidae the **R1t**-region (with **pva**) undergoes some changes which also involve **R2**. These developments are shown in fig.330n-s.

Anaplecta has **R1t** (fig.330n, **34** in fig.226) in the same relative position as e.g. *Tryonicus* (fig 330h): situated in the dorsal wall of **cbe**, connected with **R1c** to the right, articulated with **R2** to the left (**A6**). In contrast to *Tryonicus*, the left end of **R1t** shows the hook-like curvature, which is a derived feature.

Euphyllodromia has a similar ribbon-like sclerotisation in the dorsal wall of **cbe** (fig.330o), which by its position can be identified as the **R1t'**-region. The right end of this **R1t'** approaches, like in *Anaplecta*, the **R1c'**-sclerotisation immediately behind articulation **A3** but is narrowly separated from **R1c'** by membrane (at **cl** in fig.330o). The left end of **R1t'** shows, like in *Anaplecta*, a hook-like curvature, but this curved part is swollen to the interior of the phallomere by extensive thickening of the cuticle (**cwe** in fig.330o). Moreover, the left end of **R1t'** is not articulated with **R2'** but fused to it (at **6*** in fig.330o). Thus, the former sclerite **R1N'** has divided (at **cl**) into two new sclerites: **R1S'** (**R1t'**-region, now firmly connected with **R2'**) and **R1P'** (rest of the former **R1N'**). The separation of **R1t'** from **R1c'**, its fusion to **R2'**, and the **cwe**-thickening are derived features.

Nyctibora shows the same situation (fig.330r), but **R1t** (sclerite **R1S**) and the rest of **R1** (sclerite **R1P**) are slightly farther removed from each other. (i.e. the two points of division, called **cl** again, are farther away from each other). The **cwe**-thickening and its curvature are very distinct (fig.319).

In *Parcoblatta, Blaberus*, and *Byrsotria* the fusion of **R1t** and **R2** and the **cwe**-thickening are very similar to *Nyctibora* (fig.282, 283, 285 and 309, 310, 313), and **cwe** marks the border between **R2** and **R1t** (with **cwe** belonging to **R1t**). However, the condition of the right end of **R1t** varies: In *Parcoblatta* (fig.330q, 281, 282) this end of the **R1t**-region (sclerite **R1S**) is still free. It has been far removed from its previous point of contact with **R1c** (sclerite **R1P**) (or, in other words, **R1t** has been shortened; compare the **cl**-points in fig.330q and r). Instead, it has approached the opposite end of sclerite **R1P**.

In *Blaberus* (fig.330s, 309) and *Byrsotria* (fig.318) the **R1t'**-region is firmly connected with the rest of **R1'**. From the phylogenetic context, discussed later in 7.3., it follows that this is due to a secondary fusion of the sclerites **R1S** and **R1P** and does not correspond to the primary connection of these sclerotisations within the **R1N**-sclerite of *Anaplecta, Nahublattella*, and *Supella* (fig.226, 253, 330n,o,p). Therefore, the resulting sclerite, though having the same composition as **R1N**, is named differently: **R1T'**. (The sclerotisations contained within **R1N** and **R1T'** are homologous throughout but the sclerites themselves are not). Whether the fusion of **R1S** and **R1P** to form **R1T'** had as its starting point a similar situation as in *Nyctibora*, or if it was preceded by a shortening of **R1S** like in *Parcoblatta*, is unclear. (In the regioning of **R1T'** in fig.330s the former situation has been assumed, compare fig.330r).

The **R1t**-morphology of all these species also shows that the complete incorporation of **R1t'** into sclerite **R1N'** in *Nahublattella* and, in a different way, in *Supella* is in both cases a special derivation, and that the situations in *Euphyllodromia, Parcoblatta, Nyctibora*, and *Blaberus* are derived from a situation similar to *Anaplecta* (fig.330n), with **R1t** connected with **R1c** only at its right end.

The **pva**-ridge on **R1t** is very low in *Euphyllodromia, Parcoblatta* (fig.282), and *Nyctibora* (fig.319) and has been completely lost in *Blaberus* and *Byrsotria*.

The situation in *Nahublattella* could be interpreted in another way: That part of **R1N'** which near **A6** curves back to the right (right part of **34** in fig.253) could alone be the **R1t'**-region, which is shortened like in *Parcoblatta* and, by this, far away from **R1c'** with its right end. According to this (improbable) interpretation, the **R1'**-morphology of *Nahublattella* would be likewise much more primitive than in *Euphyllodromia, Parcoblatta, Nyctibora*, and *Blaberus*: There would be no fusion between **R1t'** and **R2'**, and **cwe** would be missing. Instead, some features would have to be regarded as derived peculiarities of *Nahublattella*: a fusion between the left end of **R1t'** and the left end of the posterior **R1N'**-sclerotisation (next to articulation **A6**); a reduction of the hook-curvature at the left end of **R1t'** (in the same area); an extreme shortening of **R1t'** (which in any case would be a parallelism as compared with *Parcoblatta*). In my view, the interpretation of **R1N'** of *Nahublattella* made above is by far more probable.

The dorsal lobe **fda** In *Parcoblatta* (fig.280, 281), *Nyctibora* (fig.319), *Byrsotria* (fig.318), and *Blaberus* (fig.308, 309) the posterodorsal part of the right phallomere is not an undivided lobe as in *Anaplecta* (**fda** in fig.226), *Nahublattella* (**fda** in fig.253), *Supella*, and *Euphyllodromia*, but it is, from posteriorly, divided into two lobes lying one above the other: **dla** (dorsally) and **fda** (ventrally).

Sclerite **R1P** of *Parcoblatta* resembles **R1N** of *Anaplecta*: Both sclerites articulate with **R3** (**A3** in fig.226, 229, 281, 284), have a similar shape, and largely occupy the walls of a posterior lobe (**fda** in fig.226, 281). Homology is assumed for **R1P** and **R1N** – minus the **R1t**-region of **R1N** (compare fig.330n and q). Consequently, the ventral lobe **fda** of *Parcoblatta* is assumedly the homologue of **fda** of *Anaplecta*. Apart from **r2** (fig.286), the right phallomere of both *Parcoblatta* and *Anaplecta* has only one further muscle (**r1** in fig.231, 286), which has the same course and is assumed to be homologous. The posterior insertion of **r1** is in the anteriormost dorsal wall of **fda** in *Anaplecta* but in the anteriormost dorsal wall of **dla** in *Parcoblatta*. Thus, it can be assumed that the **dla**-lobe is a new outfolding originating from the anterior dorsal wall of the formerly undivided **fda**. Hence, **fda** of *Parcoblatta* is not strictly homologous with the **fda** of *Anaplecta* and the other species. (Moreover, like in e.g. *Anaplecta*, the ventral **fda**-wall of *Parcoblatta* probably still contains the leveled vestiges of the **pia**-walls. Thus, the homology between the **fda** of *Parcoblatta* and the **fda** of e.g. *Eurycotis*, which has a well-developed **pia**-tooth, is not strict in even two respects).

In *Nyctibora* (fig.319) sclerite **R1P** and the **fda**- and **dla**-lobes take the same relative positions as in *Parcoblatta* (fig.280, 281). Additionally, however, there is a sclerite in the dorsal wall of **dla** (**R4** in fig.319, 330r). In *Byrsotria* (fig.318) the situation is essentially the same as in *Nyctibora*, but sclerite **R4'** is in two respects more derived: (1) It is expanded to the right and in contact with sclerite **R1T'** (**59** in fig.318). (2) The left end of **R4'** (**60** in fig.318) bends around the left edge of **dla** into its left ventral wall. In *Blaberus* (fig.308) the situation is like in *Byrsotria*, but **R4'** is even further expanded to the right and curves into the ventral wall of the right phallomere (**59** in fig.308, 309) where it closely approaches articulation **A3**. Moreover, the **dla**-lobe is extremely enlarged as compared with the **fda**-lobe (compare fig.308 and 318). In *Nyctibora, Byrsotria*, and *Blaberus* (fig.314) the posterior insertion of **r1** is, like in *Parcoblatta*, in the anteriormost dorsal **dla**-wall, but it is also on sclerite **R4**. (According to the insertion of **r1**, **R4** would have to be classified, by definition, as a **R1d**-sclerotisation. But since **R4** is most probably a new sclerite and not a split off part of **R1**, the designation **R4** is preferred).

The right phallomere of *Blaberus* has, in contrast to *Parcoblatta* and *Anaplecta*, not only the plesiomorphic muscles **r1** and **r2**, but also some further, certainly new muscles. Two of them run from **R4'** to the right ventral wall of **fda** (**r11a** and **r11b** in fig.314). One muscle having the same course is also present in *Nyctibora*. The other muscles (**r12-r18** in fig.314-317) have been found only in *Blaberus* (*Byrsotria* not studied); however, no specimen of *Blaberus* had all these muscles.

6.8. The muscles connecting the left complex and the right phallomere

The **b4**-muscles have been discussed in 6.7.1., 6.7.3., and 6.7.5., muscle **b3** of *Sphodromantis* in 6.5.

b2-muscles are present in *Sphodromantis* (fig.15), *Mantoida* (fig.49), *Polyphaga* (fig.110, 127, 141), *Lamproblatta* (fig.184, 198), and *Anaplecta* (fig.224, 232). The position of the right insertion is quite similar in all species: on the left part of **R3** in *Sphodromantis* and *Mantoida*, on the left margin of **R3** in *Polyphaga*, next to the left margin of **R3** and **R2** in *Anaplecta*, and next to the left margin of **R2** in *Lamproblatta*. That the **b2** of *Lamproblatta* and *Polyphaga* are homologous despite the somewhat different position of the right insertion is strongly suggested by the very similar position of the left insertion: in the right dorsal wall of the left complex, next to **L8** and to the insertions of **l9** and **l12**. In *Anaplecta, Mantoida*, and *Sphodromantis* the left insertion is rather different from that of *Polyphaga* and *Lamproblatta*: It is on the wall of the **vla**-lobe – near the right edge of **vla** in *Mantoida* and *Anaplecta*, and in the left anterior ventral wall of **vla** in *Sphodromantis*. The **b2** are certainly homologous in *Polyphaga* and *Lamproblatta* on the one hand and in *Mantoida* and *Sphodromantis* on the other. Whether the **b2** of these two groupings and of *Anaplecta* are homologous and whether **b2** is a muscle of the common groundplan of Blattaria and Mantodea or a derived element of these groupings is questionable.

b1-muscles are only present in Mantodea: *Sphodromantis* (fig.15, 16), *Mantoida* (fig.43). Muscle **b5** of *Nahublattella* (fig.235, 259, 261) and the muscles **b6** (fig.294, 316) and **b7** (fig.317) of *Blaberus* are certainly apomorphic muscles of these species.

6.9. The phallomero-sternal muscles

Phallomero-sternal muscles inserted on the right half of the subgenital plate have even numbers, those inserted on the left half have odd numbers. The insertions on the subgenital plate are designated as ventral, those on the phallomere complex or on the walls of the genital pouch as dorsal. The anterior margin of the subgenital plate is the whole margin between the right and left contacts between the subgenital plate and the paratergites of segment 9 (compare fig.333a). Fig.333 gives an overview and a homology hypothesis for the phallomero-sternal musculature of the species studied.

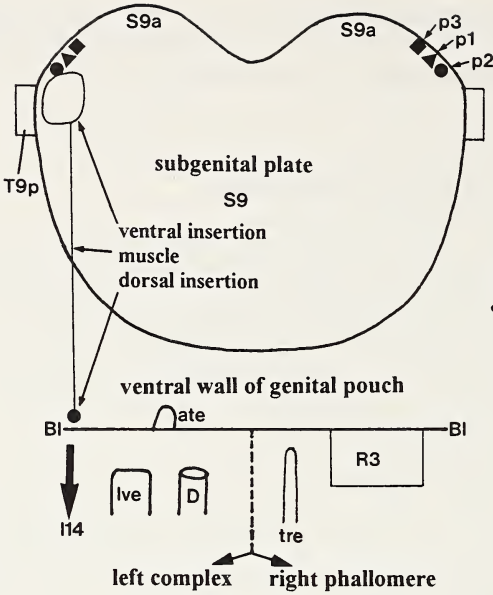
Mantoida has 6 phallomero-sternal muscles **s1-s6,** whose ventral and dorsal insertions are arranged almost symmetrically (fig.40, 333b). In my view, this is the most primitive situation within the species studied, and it is taken as the basis for the terminology. **s1** and **s2**, **s3** and **s4**, as well as **s5** and **s6** are assumed to be pairs of primitively symmetrical muscles. Thus, three pairs of **primary muscles** will be distinguished, which in the primitive situation have the following **basic arrangement**:

- **s1** and **s2** insert on the median anterior margin of the subgenital plate and run to the ventral basal line of the left complex or right phallomere, where they insert more laterally.
- **s3** and **s4** insert on the median anterior part of the subgenital plate, closely behind **s1** and **s2**, and run to the ventral basal line of the left complex or right phallomere where they insert more medially than **s1** and **s2**.
- **s5** and **s6** insert on the lateral anterior margin of the subgenital plate and run to the lateral or lateroventral walls of the genital pouch.

Within this basic arrangement, the dorsal insertion of **s2** and **s4** is on the anterior margin of sclerite **R3**, that of **s1** is on anteriormost parts of **L4**-sclerotisations (anterior **L4l**-region), and that of **s3** is on a membranous part of the basal line.

The evolution of the phallomero-sternal musculature comprises two kinds of development: (1) The morphology of the 6 **primary muscles** changes by subdivision, fusion, shift, or loss. The exact homology relations are often difficult to determine. (2) New **secondary muscles** develop, each with a characteristic course by which the homology relations can in most cases easily be determined. These secondary muscles are:

- **s7** inserts on the median anterior part of the left side of the subgenital plate and runs to the anterior part of the **lve**-pouch.
- **s8** inserts on the median anterior part of the right side of the subgenital plate and runs to the top of the **tre**-tendon.
- **s10** inserts on the median anterior part of the right side of the subgenital plate and runs to the ejaculatory duct or to an area near its opening.
- **s12** inserts on the median (or more lateral) anterior part of the right side of the subgenital



333

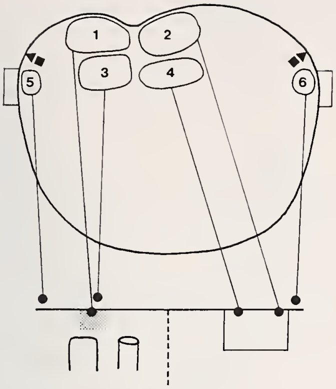
a) General scheme

Fig.333: Phallomero-sternal muscles, homology relations. – **333a** gives an overview of the mode of representation and the symbols and abbreviations used. **333b-1** (following pages) show the morphology of the various species.

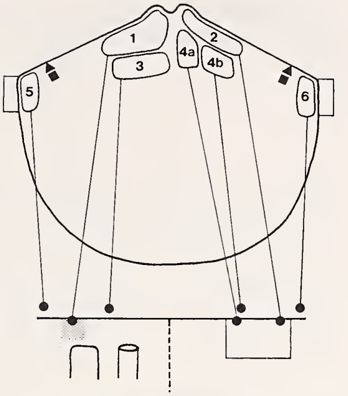
The anterior half of each figure shows the subgenital plate, with
- ventral insertions of muscles **p1, p2**, and **p3** (▲,●, and ■).
- ventral insertions of all phallomero-sternal muscles.
- paratergites of abdominal segment 9 **T9p**.

The posterior half of each figure shows the phallomere complex, with
- ventral basal line **Bl** = border between ventral + lateral walls of phallomere complex (below **Bl**) and ventral + lateral walls of genital pouch (above **Bl**).
- border between left complex and right phallomere = median vertical broken line.
- muscle **l14** (to hook **hla**; base of arrow = anterior insertion area).
- pouch **lve** (with **L2**-sclerotisations).
- ejaculatory duct **D**.
- tendon **ate**.
- tendon **tre**.
- sclerite **R3**.
- dorsal insertions of all phallomero-sternal muscles (●).
- if the dorsal insertion area of a muscle on or near the basal line of the left complex is sclerotised this is shown by a stippled field around the insertion.

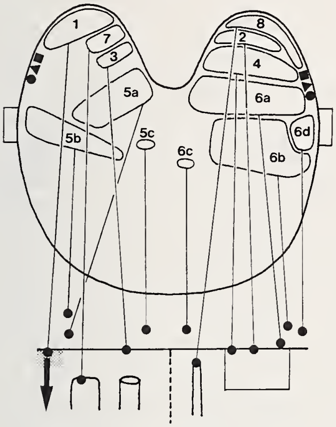
The shape of the subgenital plate is generalised, only the shape of the anterior margin (with apophyses **S9a**) corresponds with the special condition in the respective species. The numbers in the ventral insertion areas of the phallomero-sternal muscles are the numbers used in the text and in fig.1-319 to designate the muscles (e.g. **2** = **s2**, **5a** = **s5a**). Species with "S" behind their names have the phallomeres and the subgenital plate side-reversed, and a mirror-image of the original preparation is shown. Dorsal views. Further information in 6.9..



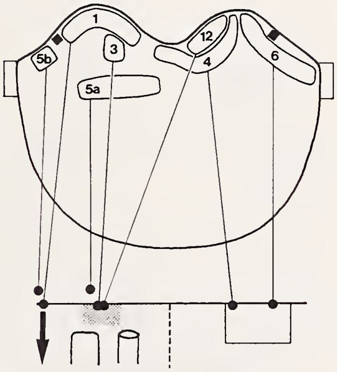
b) Mantoida schraderi



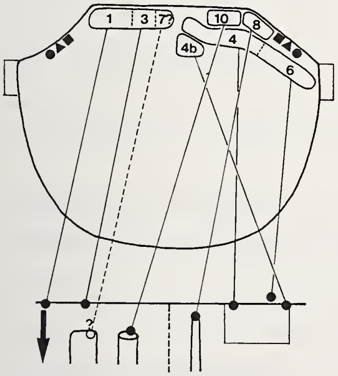
c) Sphodromantis sp.



d) Eurycotis floridana

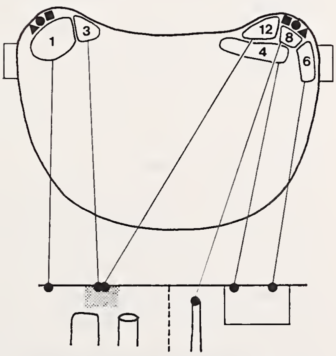


e) Lamproblatta albipalpus

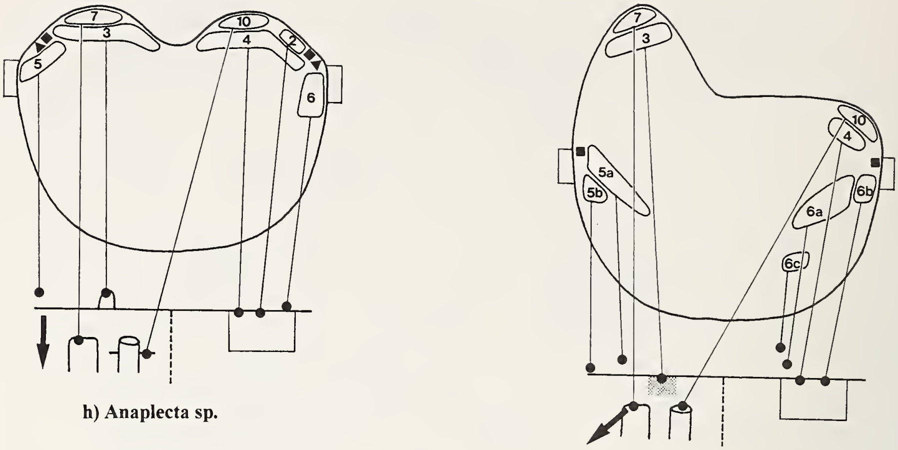


f) Cryptocercus punctulatus

333

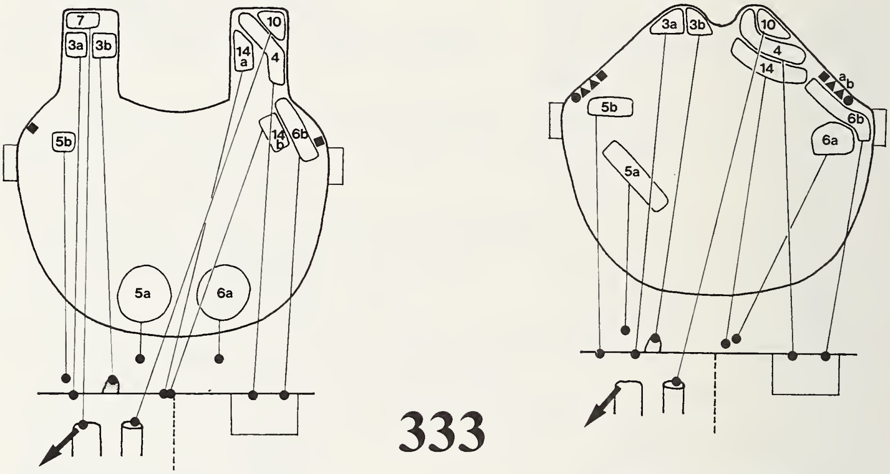


g) Polyphaga aegyptiaca



h) Anaplecta sp.

i) Nahublattella sp.^{S}



333

k) Parcoblatta lata

l) Blaberus craniifer^{S}

plate and runs to the ventral basal line of the left complex where it inserts immediately to the right of **s3**.

- **s14** inserts on the median anterior part of the right side of the subgenital plate and runs to the ventral wall of the genital pouch beneath the rightmost part of the left complex.

Mantoida and *Sphodromantis*

Mantoida (fig.40, 42, 333b) conforms with the basic arrangement, except that the dorsal insertion of **s3** is posterior (not median) to that of **s1**. *Sphodromantis* (fig.5, 7, 333c) is also close to the basic arrangement, but the right side has four muscles instead of three.

The arrangement of the insertion areas on the subgenital plate (compare **s4** in fig.40 and **s4a** and **s4b** in fig.5) and on the phallomere complex (**s4a** and **s4b** insert medially like **s4** in *Mantoida*, compare fig.7 and 42) suggests that this is due to a division of **s4**. Both species lack secondary muscles.

Eurycotis

s1, s2, s3, and **s4** conform with the basic arrangement (fig.62, 64, 333d), but **s2** is rather weak. **s5** and **s6** have divided into three (**s5a,b,c**) or four (**s6a,b,c,d**) bundles, whose insertions occupy a large area in the anterior half of the subgenital plate. However, most of these bundles are very diffuse and indistinctly bordered to each other. Moreover, it is not clear if really all these muscles are derivatives of **s5** and **s6** or if some of them are new. Of the secondary muscles **s7** and **s8** (fig.58) are present.

Anaplecta

The left side has three muscles (fig.204, 207, 333h): The secondary **s7** (fig.200) runs, like in *Eurycotis*, to the **lve**-pouch. **s5** can be identified by the lateral position of its ventral insertion and by its dorsal insertion on the lateroventral wall of the genital-pouch. The third muscle (named **s3**) might be **s1** or **s3**. It has its ventral insertion posterior to **s7** like **s3** of *Eurycotis* (**s1** of *Eurycotis* inserts anterior to **s7**, compare fig.333d and h) and has its dorsal insertion immediately anterior to **l6a** (fig.222) like **s3** in *Eurycotis* (fig.70, 73), *Polyphaga*, and *Lamproblatta* (discussion below; fig.133, 188). This muscle of *Anaplecta* is therefore regarded as **s3**; **s1** is missing.

On the right side all three primary muscles are present (**s2, s4, s6** in fig.204, 207, 333h). Their ventral insertions resemble the basic arrangement (**s2** and **s4** on the median anterior margin; **s2** anterior to **s4**; **s6** far laterally), but the **s4**-insertion is very broad, and **s2** is strongly reduced. The insertions on **R3** are side by side: **s4** on the left, **s2** in a small central area, **s6** on the right. Thus, in contrast to the basic arrangement, the dorsal insertion of **s6** has expanded to the anterior right margin of **R3** (but still occupies parts of the membranous ventral wall of the genital-pouch as well). The same is true of **s6a** of *Eurycotis* (fig.64, 333d), whose assignment to **s6** is thus confirmed by the morphology of **s6** of *Anaplecta*. Noticeably, just **s1** and **s2** have been reduced – two muscles which probably are a pair.

Apart from **s7** there is another secondary muscle: **s10**, which, however, is not directly inserted on the ejaculatory duct but more ventrally on the infolding between the lobes **vla** and **vfa** (fig.221, 222; in fig.333h this infolding is symbolised by a transverse line beneath the ejaculatory duct; compare discussion in 6.2.4.).

Lamproblatta and *Polyphaga*

On the left side, **s1** and **s3** of *Lamproblatta* (fig.173, 175, 333e) conform with the basic arrangement, but the dorsal insertion of **s1** is rather far on the left (compare *Eurycotis*, fig.70). In *Polyphaga* (fig.113, 116, 333g) both insertions of **s3** and the dorsal insertion of **s1** exactly correspond with *Lamproblatta* (**s1**: membrane anterior to the **hla**-hook, fig.127, 185), but the ventral insertion of **s1** has shifted leftward, too, and is not anterior to but to the left of **s3**. Homology can certainly be assumed for **s1** as well as for **s3**. The leftward shift of the dorsal **s1**-insertion, and that of the ventral **s1**-insertion in *Polyphaga*, might be correlated with a parallel shift of the **hla**-base from the left ventral wall (fig.65) to the left edge of the left complex (fig.117, 177). *Lamproblatta* has a lateral muscle (**s5b**) showing the **s5**-insertions of the basic arrangement. Whether another muscle having a much more median position (**s5a**) is a true part of **s5** or a new muscle is unclear. In *Polyphaga* **s5** is completely missing – possibly in consequence of the leftward shift of **s1**.

On the right side, the **s4** of *Polyphaga* and *Lamproblatta* conform with the basic arrangement and are easily identified. To the right of **s4** both species have another muscle (named **s6**) running to the anterior margin of **R3**, which might be **s2** or **s6**. Its ventral insertion is lateral (not posterior) to **s4** (fig.113, 173) and extends far laterad. This suggests it to be **s6**. Its dorsal insertion on the right anterior margin of **R3** only, not on the genital pouch, however, might suggest it to be **s2**. But since the dorsal insertion of **s6** of *Anaplecta* and *Eurycotis* has expanded to the anterior margin of **R3**, and since **s2** is small in *Eurycotis* and very small in *Anaplecta*, these muscles of *Lamproblatta* and *Polyphaga* are interpreted as **s6**; **s2** is assumed to have been lost. The restriction of the dorsal **s6**-insertion to the anterior margin of **R3** (no longer in the wall of the genital pouch) would be a derived feature of *Polyphaga* and *Lamproblatta*. (If the muscle should be **s2**, the laterad expansion of its ventral insertion would be a derived feature).

Of the secondary muscles **s12** is present (fig.133, 188): The dorsal and ventral insertions are exactly the same in both species, and, in addition, the dorsal insertion is surrounded in the same way by **s3**, **l5**, and **l6a**. **s12** is peculiar to *Lamproblatta* and *Polyphaga* (and *Ergaula*) and is assumedly a synapomorphy of these species. **s8** is present in *Polyphaga* (and *Ergaula*) but missing in *Lamproblatta*.

Cryptocercus

The left side (fig.147, 149, 333f) has only one muscle **s1+3**, with its ventral insertion along the median (not the lateral) anterior margin of the subgenital plate and its dorsal insertion only on and near the basal line (not in the more posterior walls of the genital pouch, fig.158). By this extension of the insertion areas **s5** is unlikely to contribute to this muscle and is, like in *Polyphaga*, assumed to have been lost. **s1+3** seems to be composed of the previous **s1** and **s3** since its dorsal insertion includes the areas occupied by **s1** and **s3** in *Polyphaga* and *Lamproblatta* (**s1**: anterior to the **hla**-base, compare fig.157 and 127, 185; **s3**: farther on the right, compare fig.158 and 133, 188). The dorsal insertion of **s1+3** reaches with some fibers sclerite **L2** in the **lve**-pouch; this insertion is typical for **s7**, which may therefore also contribute to **s1+3** (fig.333f).

The right side has one large primary muscle, **s2+4+6**, and, in some specimens only, a very small one, **s4b**. The ventral insertion area of the large muscle includes, in contrast to **s1+3** on the left side, the lateral anterior margin of the subgenital plate (fig.147, 333f). Thus, this muscle assumedly contains not only the median **s2** and **s4** but also the lateral **s6**. This is also suggested by the fact that the dorsal insertion (fig.168) extends far into the ventral wall of the genital pouch (compare **s6a** of *Eurycotis*, fig.64). In this latter feature *Cryptocercus* would be more primitive than *Polyphaga* and *Lamproblatta*, whose **s6**-insertion is restricted to the anterior margin of **R3**. To what extent each **s2** and **s4** contribute to the large muscle is unclear; **s2** might also be missing like in *Lamproblatta* and *Polyphaga* (as shown in fig.333f). The small **s4b** can, according to its ventral insertion posterior to the large muscle (fig.147), only be a split off part of **s4** or a new muscle but certainly not **s2**.

It is difficult to interpret this highly peculiar condition of the primary muscles. At least, the outgroup comparison between the other Blattaria and *Mantoida* strongly suggests that it is not primitive for Dictyoptera. Possibly, extensive fusions of muscles have taken place. However, there is still another possible explanation: It could be due to a retention of a nymph-like situation in adult morphology (a neotenic trait), with the differentiation of the single primary muscles not yet completed. This question could possibly be settled by an investigation of the ontogeny of the phallomero-sternal muscles in other Blattaria.

Two secondary muscles are present: **s8** to the **tre**-tendon and **s10** to the ejaculatory duct near its opening.

Nahublattella

Nahublattella (fig.237, 240, 333i) closely resembles *Anaplecta*, but the ventral insertions of the median (on the apophyses **S9a**) and of the lateral (more posteriorly on the subgenital plate) muscles are extremely far away from each other.

The secondary muscles **s7** and **s10** are easily identified by their insertions (fig.249). **s3** can, like in *Anaplecta*, be identified by its ventral insertion posterior to **s7** (compare fig.333h and i). **s1** is missing. The muscle from the right apophysis **S9a** to the anterior margin of **R3** is probably **s4**, not **s2**. (Since in *Anaplecta* **s2** is reduced, a loss of **s2** seems for *Nahublattella* more probable than a loss of **s4**).

The lateral primary muscles **s5** and **s6** have undergone a division (or new muscles have been added). The dorsal as well as the ventral insertion areas of **s5a** and **s5b** together have the same extension as those of **s5** of *Anaplecta* (compare fig.204 and 237, fig.207 and 240), and a division can readily be assumed. The same correspondence is found for the ventral insertion areas of **s6a** and **s6b** or **s6**, respectively (compare fig.204 and 237). Dorsally **s6b** of *Nahublattella* inserts on the anterior margin of **R3** like **s6** of *Anaplecta*; the dorsal insertion of **s6a**, however, is completely different (compare fig.207 and 240). Thus, for **s6a** the derivation from **s6** is not certain. The question is the same for the very delicate muscles **s6c** (fig.237, 240).

Parcoblatta and *Blaberus*

The phallomero-sternal musculature (fig.265, 267, 333k and 296, 298, 333l) can be derived from *Nahublattella* but also shows some differences.

In *Parcoblatta*, the secondary muscles **s7** and **s10** as well as the primary muscle **s4** conform with *Nahublattella*. **s3** also inserts like in *Nahublattella* but is divided into two bundles **s3a** and **s3b** (compare fig.237, 240 and 265, 267). Dorsally **s3b** inserts on the **ate**-tendon, **s3a** to the left of **ate** (fig.267). **s1** and – with the same reservations as in *Nahublattella* – **s2** are missing. Concerning these muscles, the situation in *Blaberus* is the same except that **s7** is missing. (However, **s7** is present in its typical position in *Nauphoeta*, another member of Blaberidae; fig.328i).

The lateral primary muscles of the left side (**s5**) are in *Blaberus* divided into three bundles (**s5a** – 2 bundles – and **s5b** in fig.296, 298). **s5a** and **s5b** resemble **s5a** and **s5b** of *Nahublattella* in their dorsal insertions: **s5b** near the anterior margin of **L4U'** (fig.250, 304); **s5a** in the left ventral wall of the genital pouch (fig.240, 298). The ventral insertions are similar, too, but in *Blaberus* **s5a** has shifted posteriad (fig.237, 296). The division of **s5** into **s5a** and **s5b** is assumedly homologous in *Nahublattella* and *Blaberus*. The smaller median muscle of *Blaberus*, also named **s5a**, is regarded as a median subdivision of **s5a**. In *Parcoblatta* **s5** shows a similar and certainly homologous division: The ventral and dorsal insertions of **s5b** are similar to *Blaberus* (fig.265, 267, 296, 298), but the dorsal one is somewhat more posteriorly. The ventral and dorsal insertions of **s5a** are, as compared with *Blaberus*, by far more posteriorly.

The lateral primary muscles of the right side (**s6**) are in *Blaberus* present as two bundles (**s6a** and **s6b** in fig.296, 298), which are certainly homologous with **s6a** and **s6b** of *Nahublattella*: The dorsal insertions of **s6a** and **s6b** take the same positions as in *Nahublattella* (fig.240, 298), but **s6b** has considerably expanded posteriad and now occupies the whole right margin of **R3'**. As regards the ventral insertions, **s6a** has, as compared with **s6b**, shifted far posteriad (like **s5a** on the left side!). **s6** of *Parcoblatta* shows the same division: The dorsal and ventral insertions of **s6b** are situated like in *Blaberus* (fig.265, 296), and the dorsal insertion likewise occupies the whole right margin of **R3**. The dorsal and ventral insertions of **s6a** are, as compared with *Blaberus*, shifted even farther posteriad (like those of **s5a** on the left side!).

Only *Parcoblatta* and *Blaberus* have the secondary muscle **s14**, which is divided into two bundles in *Parcoblatta* (**s14a,b**). The ventral insertion is closely behind **s4** (fig.265, 296, 333k,l). The dorsal insertion is immediately anterior to **s6a** in *Blaberus*, but, corresponding to the posteriad shift of **s6a**, far anterior to **s6a** in *Parcoblatta*.

6.10. The subgenital plate and associated structures

The subgenital plate is poor in complex structures, and hardly any character is valuable for the phylogenetic analysis in the frame of this study.

In most species the subgenital plate is asymmetrical, but the degree of asymmetry varies, and various parts are concerned: mainly the styli **S9s** and the dorsal sclerotisation **S9d** in *Anaplecta* (fig.204); the posterior edge of the plate in *Polyphaga* (fig.113, 114); mainly **S9d** in *Sphodromantis* (fig.5), *Lamproblatta* (fig.173), *Parcoblatta* (fig.265), and *Blaberus* (fig.296); **S9d** and the apophyses **S9a** in *Nahublattella* (fig.237, 238); the apophyses **S9a** and the lateral and posterior edges in *Mantoida* (fig.40); the whole subgenital plate in *Metallyticus* (fig.22). Only in *Chaeteessa* (fig.30), *Eurycotis* (fig.62), *Tryonicus* (fig.86), and *Cryptocercus* (fig.147) the subgenital plate is symmetrical or nearly so.

The apophyses **S9a** can be very different in their length and distinctness (compare *Chaeteessa*, fig.30, and *Parcoblatta*, fig.265). *Cryptocercus* has no apophyses at all (fig.147). As explained in 3.1., the areas designated as apophyses **S9d** are not in all species homologous in a strict sense, but short apophyses may be homologous with only the anterior parts of long apophyses. Such relations are obvious if *Parcoblatta* (fig.265) is compared with *Blaberus* (fig.296): In *Parcoblatta* the recess between the apophyses extends far beyond the insertions of **s14a**,**b** and nearly reaches the level of the **p3**-insertions. In *Blaberus* the recess does not even reach **s14**, much less **p3**. Thus, either the recess has deepened in *Parcoblatta*, or the posterior parts of the apophyses have fused with each other in *Blaberus*. To compare more distantly related species in this regard, however, is hardly possible.

The area designated as the dorsal sclerotisation **S9d** is rather variable and is certainly not strictly homologous in all species. In *Metallyticus* (fig.22), *Eurycotis* (fig.62), *Tryonicus* (fig.86), *Polyphaga* (fig.114), *Lamproblatta* (fig.173), *Anaplecta* (fig.204), *Parcoblatta* (fig.265), and *Blaberus* (fig.296) **S9d** is restricted to the more posterior part or even to the margins of the dorsal wall of the subgenital plate (= posterior ventral wall of genital pouch), and it is firmly connected with the ventral sclerotisation around the lateral and posterior edges of the plate. In *Sphodromantis* (fig.5) and *Cryptocercus* (fig.147) **S9d** is also continuous with the ventral sclerotisation but extends by far more to the anterior. In *Mantoida* (fig.40), *Chaeteessa* (fig.30), and *Nahublattella* (fig.237, 238) **S9d** also extends far anteriad but is isolated from the ventral sclerotisation. In *Nahublattella* **S9d** is highly elaborated (division, bristles, muscles **l33** and **l34**; fig.238, 240).

In several species, some patterns in the sclerotisation of the subgenital plate remind one of its presumable composition (true sternite, two coxites; compare in 3.1.) and might therefore be regarded as primitive. In *Eurycotis* (fig.62), *Polyphaga* (fig.113), *Cryptocercus* (fig.147), and *Nahublattella* (fig.237) an anterior (sternite?) and a posterior (transversely fused coxites?) sclerotisation are separated by a membranous field – except for a lengthwise connection of the lateralmost parts. In *Parcoblatta* (fig.265), *Blaberus* (fig.296), and *Lamproblatta* (fig.173; the anterior sclerotisation is very narrow) the field is no longer membranous but still distinctly weaker sclerotised than the other parts. In *Tryonicus* (fig.86) the sclerotisation is weaker in the anterior third, but there is no heavier sclerotisation along the anterior margin. In *Mantoida* such a zoning of the plate is only slightly indicated (not shown in fig.40). In the other Mantodea (fig.5, 22, 30) and in *Anaplecta* (fig.204) the sclerotisation of the subgenital plate is uniform. An interesting feature of *Cryptocercus* (fig.147) is that in the posterior part of the plate the lateral areas are distinctly heavier sclerotised than the median area; the transverse fusion of the coxites is probably not complete.

6.11. The peripheral muscles

The muscles **p1, p2**, and **p3** are, if present, always inserted close to each other on the anterior margin of the subgenital plate, between the median and the lateral primary phallomero-sternal muscles (fig.333b-l; fig.5, 40, 62, 113, 147, 173, 204, 237, 265, 296).

The **p1**-muscles are ventral muscles of segment 9. Their posterior insertions are on or close to the **Pv**-sclerites or, if separate **Pv**-sclerites are absent, on the anterior margin of the paraprocts **Pp**. The **p1** are rather weak (*Sphodromantis*, fig.1; *Mantoida*, fig.36; *Polyphaga*, fig.109) or even consist of very few fibers only (*Eurycotis*, fig.58; *Anaplecta*, fig.200; *Blaberus*, fig.293), or they are completely missing *(Lamproblatta, Nahublattella, Parcoblatta)*. In *Polyphaga, Anaplecta*, and some specimens of *Eurycotis* the **p1** are divided into two bundles on one or on both sides.

In *Blaberus* the **p1** are also divided into two bundles on each side; the one bundle shows the usual insertion on the anterior margin of the paraproct, but the other bundle inserts on its posterior margin (fig.293), and this is certainly a derived feature. According to McKittrick (1964), the posterior insertions of the ventral muscles of segment 9 take the same positions in the females of most Blaberidae, too.

In *Cryptocercus* the **p1** (fig.143a) are extremely broad. This is unlikely to be a primitive state since the **p1** are by far narrower in all other Blattaria as well as in *Mantoida* and *Sphodromantis*. In last-instar nymphs of *Blaberus* and *Eurycotis* the **p1** are by far broader than in the respective adults (though not as broad as in *Cryptocercus*). Hence, the broadness of **p1** of *Cryptocercus* might be a neotenic trait.

The **p2**-muscles are dorsoventral muscles of segment 9. They are either very delicate (*Eurycotis*, fig.58; *Polyphaga*, fig.109; *Cryptocercus*, fig.143a; *Blaberus*, fig.293) or completely missing *(Mantoida, Sphodromantis, Lamproblatta, Anaplecta, Nahublattella, Parcoblatta)*.

A special feature of *Eurycotis* is that the **p2** as well as the serially homologous muscles of abdominal segment 8 pass through two pairs of eyelets in the vasa deferentia (as shown in fig.58: **Vd**, **p2**, and **p2(8)**). Snodgrass (1937) finds such eyelets, in the same arrangement, also in *Blatta orientalis* (Blattinae); Pipa (1988), fig.7, describes eyelets for *Periplaneta americana*. I have additionally investigated the vasa deferentia of *Deropeltis, Periplaneta, Parcoblatta*, and *Blaberus*: There are no traces of eyelets in *Blaberus*. Eyelets or vestiges of them have been found in *Periplaneta, Deropeltis*, and *Parcoblatta*, but either the passage is more or less narrowed, or there is only a thickening of the vas deferens without any passage. The degree of eyelet reduction can be rather different in the four places (often asymmetrical; this was also the case in some specimens of *Eurycotis*) and in different specimens of a species. If passages were present in these species, these were never passed through by muscles (though very thin **p2** were often present). Pipa (1988), however, finds the **p2** passing through the eyelets in *Periplaneta* (**S-9** in his fig.7).

In last-instar nymphs of *Eurycotis* and *Blaberus* **p2** and **p2(8)** are by far stronger than in the adults of the same species, and they all run through eyelets in the vasa deferentia. The eyelets and their penetration by **p2** and **p2(8)** are assumed to be nymphal features, which in the adults can be retained to rather various extents (even within a single species). The same seems to be true of the muscles themselves. A far-reaching retention of these structures in the adult is thus regarded as a neotenic trait.

The **p3**-muscles (rectal muscles) are present in all species and have a similar fan-shape throughout. In *Cryptocercus* they are divided into two fans on each side.

The **p4**-muscles have their anterior insertions always far laterally on the anterior margin of tergite 9 **T9**. In many species they additionally extend onto the paratergites **T9p** (*Mantoida*, fig.36, 37; *Cryptocercus*, fig.143a; *Lamproblatta*, fig.169, 170; *Anaplecta*, fig.200, 201; *Parcoblatta*, fig.262, 263; *Blaberus*, fig.293, 294). In the latter case, except in *Cryptocercus*, the **p4** are divided into several bundles: throughout their length in *Mantoida* and *Parcoblatta*; only anteriorly in *Lamproblatta*, *Anaplecta*, and *Blaberus*.

The posterior insertions take rather different positions: on the lateral anterior margin of tergite 10 **T10** (*Cryptocercus*, fig.143a,b), or on the anterior margin of the paratergites 10 **T10p** (*Sphodromantis*, fig.1; *Mantoida*, fig.36, 37; *Parcoblatta*, fig.262, 263), or in the membrane median to **T10p** (*Anaplecta*, fig.200); in this latter case they can be far anteriorly (*Lamproblatta*, fig.169, 170; *Polyphaga*, fig.109; *Blaberus*, fig.294) or extremely far medially (left **p4** of *Eurycotis*, fig.58; *Nahublattella*, fig.235).

In *Cryptocercus* the insertion on tergite 9 and that on tergite 10 take the same relative position (compare fig.143a and b), and **p4** is clearly a dorsal muscle of segment 9. The **p4** of the other species are assumed to be the same dorsal muscles, and the posterior insertion is assumed to have undergone a ventromediad and anteriad shift which is variously pronounced in the different species. The homology of these **p4** is suggested by the constant position of the anterior insertion and by the following fact: In last-instar nymphs of *Eurycotis* and *Blaberus* the posterior **p4**-insertion is by far more laterally than in the adults; that means, it shifts mediad during late ontogeny. In the various species, the final position of the posterior **p4**-insertion in the adult might depend on the extent to which the adult character state prevails against the nymphal state. A dorsolateral position (like in *Cryptocercus*, fig.143b) is probably a neotenic trait. However, in some species this could also be a primitive feature.

In *Periplaneta americana*, whose posterior **p4**-insertions have a similar ventromedian position as in *Eurycotis* (compare fig.58), the innervation of **p4** is known (Pipa 1988): It is accomplished by a nerve-branch (the common base of **4A1c** and **4A1d** in Pipa) which innervates, apart from **p4** (**359**, **360** in Pipa), the various groups of dorsal muscles (**M** and **MDM9** in Pipa). This is consistent with the assumption that even those **p4** having their posterior insertions far medially are true, though modified, dorsal muscles.

The **p5**-muscles are dorsoventral muscles of segment 10. Dorsally they always insert on the lateral anterior margin of tergite 10 **T10**. Their ventral insertions are on or near the **Pv**-sclerites (*Eurycotis*, fig.58; *Lamproblatta*, fig.169; *Anaplecta*, fig.200; *Nahublattella*, fig.235) or, if separate **Pv**-sclerites are missing, on the anterior margin of the paraprocts **Pp** (*Sphodromantis*, fig.1; *Polyphaga*, fig.109; *Cryptocercus*, fig.143a; *Parcoblatta*, fig.262; *Blaberus*, fig.293). Hence, the position of the **p5**-insertions (**Pv**-sclerites or anterior margin of paraprocts **Pp**) differs in the same way as in the **p1**-muscles. The insertions of **p1** and **p5** suggest that in those species without separate **Pv**-sclerites the **Pv**-sclerotisations have become incorporated into the anterior part of the paraprocts. (This part of the paraprocts is then labelled **Pv** in the figures). Moreover, the insertions of **p1** and **p5** (ventral muscles of segment 9, dorsoventral muscles of segment 10) suggest that the **Pv**-sclerites (or the **Pv**-parts of the paraprocts) are sternal sclerotisations of abdominal segment 10. However, this question cannot be finally settled here.

The **p6**-muscles are dorsoventral muscles of segment 9. The dorsal insertion is always far laterally on tergite 9 **T9**. The ventral insertion is either close to the line of contact between the lateral margin of the subgenital plate and the paratergite of segment 9 **T9p** (*Eurycotis*, fig.69; *Cryptocercus*, fig.146; *Lamproblatta*, fig.172; *Anaplecta*, fig.203; left muscle of

Polyphaga, fig.112a) or slightly posterior to this area (*Mantoida*, fig.39; *Sphodromantis*, fig.4). In *Polyphaga* the ventral insertion has expanded into the lateral wall of the genital pouch (left muscle, fig.112a) or has completely shifted to this area (right muscle, fig.112b). In *Nahublattella* (fig.237), *Parcoblatta* (fig.265), and *Blaberus* (fig.296) the **p6** insert distinctly more medially on the subgenital plate.

The **p7**-muscles have their anterior insertions far medially in the membrane anterior to paraprocts and **Pv**-sclerotisations; their posterior insertions are far laterally where the paratergites 10 **T10p** meet the paraprocts **Pp** (articulations **A99**; lateral to the posterior **p1**-insertions). **p7** is well-developed in *Mantoida* (fig.37), *Sphodromantis* (fig.2), *Lamproblatta* (fig.170), and *Cryptocercus* (fig.144). In *Lamproblatta* the posterior (or lateral) insertion of the left **p7** has distinctly shifted anteriad. In *Eurycotis* **p7** is represented by only very few fibers (fig.59). In the other species no **p7** have been found.

The muscles **p8** and **p9** will not be discussed: Their homology relations are uncertain since they are not clearly distinguishable from other muscles of the anal region. The muscles **p10** of *Cryptocercus* (fig.144) are probably subdivisions of the **p5**-muscles.

The muscles **p1-p7** are certainly present in the common ground-plan of Blattaria and Mantodea. **p3** and **p5** are very uniform in the species studied. The differences in the morphology of **p1, p2**, and **p4** are assumed to be of limited value for a phylogenetic analysis, because these differences probably depend on the extent to which nymphal features are retained in the adult. As regards **p6**, the mediad shift of the ventral insertions could be a synapomorphy of the species concerned.

6.12. The terminal part of the abdomen

The homology relations of most elements of this area are quite evident and need no discussion. The homologies concerning the supraanal lobe **spl**, the epiproct **Ep**, and the tergite 10 **T10** are discussed in 3.1. The homology between the **Pv**-sclerites and the anterior part of the paraprocts **Pp** (in species without separate **Pv**-sclerites) is discussed in 6.11.. There are hardly any features valuable for a phylogenetic analysis, but the following features are worth mentioning and might gain some more value in future investigations including more species.

The area where the paraproct **Pp**, the **Pv**-sclerite, and the paratergite 10 **T10p** meet each other shows in several species some peculiarities. However, the ground-plan condition of this area is in most respects uncertain since Mantodea seem to have this area highly modified – similar to but certainly independently of certain Blattaria – and since the outgroup comparison with other Ectognatha suffers from the uncertainty of homology relations. Hence, the plesiomorphic or apomorphic nature of these peculiarities is debatable. A rather primitive condition might be assumed to be represented in e.g. *Eurycotis* (fig.59): The lateral tip of **Pp** articulates (**A99**) with the ventromedian tip of **T10p** laterally and is in close vicinity to the lateral end of a completely free **Pv** anteriorly. If the **Pv**-sclerites really represent the medially divided sternite 10 (compare in 6.11.), their complete isolation could be plesiomorphic. *Tryonicus* (fig.83), whose **Pv**-sclerites are fused to the paraprocts laterally, would then have a more derived state of this character. In the species having no separate **Pv**-sclerites by fusion to **Pp** (e.g. *Mantoida*, fig.37, *Polyphaga*, fig.110) this character would be even more derived. The fusion of the paraprocts **Pp** and the paratergites **T10p** in *Lamproblatta* (partial; fig.170), *Anaplecta, Mantoida*, and *Sphodromantis* (complete; fig.201, 37, 2), corresponding to a partial (*Lamproblatta*) or complete loss of **A99**, is certainly a derived feature. The presence of two articulations per side is peculiar to *Lamproblatta* (**A97** and **A99** in fig.169, 170). The interpretation in this species is done in accordance with *Eurycotis* (fig.59) and *Tryonicus* (fig.83): The lateral articulation is the true **A99**; **A97** is assumed to be a new articulation within the paraproct **Pp**.

In several species tergite 10 **T10** has undergone a complete longitudinal division by a median stripe of membrane (*Polyphaga*, fig.109; *Nahublattella*, fig.234; *Blaberus*, fig.293) – certainly a case of threefold parallel evolution. The membranous area **21** of *Lamproblatta* (fig.169) might represent an early stage of such a division.

The articulation **A98** between the cercal base and tergite 10 has been lost only in *Polyphaga* and *Blaberus* – certainly another case of parallel evolution.

The ventral sclerotisation of tergite 10 **T10v** is only in *Anaplecta* separated from the dorsal main part of **T10** (fig.200). However, the **T10v**-sclerites of *Anaplecta* could also be homologous with the **Cc**-sclerites of the other species (compare fig.200 and e.g. 58).

The various paired sclerites median to the cercal base (**Ca, Cb, Cc**) are certainly homologous in the way expressed by the designations. All three pairs are present only in (some) Blattaria but not in *Mantoida* and *Sphodromantis* (*Chaeteessa* and *Metallyticus* not investigated). Sclerites median to the cercal base are also present in e.g. Caelifera (Snodgrass 1935, fig.7), but whether there is any kind of homology with the Blattarian sclerites is unknown. It is therefore also unclear if some or all of these sclerites are elements of the Dictyopteran ground-plan or derived features of Blattarian subgroups or of Blattaria as a whole. **Ca**-sclerites are present in *Eurycotis* (fig.58, 59), *Tryonicus* (fig.83, 84), *Lamproblatta* (fig.169, 170), *Anaplecta* (fig.200), *Nahublattella* (fig.234, 235), and *Parcoblatta* (fig.262, 263), and they are crescent-shaped in most species. Except in *Tryonicus* and *Lamproblatta* the **Ca** extend along distinct curved **Ca**-bulges. **Cc**-sclerites are present in *Eurycotis* (fig.58, 59), *Tryonicus* (fig.83, 84), *Lamproblatta* (fig.169, 170), and possibly *Anaplecta* (fig.200: **T10v**?). **Cb**-sclerites are peculiar to *Lamproblatta* (fig.169, 170). In *Polyphaga, Cryptocercus*, and *Blaberus* all three pairs are missing, but in *Polyphaga* and *Blaberus* at least the **Ca**-bulges are distinct.

A distinct supraanal lobe **spl** has been found in Mantodea (fig.1, 36) and in *Eurycotis, Tryonicus, Cryptocercus, Lamproblatta, Parcoblatta*, and *Blaberus* (fig.58, 83, 143a, 169, 262, 293). An epiproct **Ep** is present in Mantodea (fig.1, 36) but never in Blattaria.

6.13. The asymmetry of the phallomere complex

The right phallomeres of the Mantodean species, especially *Chaeteessa*, and of *Eurycotis* are very similar in the arrangement of the sclerotisations (**R1**, **R2**), the formative elements (invagination **cbe**, lobe **fda**, tooth **pia**, ridge **pva**, apodeme **age**), the main muscles (**r1,**

r2, r3, s2, s4), and some morphological details (keel **3**, edge **16**). The right phallomeres of all other Blattaria studied can be derived from that of *Eurycotis* without any problems; especially the area comprising sclerites **R2** and **R3**, invagination **cbe**, and muscle **r2** is very similar in all species. Therefore, homology is assumed for all these right phallomeres. This assumption also includes those species with the right phallomere situated on the left side (*Nahublattella, Supella, Euphyllodromia, Byrsotria*, and *Blaberus* investigated in this paper): The right phallomeres of these species can be integrated into the homology hypothesis without any problems, and the right phallomeres of *Blaberus* and *Byrsotria* (situated on the left side) and the right phallomere of *Nyctibora* (situated on the right side) are nearly identical. (The only principal difference is the fusion of **R1P** and **R1S** to form **R1T** in the two blaberid species).

The left complexes of *Mantoida* and of *Archiblatta* and *Eurycotis* are quite similar in the principal arrangement of the sclerotisations (**L1, L2, L4**), the formative elements (e.g. pouches **lve** and **pne**, ventral lobe **vla**, apodeme **swe**, processes **paa** and **pda**), the main muscles (**l2, l3, l4, l6, l9, s1, s3**), the genital opening, and some morphological details (**L4d**-region). Most of the morphological gaps between these species are bridged by other Blattaria, e.g. *Tryonicus* (shape of **paa** and **pda** and relation between them), *Polyphaga* (shape of sclerites **L1** and **L2**, position of phallomere-gland opening), or *Cryptocercus* (muscle **l1**). The left complexes of the other Blattaria (e.g. *Parcoblatta*) can be extremely different from those of *Archiblatta* and *Eurycotis*, but the morphology of each species can, if several other species are included in the comparison, be traced back to the basic pattern. Therefore, homology is assumed for all these left complexes. This assumption likewise includes those species with the left complex situated on the right side (*Nahublattella, Supella, Euphyllodromia, Blaptica, Nauphoeta*, and *Blaberus* investigated in this paper): The left complexes of these species can be integrated into the homology hypothesis without any problems. The left complex of *Blaberus* (situated on the right side) and the left complex of *Parcoblatta* (situated on the left side) are very similar; concerned are the principal arrangement and shape of most cuticular elements, the course of most muscles, as well as many details (**ate**-tendon, **hge**-groove, notch **45**). Differences between *Blaberus* and *Parcoblatta* are in most cases bridged by other species of Blattellidae and Blaberidae: *Loboptera* and *Nyctibora* (orientation as in *Parcoblatta*) have, like *Blaberus*, a sclerite **L4U**, which is missing in *Parcoblatta*. *Nauphoeta* (orientation as in *Blaberus*) has, like *Parcoblatta*, a muscle **s7**, which is missing in *Blaberus*. The **lve**-apodeme and the **via**-process of *Nyctibora* (orientation as in *Parcoblatta*) and *Nauphoeta* (orientation as in *Blaberus*) are very similar and do not show the strong differences as present between *Parcoblatta* and *Blaberus* (which are due to the differently directed rotation of this area).

From the homology of the right phallomeres and from that of the left complexes it follows that the asymmetry of the whole phallomere complex is homologous in all species studied. Thus, the asymmetry of the phallomere complex is a feature of the common ground-plan of Blattaria and Mantodea (and maybe Isoptera). Moreover, from a comparison of the ground-plan morphologies of the left complex (fig.321e,g) and of the right phallomere (fig.321f,h) it follows that the asymmetry of the phallomere complex was in the common ground-plan of Blattaria and Mantodea already as extreme and of the same very special kind as in the extant species. For the investigated members of Plectopterinae

(Nahublattella, Euphyllodromia, Supella) and Blaberidae *(Nauphoeta, Byrsotria, Blaptica, Blaberus)* it is thus evident that the phallomere complex has undergone a change of its left-right-asymmetry (like a mirror-image): This hypothesis first proposed by Bohn (1987) is strongly supported, and many new arguments are now available. According to e.g. Bohn (1987), the phallomere complex of most species of *Ectobius* (Ectobiinae) is normally orientated, but some species show the same orientation as Blaberidae. The latter species, as compared with the former, clearly show that a reversal of the left-right-asymmetry must be regarded as a possible evolutionary pathway.

Vestiges of a bilateral symmetry or side-homologies within the phallomere complex are revealed in only very few respects: (1) The primary phallomero-sternal muscles **s1** and **s2** are assumed to be side-homologous (e.g. fig.37), and side-homology might also be assumed for the areas of their dorsal insertions. In the primitive case (compare in 6.9.) these are the anterior **L4l**-region on the left side and the anterior margin of **R3** on the right side. These two areas have additionally in common that the margin of the sclerotisation is more or less groove- or beam-like (apodemes **swe** or **age**). (2) The transverse phallomere muscles (**b**-muscles) might be assumed to have primitively a symmetrical course, and their left and right insertion areas might be side-homologous. The situation in *Mantoida* might be interpreted in this way: The insertions of muscle **b1** (fig.43) are next to those of the side-homologous **s3** (left side) and **s4** (right side), and the resulting side-homology would again concern the (median) anterior margins of **R3** and **L4**. (3) The dorsal transverse muscles **b4a** and **b4b** (fig.48, 58, 109) have their right insertions close to each other, but the left insertions are quite distant from each other. From their course it can be at most deduced that there is some kind of side-homology between the dorsomedian parts of the left complex and of the right phallomere. As regards the remaining parts of the right phallomere and of the left complex, there are in no species any similarities in the positions, in the special shapes, or in the muscular connections of elements which show similar spatial interrelationships on both sides. Hence, no further side-homologies can be reliably assumed.

The primary phallic lobes of nymphal Blattaria and Mantodea are certainly homologous with those of the other Ectognatha (in a more or less strict sense). In most other Ectognatha (also in the most primitive: Archaeognatha, Zygentoma) the external genitalia developing from these phallic lobes are bilaterally symmetrical. Hence, the male external genitalia have certainly been bilaterally symmetrical in some early members of the common stem-group of Blattaria and Mantodea. However, from this it cannot be concluded that there must be extensive vestiges of this bilateral symmetry in the sclerotisations, in the formative elements, or in the musculature of the phallomere complex of the extant species (or of the later members of the common stem-group): The sclerotisations, muscles, and formative elements present in the common ground-plan of Blattaria and Mantodea (or more or less extensive parts of them) might have evolved later – at a time when the extreme asymmetry had already established. Nothing is known about homology relations between these Dictyopteran phallomere elements and the elements of the male genitalia in other insect groups, and hence there is no information about which elements have already been present when the Dictyoptera branched off from their (unknown; Kristensen 1995) sister-group.

7. THE GROUND-PLAN AND THE EVOLUTION OF THE PHALLOMERE COMPLEX AND THE PHYLOGENY OF BLATTARIA AND MANTODEA

In the sections of chapter 6 many features of the common ground-plan of Blattaria and Mantodea have been reconstructed. This ground-plan will be given completely in 7.1.

In 7.2. and 7.3. the evolution of the phallomere complex will be described for Mantodea and for Blattaria. This will be done in accordance with a phylogenetic hypothesis which results as the most parsimonious solution from the distribution of the phallomere character states analysed in chapter 6. In this description, all derived character states present in the various subgroups will be listed, and these derivations are regarded as autapomorphies of the respective subgroups. For each autapomorphy the section of chapter 6. in which the respective feature has been discussed will be given. Most of the phallomere characters are consistent with each other in the distribution of their states over the subgroups defined in 7.2. and 7.3., and this phylogenetic hypothesis is thus highly supported. Some derived character states which appear as autapomorphies of single species in the frame of the sample of species included in this investigation and which are uninformative in the present analysis will also be mentioned, since in later investigations they might be detected in other species, too, and might then serve as synapomorphies and help in integrating further species into this phylogenetic hypothesis.

A survey of all assumed aut/synapomorphies is given in 7.4. – together with a phylogenetic tree (diagram 1) showing the most parsimonious solution.

For some characters the polarity of the states does not become unambiguously clear from the discussions and informations given in chapter 6, and the respective interpretations given in 7.1.-7.4. are not yet sufficiently substantiated. The evolution of these characters and the polarity of their states will be discussed in 7.5. The single topics will be designated with letters and referred to in 7.2. and 7.3.

For some characters there will, despite the previous discussions, remain some doubt in terms of polarity. In some other characters whose polarity is rather clear the distribution of the character states over the species is in some way inconsistent with the phylogenetic hypothesis in 7.2. and 7.3. The respective (possibly or clearly) derived character states and the groupings they would suggest will be listed in 7.6. All these inconsistencies will be also mentioned in 7.2. and 7.3.

In the following discussions, assemblages of species regarded as holophyletic are called “subgroups” and numbered according to their hierarchy. Assemblages not regarded as holophyletic are called “groupings” and are designated with capital letters for cross reference. The character states which are assumed to be autapomorphies of subgroups, and also the character states whose role as possible autapomorphies is discussed but regarded as improbable, are, for easy reference, numbered (bold printed and put in brackets, e.g. (**45**)).

7.1. The common ground-plan of the phallomere complex of Blattaria and Mantodea

Fig.321a-p shows the cuticular elements and the muscles of the phallomere complex and of the other parts of the male postabdomen as they have assumedly been in this ground-plan. For some characters, however, the ground-plan state could not be resolved, since

- the respective elements are (probably) present in the ground-plan of Blattaria but completely absent in Mantodea: presence or absence of **hla**-hook, **nla**-process, **dca**-processes, **tre**-tendon, sclerites **L3** and **R2**, articulations **A6**, **A7**, **A8**, and **A9**, muscles **l14**, **r6**, **s7**, and **s8**.
- the respective elements are present in the ground-plan of Mantodea but completely absent in Blattaria: presence or absence of muscles **r4** and **b1**.
- the condition of the respective elements is different in the ground-plan of Mantodea and in that of Blattaria: connection or separation of the **L4**-sclerotisations **L4v/L4c**, **L4l**, and **L4n** in the anterior ventral wall of the left complex; presence or absence of the curvature (dorsad and back to the left) of the right parts of **L2** and **lve**; connection or separation of the **R1**-regions **R1d** and **R1v** posterior to the membranous area **17**.
- the homology relations between Blattaria and Mantodea or within Blattaria are questionable: presence or absence of **loa**-process, **L5**-sclerite, **L4c**-region, muscles **l7**, **l13/b3**, and **b2**.

In fig.321 the elements or properties concerned are omitted or supplied with question-marks. As regards all the data in 7.1., compare in 6.1.2., 6.2.2., 6.3.2., 6.4.2., 6.5., 6.7.2., 6.8., 6.9., and 7.5.

Cuticular elements

Left complex

L1 is an undivided sclerite in the central dorsal wall of the left complex. A large anterior part of **L1** (**L1a**-region) is situated in a deep and distinct **pne**-pouch and is hood-shaped (but not plateau-like anteriorly). The right posterior part of **L1** is a distinct arm-like extension (**L1m**-region). There is possibly another arm-like extension formed by the left posterior part of **L1** (**L1l**-region). **L1l** and **L1m** do not join each other ventrally to form a sclerite-ring (no region **L1r**). The membranous part of the **pne**-wall has a roughly dorsal position and receives the opening of the phallomere-gland **P**. A completely sclerotised **loa**-process is probably present. Whether there are **dca**-processes is not decidable (omitted in fig.321).

The pouch **lve** lies ventral to the **pne**-pouch. **L2** is an undivided arch-shaped sclerite which extends along the edges **7** of the **lve**-pouch and is (almost) completely restricted to its dorsal wall. Whether the right parts of **lve** and **L2** are level or curved dorsad and back to the left is not decidable (curvature omitted in fig.321). The right end of **L2**, or its dorsal left end if the right parts of **L2** are up- and recurved, (**L2m**-region) shows a narrow (not hinge-like) articulation **A2** with **L1m**. The left end of **L2** (**L2p**-region) leaves the **lve**-pouch posteriorly, bends into the dorsal wall, and forms the sclerotisation of the **paa**-process (**L2d**-region). **paa** is completely sclerotised, short, and somewhat upcurved. The ventral wall of the **lve**-pouch is mostly membranous and is at the same time the left anterior part of the dorsal wall of the **vla**-lobe. The ejaculatory duct **D** opens into the right anterior part of the dorsal **vla**-wall. Both the presence of a small sclerite **L5** in the dorsal **vla**-wall and, if present, its exact position are questionable.

The ventral wall of **vla** is part of the ventral wall of the left complex and is sclerotised by the right posterior part of **L4** (**L4v**-region). The ventral wall of **vla** is for most or all of its length confluent with the remaining ventral wall of the left complex (i.e. only most posteriorly **vla** has a free left edge **61**, or edge **61** is missing). The **lve**-pouch and the **vla**-lobe are rather broad but do not reach the left edge of the left complex.

The **L4**-sclerotisations as a whole form an arch (open posteriorly) in the ventral wall and at the left edge of the left complex. The **L4**-regions **L4l**, **L4d**, **L4n**, and **L4v** (and possibly **L4c**) are present. The ventral wall between these regions is membranous. The morphology of the **L4l**- and **L4d**-regions is like in *Mantoida* and *Archiblatta*: **L4l** is undivided and extends over the left anterior margin and the whole left edge of the left complex. In the dorsal wall **L4l** is restricted to the left margin. The posteriormost part of **L4l** sclerotises a short bulge-like process **pda**, which takes a position immediately to the left of the **paa**-process and whose sclerotisation is connected with the **L2d**-sclerotisation of **paa**. The **swe**-apodeme extends over most of the length of **L4l**. In its anterior part **swe** is beam-shaped by cuticular thickening, in its posterior part it is groove-like. **L4d** is distinctly prominent from the outline of **L4l** and directed to the right (and possibly slightly anteriad). The **L4n**-region is present; whether it is connected with or separated from the **L4l**-region cannot be decided. The **nla**-process on **L4n** is possibly also present (according to its functional correlation with **l14** and **hla**; discussion in 7.5. (**M**), (**N**)). Whether the **L4c**-region is present is not decidable. (If it should be present, it is certainly firmly connected with the **L4v**-region right-posterior to it. At least, there is no separate sclerite **L4F**). Whether the **L4v**-region (or the **L4c**-region, if present) is connected with or separated from the anterior end of the **L4l**-region is unclear. The **hla**-hook and its **L3**-sclerite are probably present. If this is true, the ground-plan condition of **hla** and **L3** can be assumed to correspond with the ground-plan situation in Blattaria (compare in 7.3.).

Right phallomere

Sclerite **R3** lies more or less transversely in the anteriormost ventral wall. At least its right margin and the right part of its anterior margin form a groove- (or somewhat beam-) like apodeme **age**, which reaches the **A3**-articulation. The **age**-groove bears a keel **3**. The right posterior end of **R3** has an articulation **A3** with the **R1c**-region. Posterior to **R3** the ventral wall of the right phallomere curves dorsad and somewhat anteriad to form a large invagination **cbe**.

The posterior part of the right phallomere is composed of a dorsal lobe **fda** and of a ventral tooth **pia**. **fda** and **pia** are confluent along the right edge of the right phallomere and diverge to the left. **R1** is probably an undivided sclerite (or, with less probability, it is divided into three sclerites **R1F**, **R1G**, and **R1H**, corresponding to the regions **R1c+R1t**, **R1v**, and **R1d**, by the articulations **A8** and **A9**). **R1** occupies the area behind the **A3**-articulation (**R1c**-region), part of the right-dorsal wall of the **cbe**-invagination (**R1t**-

region), the dorsal (and possibly part of the ventral) wall of **fda** (**R1d**-region), and the dorsal and ventral walls of **pia** (**R1v**-region). The regions **R1c** and **R1t** form a distinct angle along the edge **16**. Along its posterior margin **R1t** has a posteriad-directed ridge **pva**. At and near the posterior right edge of the right phallomere there is a membranous area **17**. The dorsal and ventral parts of **R1** are (probably) connected anterior to this area but separated (or only narrowly connected) posterior to it.

The presence of sclerite **R2** and of its articulations **A6** and **A7** is questionable. The membranous stripe **4** and probably the articulations **A8** and **A9** and the **tre**-tendon are missing.

Musculature

Muscles certainly present in the ground-plan (all shown in fig.321l-p)

l1: from the dorsal wall of the **pne**-pouch to the **L4d**-region (6.1.1., 6.3.4.).

l2: from sclerite **L1** in the left wall of the **pne**-pouch to the **swe**-apodeme on the **L4l**-region (6.1.1., 6.3.1.).

l3: from sclerite **L1** in the posterior ventral wall of the **pne**-pouch to the **L2a**-region in the anterior dorsal wall of the **lve**-pouch (6.1.1., 6.2.1.).

l4: from the **L2a**-region anteriorly in the **lve**-pouch to the **swe**-apodeme on the **L4l**-region (insertion on **swe** ventral to **l2**) (6.2.1., 6.3.1.).

l5: from the anterior ventral wall of the left complex to the left(-anterior) edge of the **lve**-pouch (6.2.1.).

l6a: from the anterior ventral wall of the left complex to the right(-anterior) edge of the **lve**-pouch (6.2.1.).

l6b: from the ventral wall of the left complex to the membranous ventral wall of the **lve**-pouch at or near the genital opening (ventral insertion posterior to **l6a**) (6.2.1.).

l9: transversely within the dorsal wall of the left complex (6.5.).

b4a, **b4b**: connect the dorsal parts of the left complex and of the right phallomere; left insertions in the right marginal area of the **lve**-pouch (**b4a**) or in the dorsal wall dorsal to the **pne**-pouch (**b4b**); right insertions on the dorsal anterior margin of the **fda**-lobe (on the **tre**-tendon, if it is present in the ground-plan) (6.7.1.).

r1: from the right margin of sclerite **R3** (to the right of keel **3**) to the **R1d**-region in the dorsal wall of the **fda**-lobe (6.7.1.).

r2: from sclerite **R3** to the **cbe**-invagination and the **R1t**-region (and to sclerite **R2**, if it is present in the ground-plan) (6.7.1.).

r3: from the **R1c**-region to the **R1v**-region in the dorsal wall of the **pia**-tooth (6.7.1.).

s1: from the left median anterior margin of the subgenital plate to the lateral ventral basal line of the left complex (on the **L4l**-region) (6.9.).

s2: from the right median anterior margin of the subgenital plate to the lateral ventral basal line of the right phallomere (on sclerite **R3**, to the left of keel **3**) (6.9.).

s3: from the left median anterior part of the subgenital plate (posterior to **s1**) to the median ventral basal line of the left complex (on membrane) (6.9.).

s4: from the right median anterior part of the subgenital plate (posterior to **s2**) to the median ventral basal line of the right phallomere (on sclerite **R3**) (6.9.).

s5: from the left anterior margin of the subgenital plate to the left(-ventral) wall of the genital-pouch (6.9.).

s6: from the right anterior margin of the subgenital plate to the right(-ventral) wall of the genital-pouch (6.9.).

Muscles possibly present in the ground-plan (except for **l14** omitted from fig.321l-p)

l7: longitudinally within the posterior left ventral wall of the left complex (6.5.).

l13, **b3**: from the ejaculatory duct **D** to the dorsal wall of the **vla**-lobe posterior to or to the right of the genital opening (6.5.).

l14: from the **L4n**-region on or near the **nla**-process to sclerite **L3** and the **hla**-hook (6.4.2.).

r4: from the **R1d**-region in the left dorsal wall of the **fda**-lobe to the left ventral wall of the **fda**-lobe (6.7.1., 6.7.3.).

r6: from the **R1c**-region to the **R1d**-region (6.7.1., 6.7.6.).

b1: from the left margin of sclerite **R3** to the anteriormost ventral wall of the left complex (6.8.).

b2: from the left margin of sclerite **R3** to an area next to the right end of the **lve**-pouch (6.8.).

s7: from the left anterior margin of the subgenital plate to the **lve**-pouch (6.2.4., 6.9.).

s8: from the right anterior margin of the subgenital plate to the **tre**-tendon (6.7.1., 6.9.).

Asymmetry

From the features of the ground-plans of the left complex and the right phallomere it follows that the very special kind of extreme asymmetry – corresponding to the extreme differences between these two ground-plans – is also a feature of the ground-plan.

7.2. The evolution of the phallomere complex and the phylogeny in Mantodea (= subgroup 1.)

The ground-plan of the phallomere complex of Mantodea

The features listed subsequently can be ascribed to the ground-plan of Mantodea since they are true either of all investigated species (cuticular elements) or at least of *Sphodromantis* and *Mantoida* (muscles), which are representatives of the two basal sister-groups (subgroups 1.1. and 1.2., see below). For all these features it is not clear whether they belong to the common ground-plan of Blattaria and Mantodea or whether they are autapomorphic for Mantodea.

The following elements are absent: sclerotisations **L3**, **R2**; formative elements **dca**-processes, **hla**-hook, **nla**-process, **tre**-tendon; articulations **A6**, **A7**, **A8**, **A9**; muscles **l14**, **r6**, **s7**, **s8**. The **L4**-sclerotisations **L4v/L4c**, **L4l**, and **L4n** are firmly connected with each other in the anterior ventral wall. The right parts of **L2** and **lve** are level. The **loa**-process is present. The membranous part of the **pne**-wall is right-dorsal. The regions **R1d** and **R1v** are not connected with each other posterior to the membranous area **17**. The muscles **r4** and **b1** are present.

Subgroup 1.1.: *Mantoida*

The phallomere complex of *Mantoida* is rather close to the Mantodean ground-plan but also has some derived features: On the left complex, the **L4n**-region has been lost (6.3.1., 6.3.3.). On the right phallomere, the **R1t**-region (with the **pva**-tooth) has been separated from the **R1c**-region (6.7.1., 6.7.3.; like in *Metallyticus*: compare **(G)** in 7.5. and grouping B **(123)** in 7.6.).

Subgroup 1.2.: *Chaeteessa* + *(Metallyticus* + *Sphodromantis*)

There are some conspicuous autapomorphies on the left complex: The ventral wall has developed the **L4b**-region which occupies all the interspaces between the primary **L4**-regions **L4v/L4c**, **L4n**, and **L4l** and makes the ventral wall completely, or nearly so, sclerotised (6.3.3.; in the primitive case **L4b** is distinctly weaker than the primary **L4**-regions). The **swe**-apodeme has been lost or reduced to vestiges (6.3.3.). In the dorsal wall the **L4l**-region has strongly expanded to the right (6.3.3.). The **L4d**-region, if present at all, is no longer prominent from the outline of the **L4l**-region (6.3.3.). Possibly in correlation with this expansion of **L4l**, the **pne**-pouch has rotated (clockwise as seen from behind), and the membranous part of its wall is somewhat more on its right side (6.1.3.). The distal part of the right posterior extension **L1m** of sclerite **L1** curves into the dorsal wall of the **lve**-pouch, and **L1m** and **L2** are therefore in the same plane in the area of articulation **A2** (6.1.3.). The **lve**-pouch has become distinctly narrower (6.2.3.). Sclerite **L2** in its dorsal wall has lost its primitive arch-shape (probably by a fusion of the arms of the arch, **L2p** and **L2m**) and is now ribbon- or plate-like (6.2.3.; compare (**B**) in 7.5.). At least the **paa**-process has distinctly lengthened (6.2.3.). Whether the **pda**-process has lengthened is not assessable since **pda** has been lost in *Chaeteessa*. The sclerotisations of **pda** and **paa** (or, to apply this character state also to *Chaeteessa*, the **L4**- and **L2**-sclerotisations of the corresponding area) have been separated from each other (6.2.3.; compare (**A**) in 7.5.).

On the right phallomere, the **R1c**-region has been divided by the membranous stripe **4** separating the sclerites **R1A** and **R1B** (**R1A** and **R1C** in *Metallyticus*) (6.7.1., 6.7.3.).

Subgroup 1.2.1.: *Chaeteessa*

The left complex has a membranous pouch **pbe** between the **pne**- and **lve**-pouches (fig.34). The **pda**-process has been lost (6.2.3., 6.3.3.). The **loa**-process has also been lost (assuming that at least the **loa** of *Mantoida* and *Metallyticus* + *Sphodromantis* are homologous; 6.1.3.). The **vla**-lobe has considerably broadened as compared with the narrow **lve**-pouch (fig.32), and the genital opening has come into a position far to the right of the **lve**-pouch (6.2.3.). On the right phallomere, sclerite **R3** bends to the right along its left margin (6.7.3., fig.32). The keel-apodeme **3** has been lost (6.7.3.). The utmost right-posterior part of the **age**-groove (near articulation **A3**) has been reduced (6.7.3.).

Subgroup 1.2.2.: *Metallyticus* + *Sphodromantis*

Most of the autapomorphies are on the left complex: The dorsal and ventral parts of **L4** have been separated by articulation **A1** at the left edge of the left complex, which divides the **L4l**-region (sclerites **L4A** and **L4B**; 6.3.3.). The ventral wall is uniformly sclerotised since the **L4b**-region has become as heavy as the primary **L4**-regions (6.3.3.). The **L1**-extension **L1m**, which curves into the dorsal **lve**-wall, as well as articulation **A2** have become much broader (6.1.3.). The curving part of **L1m** now also sclerotises the **afa**-process on the anterior part of the edge **1** between the **pne**- and **lve**-pouches (6.1.3.; this autapomorphy is uncertain since the homology of **afa** with the elements called **afa** in *Mantoida* and *Chaeteessa* is not certain, and since **afa** of *Metallyticus* is nothing but a shallow bulge). Sclerite **L1** is, at least in its posterior part, divided by a stripe of membrane **2** within the **L1m**-region (6.1.3.). On the right phallomere, the deepening of the left part of the **age**-groove is very abrupt – certainly also a derived condition (6.7.3.).

Subgroup 1.2.2.1.: *Metallyticus*

The restriction of **L4** (**L4B**-sclerite) to the anterior part of the dorsal wall seems to be an autapomorphy since in both *Chaeteessa* and *Sphodromantis* **L4** or **L4B** occupies the whole dorsal wall (6.3.3.). The phallomere-gland **P** has probably been lost (at least, it was not found; 6.1.3.). The **R1t**-region (with the **pva**-tooth) has separated from the **R1c**-region (6.7.1., 6.7.3.; like in *Mantoida*: compare (**G**) in 7.5. and grouping B (**123**) in 7.6.). The **R1d**-region has expanded into the ventral wall of the **pia**-tooth and has largely ousted the membranous area **17** (6.7.3.).

Subgroup 1.2.2.2.: *Sphodromantis*

There are several autapomorphies: The **L1m**-extension has become extremely broad (fig.323a; 6.1.3.). Sclerite **L1** is now completely divided by the membranous stripe **2** (sclerites **L1A** and **L1B**; 6.1.3.). The **afa**-process is highly elaborated (fig.10; 6.1.3.). The membranous part of the **pne**-wall with the phallomere-gland opening has undergone a further rotation to the ventral side of the **pne**-pouch (6.1.3.). The sclerotisation of the **loa**-process has been strongly reduced (6.1.3.). The tongue-like deepening of the anterior part of the **lve**-pouch and of **L2** to the left is certainly also a derived feature since **lve** and **L2** are narrow in both *Metallyticus* and *Chaeteessa* (6.2.3.). On the right phallomere, the crescent-like curvature and the extreme deepening of the left part of the **age**-apodeme and the resulting pouch **5** in the ventral wall of the genital pouch are derived features (fig.6; 6.7.3.). The posterior part of the **pia**-tooth and its **R1v**-sclerotisation have been reduced (6.7.3.).

LaGreca (1954) investigated the phallomeres of species of Amorphoscelididae, Eremiaphilidae, Hymenopodidae, Mantidae, and Empusidae. Not many of the characters dealt with in this chapter are recognisable in the figures of LaGreca or discussed in his text, but at least three features are present in all these species: (1) **L4** always occupies the whole ventral wall of the left complex: the **L4b**-sclerotisation is present. (2) The sclerotisations of **paa** and **pda** are always separated from each other. (3) **L4** is always divided into a dorsal (**L4B**) and a ventral (**L4A**) sclerite: the articulation **A1** is present. (1) and (2) suggest that these families all belong to subgroup 1.2.; (3) additionally suggests that they all belong to subgroup 1.2.2.

7.3. The evolution of the phallomere complex and the phylogeny in Blattaria (= subgroup 2.)

The ground-plan of the phallomere complex of Blattaria

The features listed subsequently can be ascribed to the ground-plan of Blattaria since they are true either of all investigated species or at least of representatives of the two basal sister-groups (subgroups 2.1. and 2.2., see below). For all these features, except for the last-mentioned (reduction of muscle **s2**), it is not clear whether they belong to the common ground-plan of Blattaria and Mantodea or whether they are autapomorphic for Blattaria.

The following elements or properties are assumed to be present in the ground-plan since they are found in all Blattaria: sclerotisations **L3**, **R2**; formative element **hla**-hook. The **L4v**-region (in close connection with the **L4c**-region, if **L4c** is present) is separated from the regions **L4l** and **L4n**. The regions **R1d** and **R1v** are connected with each other (narrowly in the primitive case) posterior to the membranous area **17**.

The following elements or properties occur only in part of the investigated species but are assumed to be present in the ground-plan since they are found in representatives of the two basal sister-groups: formative elements **dca**-processes, **nla**-process, **tre**-tendon, **rge**-groove; articulations **A6**, **A7**, **A8**, **A9**; muscles **l14**, **r6**, **s7**, and **s8**. The right parts of **L2** and of the **lve**-pouch curve dorsad and back to the left. The base of the **hla**-hook is in the left anterior ventral wall of the left complex, and the introversible membranous basal part **30** of **hla** is narrow. The **dca** are two membranous cushions posterior to **L1**.

Another ground-plan feature of Blattaria might be that muscle **s2** is distinctly thinner than its left counterpart **s1** (6.9.); this situation is distinct in *Eurycotis* (fig.62: **s2** weak), *Polyphaga*, and *Lamproblatta* (fig.113, 173: **s2** lost). In *Cryptocercus* the condition of **s2** is not assessable; in *Anaplecta, Nahublattella, Parcoblatta*, and *Blaberus* **s2** is also weak or absent, but, in addition, **s1** has been completely lost. The situation in the Mantodean ground-plan, with **s1** and **s2** of similar stoutness (*Mantoida*, fig.37, 40), is regarded as more primitive than in all Blattaria since both muscles as well as their symmetry are preserved. An asymmetry in the stoutness of **s1** and **s2** is assumed to be an autapomorphy of Blattaria.

Subgroup 2.1.: *Archiblatta* + *Eurycotis* (and *Periplaneta, Blatta, Deropeltis*)

Periplaneta, Deropeltis, and *Blatta* have been studied only in part, but at least all the derived features listed subsequently are also present in these species. The muscles have not been studied in *Archiblatta*.

Most of the autapomorphies are on the left complex: The anteroventral part of the **lve**-pouch is, like a tongue, deeply invaginated to the left (6.2.1.). The posteroventral part of the **lve**-pouch has strongly receded to the right (or is even more reduced: *Eurycotis*; 6.2.1.). Correlated with the latter feature is that the **paa**-process has shifted far to the right and is far away from the **pda**-process (6.2.1.). The sclerotisations of **pda** (**L4l**-region) and **paa** (**L2d**-region) have, possibly again in correlation with the previous feature, been separated from each other (like in some other subgroups: compare (**A**) in 7.5.; 6.2.1.). The **L4c**-region is highly elaborated (or **L4c** is as a whole an autapomorphy of this subgroup), and there is a distinct **L4F**-sclerite (6.2.1., 6.3.1.). The ventral insertions of the **l5**-muscles (**l5a** and **l5b** in *Eurycotis*) have shifted posteriad and take a position on **L4F** (6.3.1.; **l5a**,**b** could also be new muscles, but this would be a derived condition, too). The left insertion of muscle **b4b** has shifted to the top of the **pne**-pouch (6.1.4., 6.7.1.). The anterior part of sclerite **L1** (**L1a**-region) has been leveled, and muscle **l1** has been lost (6.1.4.; these two derived features, however, are also present in other subgroups of Blattaria: compare grouping M **(24)** and grouping R (**25**) in 7.6.). On the right phallomere, the **R1t**-region has enlarged and occupies most of the **cbe**-invagination including its anterior wall (6.7.4.).

Subgroup 2.1.1.: *Archiblatta*

On the left complex, the **paa**-process has lost most of its sclerotisation (**L2d**-region; 6.2.1.). On the right phallomere, the **R1t**-region has expanded to sclerotise the entire **cbe**-invagination and has developed a broad connection with sclerite **R2** (6.7.4.). Whether the condition that the anterior **L4c**-region forms an isolated sclerite **L4E** is an apomorphy of *Archiblatta* (and *Periplaneta, Blatta, Deropeltis*) or the plesiomorphic state within subgroup 2.1. is not decidable (6.3.1.).

Subgroup 2.1.2.: *Eurycotis*

As compared with *Archiblatta*, the cuticular elements of the left complex show many derived features: The **L4d**-region, if present at all, is no longer prominent from the outline of the **L4l**-region (6.3.1.). The posteroventral part of the **lve**-pouch is extremely reduced (6.2.1.). Sclerite **L2** has lost the arch-shape and is plate-like: the arms of the arch, **L2m** and **L2p**, are assumed to have fused (6.2.1.; like in the Mantodean subgroup 1.2.; compare **(B)** in 7.5.). Within the **vla**-lobe there is a deep incision **9** (6.2.1.). The **mla**-lobe covering **L4F** has evaginated from the ventral wall (6.3.1., fig.63, 69). The **pne**-pouch has become less distinct (6.1.4.). The left-dorsal wall of **pne** contains two probably new sclerites **L6A**,**B** (6.1.4., 6.5.).

As compared with *Periplaneta, Blatta*, and *Deropeltis*, the muscles also show some derived features: The right insertion of **l2** has shifted from sclerite **L1** to the adjacent membrane (6.1.4.). Muscle **l3** has divided into three bundles **l3a**,**b**,**c** (6.1.4., 6.2.1.).

The following derived features have not been investigated in the other species of subgroup 2.1., and it is unclear whether they are autapomorphies of *Eurycotis* or of a larger holophyletic group within 2.1.: **l15** (fig.70) and some muscles in the **mla**- and **vla**-lobes (**l13**-group except for **l13h**, 6.5.; **l16**, **l17**, **l18**; fig.71-73) are new. The presence of a separate muscle **r5** might also be derived (fig.80; this could be a new muscle or a split off part of **r1**).

Subgroup 2.2.: *Tryonicus + (Cryptocercus + (Lamproblatta + (Ergaula + Polyphaga))) + (Anaplecta + (Nahublattella + (Supella + (Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)))))))*

The most important synapomorphy of all these species is that the **L4l**-region reveals the same division (at **A5** or (**A5**) in fig.329e-h): As far as the various substructures are preserved, and as far as no further subdivisions of the **L4l**-region have occurred, the anteroventral part of **L4l** bears the left insertions of **l2** and **l4** and forms a sclerite (**L4K**) together with the **L4n**-region or its vestiges. The posterodorsal part contains the **pda**-sclerotisation and, at its connection with the **paa**-sclerotisation (**L2d**-region), the posterior **l10**-insertion and forms a sclerite (**L4N**) together with the **L4d**-region. The **L4l**-, **L4d**-, and **L4n**-morphology of all species comprised in this subgroup follows this description (muscles not known in *Tryonicus*) or can be derived from this situation (6.3.1., 6.3.4.). (This division is completely different from the division of the **L4l**-region in the Mantodean subgroup 1.2.2. where the **l2**- and **l4**-insertions are together with **L4d** on the dorsal **L4B** and the **pda**-sclerotisations together with the **L4n**-region on the ventral **L4A**; fig.329c).

Additionally, the **swe**-apodeme has been completely lost (6.3.1., 6.3.4.). (**swe** has also been reduced in the Mantodean subgroup 1.2. The loss might be correlated with the division of **L4l** in both groups, for which region there is now no longer any need to be stiffened. For *Chaeteessa*, however, this explanation does not fit).

In its ground-plan subgroup 2.2. probably possesses a muscle **l10** from the **lve**-pouch to the common sclerotisation of **paa** and **pda**. (However, this feature is not investigated in *Tryonicus*, and homology is not certain for **l10** of *Cryptocercus*. In some members of subgroup 2.2.3.2.2.2. **l10** is missing, but this is certainly a secondary loss, compare (**R**) in 7.5). **l10** might be a posterior part of the ground-plan muscle **l4**, which might have divided together with the **L4l**-region (its left insertion area); in this case, the similar division of **l4** and the shift of the posterior part of its left insertion to the **paa**- and **pda**-sclerotisation would be an autapomorphy of this subgroup.

The **L4d**-sclerotisation has rotated (counterclockwise as seen from above): In *Tryonicus* **L4d** is directed anteriad; in the other species **L4d** is directed to the left, or, after a further rotation, dorsad (*Lamproblatta*), or it has been lost (6.3.4.).

On the right phallomere, the **pia**-tooth has been lost (6.7.6.). The regions **R1d** and **R1v** have developed a broad connection at the posterior edge of the **fda**-lobe (i.e. the former sclerites **R1G** and **R1H** have broadly fused to form **R1J**; 6.7.6.). (In some more derived species **R1J** has additionally fused with **R1F**, the sclerites **R1M** or **R1N** being the results).

A possible autapomorphy is the extreme reduction of muscle **s2** (more than in the Blattarian ground-plan and in subgroup 2.1.); this feature, however, has not been investigated in *Tryonicus* and is not assessable in *Cryptocercus* (6.9.). Another possible autapomorphy is the sclerite-ring formed by the posterior part of **L1** (by the regions **L1l**, **L1m**, and **L1r**; 6.1.1., 6.1.4.; compare (**P**) in 7.5.).

For this subgroup 2.2. there are two possibilities for the next subordinate sister-group relation; both are supported by derived character states or possible autapomorphies. Hence, there is a trichotomy not resolvable with the present state of knowledge. Alternative B, followed in fig.322 and 330, might be more probable.

Alternative A: Holophyly of **Subgroup 2.2.1. + Subgroup 2.2.3.** is supported by two derived character states of the **hla**-hook: The introversible membranous basal part **30** of **hla** has become more extensive (**hla** can therefore be retracted more deeply into the left complex; 6.4.3.). The base of **hla** has shifted posteriad (6.4.3.). These two features are possibly intercorrelated (compare (**M**), (**N**) in 7.5.). A posteriad shift of the **hla**-base, however, is also present in *Cryptocercus* (fig.151; compare in 7.7.).

Alternative B: Holophyly of **Subgroup 2.2.2.** + **Subgroup 2.2.3.** is supported by three derived character states of the regions **L4l** and **L4d**: The anterior and posterior parts of the **L4l**-region (in the primitive case included in the **L4K**- and **L4N**-sclerites) are still hinged to each other in *Tryonicus* (articulation **A5**) but always far removed from each other in the species of these subgroups (6.3.4.). The utmost right-anterior part of the **L4l**-region, which in *Tryonicus* extends rightward anterior to the **L4n**-region, has been lost (6.3.4.). The **L4d**-ribbon has further rotated (counterclockwise as seen from above) and is now directed to the left. (In *Lamproblatta* **L4d** has additionally rotated into a dorsoventral orientation; in subgroup 2.2.3. **L4d** has been preserved only in *Nahublattella*; 6.3.4).

Subgroup 2.2.1.: *Tryonicus (parvus* and *angustus)*

Synapomorphies of the two species of *Tryonicus* investigated in this paper are the rotation of the **pne**-pouch (counterclockwise as seen from behind; extreme in *T. parvus*; 6.1.4.), the enlargement and plate-like condition of the **L1m**-region, and the consequently hinge-like condition of articulation **A2** (6.1.4.). The anterior part of **L1** has become level (6.1.4.; like in the subgroups 2.1. and 2.2.3.; compare grouping M (**24**) in 7.6.).

Derived features of *T. parvus* (characters not investigated in *T. angustus*) are the extension **R2m** of sclerite **R2** and the loss of the **age**-apodeme (6.7.4.; both features also in *Lamproblatta*: compare grouping G (**129**) and (**130**) in 7.6.). The sclerite bridge **L3a** which connects the **L4n**-region and **L3** and crosses the **hla**-base **30** is probably also derived (6.4.3.).

Subgroup 2.2.2.: *Cryptocercus* + *(Lamproblatta* + *(Ergaula* + *Polyphaga))*

On the left complex, sclerite **L4K** has been reduced in a specific way (6.3.4.): The parts of **L4K** which in the ground-plan of subgroup 2.2. (as in *Tryonicus*) take a position right-ventral to the **hla**-base have been lost. This concerns mainly the **L4n**-region, and the anterior insertion of **l14** (muscle lost in *Polyphaga* and *Ergaula*) is at least mostly on membrane. (In *Polyphaga* and *Ergaula* this reduced **L4K** has shifted to the ventral side of the **hla**-base). Probably in consequence of this **L4n**-reduction, the **nla**-process has been lost (6.3.4.).

Muscle **l2** shows a shift to the anterior: This concerns a gradual anteriad shift of the left insertion (6.3.4.; least distinct in *Cryptocercus*: insertion still on sclerite **L4K**, i.e. on region **L4l**) and a complete anteriad shift of the right insertion from the left wall of the **pne**-pouch to its top (6.1.4.). That the anterior face of the **pne**-pouch, i.e. of sclerite **L1**, has become plateau-like (6.1.4.; distinct in *Cryptocercus, Polyphaga*, and *Ergaula*; plateau vestigial in *Lamproblatta)* is possibly correlated with the shift of **l2** and is also assumed to be an autapomorphy of this subgroup. That this feature of **pne** is obsolete in *Lamproblatta* is assumed to be a secondarily derived condition, possibly correlated with the apomorphic right-anteriad shift of **pne** by which the insertion angle of **l2** on **pne** has become very acute.

Another possible autapomorphy might be the complete loss of muscle **s2**, which feature, however, is not assessable in *Cryptocercus* (6.9.). (The loss of **s2** in subgroup 2.2.3.2. is certainly a case of parallel evolution since **s2** is present in *Anaplecta*.)

Subgroup 2.2.2.1.: *Cryptocercus*

The left complex has several derived features: The right part of **L2**, which is upcurved in other Blattaria, has been reduced; in consequence, the respective right-dorsal part of the **lve**-pouch has been reduced, and the contact between **L2** and **L1** (articulation **A2**) has been lost (6.1.4., 6.2.4.). The left edge **61** of the **vla**-lobe has expanded almost to the anterior margin of the left complex; in consequence, the left-ventral part of the **lve**-pouch has also been extremely reduced (6.2.4.; a similar derived state is present in *Tryonicus* and in *Anaplecta*: compare grouping C (**124**) in 7.6.). The **pda**-sclerotisation (posterior **L4l**-region) has been reduced and also separated from the **paa**-sclerotisation (**L2d**-region) (6.2.4., 6.3.4.; the separation of **L4l** and **L2d** has also developed in the subgroups 1.2. and 2.1.: compare (**A**) in 7.5.). New muscles of *Cryptocercus* are **l19** (6.4.3.), **r7** (6.7.5.), **r8** (6.7.4.), and possibly **l7** (6.5., 7.1.).

There are some derived features in the phallomero-sternal and peripheral musculature: **s1** and **s3**, and probably **s7**, are fused (6.9.). **s4** and **s6**, and **s2** if present, are fused (6.9.). The **p1** are extremely broad. The posterior insertions of the **p4** are far laterally (6.11.). All these seemingly primitive features are assumed to be neotenic traits; that they are not primitive but derived results from the outgroup comparison with Mantodea. **s5** has been lost (6.9.; like in *Polyphaga* and *Ergaula*: compare grouping H (**131**) in 7.6.).

Subgroup 2.2.2.2.: *Lamproblatta + (Ergaula + Polyphaga)*

There are many autapomorphies on the left complex: **L8** is a new sclerite in the right dorsal wall, with the insertions of **l12**, **l9**, and **b2** upon it or in its immediate vicinity (6.5.). **L7** is a new sclerite on the right part of the **vla**-lobe (or on the **lba**-lobe, which is a right part of **vla**; 6.5.). The muscles **l11** (6.3.4.), **l12** (6.2.4., 6.5.), and **s12** (6.2.4., 6.3.4., 6.9.) are also peculiar to this subgroup. The **L4**-plate in the ventral **vla**-wall has expanded to include the dorsal insertion of muscle **s3** (new region **L4a**, larger sclerites **L4R** and **L4M**; 6.3.4.). The left insertion of **l2** has shifted further anteriad and away from sclerite **L4K** (or region **L4l**; 6.3.4.). The **lve**-pouch has expanded almost to the left edge of the left complex (6.2.1., 6.2.4.).

Other derived features could possibly also be autapomorphies of this subgroup: If **s2**-parts should be included in **s2+4+6** of *Cryptocercus*, **s2** would have been lost in subgroup 2.2.2.2. (6.9.). The dorsal insertion of muscle **s6** has become restricted to the anterior margin of sclerite **R3** (6.9.). (If the muscle named **s6** should be **s2**, the loss of **s6** and the laterad expansion of the ventral **s2**-insertion would be the autapomorphies). If **s7** really is a ground-plan muscle of Blattaria (compare (**L**) in 7.5.), and if vestiges of **s7** are included in **s1+3** of *Cryptocercus*, the complete loss of **s7** would also be an autapomorphy of subgroup 2.2.2.2. (6.9.). Muscle **l1** has been lost. (However, **l1** has certainly been lost several times: at least also in the subgroups 2.1., 2.2.3.1., and 2.2.3.2.2.; compare grouping R (**25**) in 7.6.)

Subgroup 2.2.2.2.1.: *Lamproblatta*

There are many derived features on the left complex. **L2** has divided into three sclerites: **L2A** in the left part of the **lve**-pouch, **L2B** in the right part of the **lve**-pouch, and **L2C** on the **paa**-process (6.2.4.). **L4N** has divided into two sclerites: **L4S** containing the **L4d**-region, **L4T** on the **pda**-process (6.3.4.). (The sclerotisations of **paa** and **pda** remain connected). Around articulation **A4** (between **L2A** and **L2B**) the **lve**-pouch has developed a deep recess (6.2.4.). The **L4d**-region has rotated into a dorsoventral orientation (6.3.4.). The processes **paa** and **pda** have elaborated the cuticular invaginations **boe** and **sbe** (fig.182). The muscles **l20**, **l21**, **l22**, **l23**, and **l24** have evolved (fig.184-188). Muscle **l4** has been lost (like in *Anaplecta*: compare grouping K **(133)** in 7.6.).

On the right phallomere, the **tre**-tendon and its muscles **b4** and **s8** have been lost (6.7.5.; like in subgroup 2.2.3.: compare **(I)** in 7.5. and grouping E **(73)** in 7.6.). The **age**-groove has been lost (6.7.4.), and sclerite **R2** bears an extension **R2m** to the left (6.7.4.; both features also in *Tryonicus*: compare grouping G **(129)** and **(130)** in 7.6.). Muscle **r1** has been lost (6.7.6.).

Subgroup 2.2.2.2.2.: *Ergaula* + *Polyphaga*

There are many autapomorphies on the left complex: Sclerite **L4K** has shifted to the posteroventral part of the **hla**-base (6.3.4.). Muscle **l14** has been lost and functionally replaced by **l4** (6.3.4., 6.4.3.). The **L4**-plate in the ventral **vla**-wall has undergone a further expansion (new region **L4x**, larger sclerite **L4M**) and includes now the left insertion area of **l2** (6.3.4.). Additionally, this **l2**-insertion has shifted further anteriad and also ventrad (6.3.4.). The cuticular area around sclerite **L7** has been elaborated as a new lobe **lba** which represents the rightmost part of the **vla**-lobe (6.5.).

On the right phallomere, the sclerites **R2** and **R3** have fused (and articulation **A7** has been lost; 6.7.4.). The large sclerite **R1M** has developed, either by a posteriad expansion of the former **R1F** alone or, more probably, by an additional fusion of **R1F** and parts of the former **R1J** (6.7.6.; with the loss of the membranous area **17** and of the articulations **A8** and **A9** as a result; compare **(H)** in 7.5.). Probably in correlation with this feature (in its latter interpretation) muscle **r3** has been lost (6.7.6.). (The fusion of **R1F** and **R1J** and the loss of **r3** have also been achieved in subgroup 2.2.3.: compare grouping F **(128)** and **(64)** in 7.6.). The **rge**-groove on the **R1c**-region has distinctly expanded posteriad (6.7.6.). The **pva**-ridge on the **R1t**-region has achieved a longitudinal orientation and has likewise expanded posteriad (6.7.6.). (That means, within the **R1M**-sclerite, as compared with the **R1F**-sclerites, the regions **R1c** and **R1t** have expanded posteriad). Sclerite **R2** has expanded to occupy most of the **cbe**-invagination and is connected with **R1t** in the dorsal wall of **cbe** (6.7.4.). The articulation **A6** between **R2** and **R1t** has been lost (6.7.4.). (Since a fusion of **R1t** and **R2** does not necessarily result in a loss of **A6** – compare *Archiblatta* in 6.7.4. – each of the two latter features is regarded as an autapomorphy of its own.)

Subgroup 2.2.2.2.2.1.: *Polyphaga*

The only derived feature known as compared with *Ergaula* is the ventral gap in the sclerite ring formed by the posterior part of **L1** (6.1.4.). **r9** is a new muscle (6.7.4.; *Ergaula* not investigated).

Subgroup 2.2.2.2.2.2.: *Ergaula (capensis* and *capucina)*

On the left complex, the anteriormost part of **L4M** has split off to form an isolated sclerite (with the insertions of **s3** and **s12**; 6.3.4.). Sclerite **L4K** has shifted somewhat farther anteriad (6.3.4.). The dorsal part of **L4K** within the **hla**-base has shortened and fused to the ventral anterior margin of sclerite **L3** (6.3.4.). Muscle **l11** has distinctly enlarged (6.3.4.; investigated only in *E. capucina*). The **paa**-process has been lost (6.3.4.). On the right phallomere, **R2** has broadened, and **R3** is now for most of its breadth confluent with **R2** (6.7.4.). The weak lines **A7*** and **13**, representing the fusion lines between **R2** and **R3** or **R2** and **R1t**, respectively, in *Polyphaga*, have been lost (6.7.4.).

Subgroup 2.2.3.: *Anaplecta* + *(Nahublattella* + *(Supella* + *(Euphyllodromia* + *(Parcoblatta* + *(Nyctibora* + *(Blaberus* + *Nauphoeta* + *Blaptica* + *Byrsotria))))))*

All these species belong to Blattellidae and Blaberidae sensu McKittrick (1964). In *Anaplecta, Nahublattella, Parcoblatta*, and *Blaberus* the whole phallomere complex has been investigated, including its muscles. In the other species only certain parts or elements have been studied, or their presence or absence has been checked (mainly the elements listed in 5.15.). It will be exactly specified which derived features are known to be present in which of these species. *Ectobius* and *Loboptera* will not be considered in the following analysis since too few features have been investigated to correctly assess and assign these species, which are probably highly modified in their phallomere morphology.

At least the following apomorphies are present in all species comprised in this subgroup: On the left complex, the introversible membranous basal part **30** of the **hla**-hook has become very extensive, and **hla** can be almost completely retracted (6.4.3.). The **hla**-base has shifted to the left posterior edge of the left complex (6.4.3.). (These two features are possibly intercorrelated; compare (**M**), (**N**) in 7.5). The left part of the left complex, which contains the **hla**-base, has been separated from the parts more to the right by the **fpe**-infolding (6.4.3.). The anterior part of the **lve**-pouch has been elaborated as a tube-like **lve**-apodeme (6.2.4.). The common sclerotisation of the processes **paa** and **pda** has become stout and ring-shaped in its basal part (6.2.4.). (The resulting very close relation of **paa** and **pda** and their sclerotisations might be the basis for the formation of the **via**-process with an elongated common basal part of **paa** and **pda** in subgroup 2.2.3.2.).

On the right phallomere, the **tre**-tendon and its muscles **b4** and **s8** have been lost (like in *Lamproblatta*: compare (**I**) in 7.5. and grouping E (**73**) in 7.6.; 6.7.5.). Sclerite **R1N** has developed by a fusion of the former **R1F** and **R1J** (6.7.6.; the loss of the membranous area **17** and of the articulations **A8** and **A9** are concomitant derivations; all regions of **R1** are now included in one sclerite, like in the common ground-plan of Blattaria and Mantodea). The loss of muscle **r3** is probably correlated with this feature (6.7.6.). (The fusion of **R1F** and **R1J** and the loss of **r3** have also been achieved in subgroup 2.2.2.2.2.: compare grouping F (**128**) and (**64**) in 7.6. and (**H**) in 7.5.). The **rge**-groove on the **R1c**-region has been lost (6.7.6.; compare (**J**) in 7.5.). The median end of the **R1t**-region has developed a hook-like curvature (6.7.6.). (This feature is absent in *Supella*; it is assumed to be rendered unrecognisable by the extreme expansion of sclerite **R1N'**. In subgroup 2.2.3.2.2.2. this curved area forms the **cwe**-thickening).

The following features have been investigated only in *Anaplecta, Nahublattella, Parcoblatta*, and *Blaberus*: Muscle **s1** has been lost (6.9.). The muscles termed **l5** in *Anaplecta* and *Nahublattella* are possibly new muscles, or they are true **l5** with the anterior insertion shifted to the **L4n**-region; in any case, one of these character states is probably apomorphic for subgroup 2.2.3. (6.2.4., 6.3.4.). (In *Parcoblatta* and *Blaberus* **l5** has been lost or integrated into **l6b**).

Subgroup 2.2.3.1.: *Anaplecta*

On the left complex, sclerite **L1** and the **dca**-processes have been lost (like in all or many species of subgroup 2.2.3.2.2., compare grouping L **(109)** and **(110)** in 7.6.; according to McKittrick (1964), however, **L1** is present in another species of *Anaplecta*; 6.1.4.). The **pne**-pouch is therefore completely membranous; it has been reduced to a shallow depression in the central dorsal wall. (**pne** has been lost completely in all or many species of subgroup 2.2.3.2.2., compare (**111**) in 7.4. and grouping L (**134**) in 7.6.; 6.1.4.). Muscle **l4** has been lost (6.2.4., 6.3.4.; like in *Lamproblatta*: compare grouping K (**133**) in 7.6.). Some membranous foldings have developed in the area of the **lve**-pouch, e.g. **vfa** and **vpe** (6.2.4.). The **gta**-process (6.2.4., fig.215) and the **vte**-tendon (fig.208) have evolved. The **L4d**-region has been lost (like in subgroup 2.2.3.2.2., compare grouping L (**95**) in 7.6.). Muscle **l1** has been lost (like in some other subgroups: compare groupings L and R **(25)** in 7.6.). **l25** and **l26** are probably muscles peculiar to *Anaplecta*. (However, **l26** might be homologous with **l6a** of *Nahublattella, Parcoblatta*, and *Blaberus*; 6.3.4.).

The firm connection between the **nla**-process and the top of the **lve**-apodeme might be autapomorphic for *Anaplecta*. According to its possible correlation with the translocation of the anterior **l14**-insertion from **nla** to the top of **lve**, however, this feature could also be an autapomorphy of the whole subgroup 2.2.3., lost again at the base of subgroup 2.2.3.2. (compare (**M**), (**N**) in 7.5.; 6.4.3.). That there are two phallomere gland openings in a rather peculiar position – possibly new organs – could also be either a derived feature of *Anaplecta* alone or an autapomorphy of subgroup 2.2.3., with a loss of one opening and a deplacement of the other at the base of subgroup 2.2.3.2. (6.6.).

Subgroup 2.2.3.2.: *Nahublattella + (Supella + (Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)))))*

At least the following apomorphies are present in all species listed: The anterior insertion of muscle **l14** has been translocated from the **L4n**-region on the **nla**-process to the **L2a**-region on top of the **lve**-apodeme (6.4.3.; or, if the homology of the **l14**-muscles should not be true, a new muscle from **L2a** to **L3** has developed). The size of the **vla**-lobe has distinctly decreased (6.2.4., 6.3.4.). The common base of the **paa**- and **pda**-processes has been elongated and forms, together with **paa** and **pda**, the **via**-process (6.2.4., 6.3.4.). The right posterior dorsal part of the left complex – the part dorsal to the right half of the **lve**-pouch – has been reduced (6.2.4.). The division of **L2** into **L2D** (within the **lve**-pouch) and **L2E** (together with **L4N** on the **via**-process) by articulation **A10** can also be regarded as an autapomorphy of this group since this situation is present in both the subordinate sister groups 2.2.3.2.1. and 2.2.3.2.2. (The absence of this division and of **A10** is regarded as a secondary loss having occurred several times within subgroup 2.2.3.2.2.: compare (**Q**) in 7.5.).

The following derived features are also assumed to be autapomorphies of subgroup 2.2.3.2. but have been investigated in sufficient detail only in *Nahublattella, Parcoblatta*, and *Blaberus*: On the left complex, **L4K** has divided into the sclerites **L4U** and **L4V** – with the **nla**-process probably still present on **L4V'** of *Nahublattella*. (In *Blaberus* and possibly also in *Parcoblatta* **L4V** has been completely lost; 6.3.4.). Sclerite **L4G** (**L4v**-region) in the ventral **vla**-wall has been lost (6.3.4.). The right insertion of muscle **l2** has shifted to the membranous basal part **30** of the **hla**-hook (6.3.4.). Muscle **l30** has developed, having a longitudinal course in the ventral wall of the left complex (6.5.). Muscle **s2** has been lost (6.9.; like in subgroup 2.2.2. or 2.2.2.2.: compare above). The muscles **s5** and **s6** have divided into **s5a** and **s5b** or **s6a** and **s6b**, respectively (or, new muscles **s5a** and **s6a** have developed; 6.9.). The **p4**-insertions on the subgenital plate have shifted mesad (6.11.).

Subgroup 2.2.3.2.1.: *Nahublattella*

On the left complex, the sclerotisation **L2E'+L4N'** of the **via**-process has been divided transversely by the membrane ring **39** (6.2.4.). The **nla**-process, if actually **nla**, has become whip-shaped (6.3.4.). The central dorsal wall contains a bristle area **35** (fig.242). The muscles **l27**, **l28**, **l29**, **l31**, **l32**, and **l35** have developed (fig.240, 249-252). On the right phallomere, sclerite **R2** has become plate-like, bearing the highly elaborated evaginations **42** and **43** (6.7.4.). The **R1t**-region has probably completely fused to the rest of sclerite **R1N'** (6.7.6.). There is a new muscle **r10** (6.7.6.). The dorsal sclerotisation **S9d** of the subgenital plate is highly elaborated, divided, and provided with the new muscles **l33** and **l34** (6.10.).

Subgroup 2.2.3.2.2.: *Supella + (Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria))))*

At least the following apomorphies are present in all species listed (with the exceptions mentioned): On the left complex, the **hla**-hook has evolved a **hge**-groove with a notch **45** in its ventral wall (6.4.3.). (In *Nyctibora* and *Nauphoeta* **hge** is not that distinct, and the notch **45** is missing; this is probably due to secondary reduction). The **ate**-tendon has become very long and narrow (6.3.4.). (That **ate** is rather short in *Blaberus, Blaptica*, and *Byrsotria* is interpreted as a secondary reduction since **ate** is very long and thin in *Nauphoeta*, and since these four species form the holophyletic subgroup 2.2.3.2.2.2.2.2.2.). Sclerite **L4V** (essentially the **L4n**-region) has been reduced to a small sclerite in the dorsal wall of the **ate**-tendon or has been completely lost (or, **L4V** has been generally lost, and the sclerite within **ate**, present only in *Parcoblatta, Nyctibora*, and *Blaptica*, is a new one; 6.3.4.). The **nla**-process has been lost (6.3.4.). The **via**-process is no longer branched, i.e. **paa** and **pda** are no longer distinct (6.2.4.). The right posterior branch of **L2**, whose distal part sclerotises the **psa**-process in *Nahublattella*, has been completely lost (6.2.4.). The **L4d**-region has been lost (6.3.4.; like in *Anaplecta*: compare grouping L (**95**) in 7.6.). The ventral extension **28** of **L2**, present in *Anaplecta* and *Nahublattella*, is lacking; this is also assumed to be a derived feature (6.2.4.; compare the possible homology of **28** and **L5**: 6.5.).

The following apomorphies have been investigated only in *Parcoblatta* and *Blaberus*; they might be autapomorphies of the whole subgroup 2.2.3.2.2. or of any subordinate subgroup containing at least *Parcoblatta* and *Blaberus*: The **age**-groove has been restricted to the anterior part of sclerite **R3**, i.e. the **age**-part along the posterior right margin of **R3** has been lost (6.7.4.). Muscle **l14** has divided into two bundles **l14a** and **l14b** (6.4.3.; this division is completely different from the division of **l14** in *Eurycotis*). Muscle **l3** has been lost (6.1.4., 6.2.4.). The muscles **l36**, **l37**, and **l38** have developed (fig.276-278, 303, 307; 6.4.3.). Muscle **l5** has been lost or integrated into **l6b** (6.2.4.). Muscle **l6a** has distinctly enlarged (6.2.4.). Muscle **s3** has divided into two bundles **s3a** and **s3b** (6.9.). The muscles **s14** or **s14a,b** are new (6.9.). The dorsal insertion of muscle **s6b** has expanded posteriad to occupy the entire right margin of sclerite **R3** (6.9.). The ventral insertions of **s5a** and **s6a** have shifted posteriad (6.9.). Some further derived features of *Parcoblatta* and *Blaberus* are also present in *Anaplecta* but not in *Nahublattella* (compare grouping L **(109)**, **(110)**, **(134)**, and **(25)** in 7.6.): Sclerite **L1**, the **dca**-process(es), and muscle **l1** have been lost. The **pne**-pouch, which has become indistinct in *Anaplecta*, has been completely lost (6.1.4.).

Subgroup 2.2.3.2.2.1.: *Supella*

Sclerite **R1N'** has extremely expanded to occupy the entire dorsal wall of the **cbe**-invagination (6.7.6.). The indistinctness of the **R1t'**-region and the lack of a hook-like curvature at the median end of **R1t'** (present in the ground-plan of subgroup 2.2.3.) are assumed to be results of this expansion.

Subgroup 2.2.3.2.2.2.: *Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)))*

All species listed share some very important derived features on the right phallomere (6.7.6.): The median ends of the **R1t**-region and of sclerite **R2** have fused: loss of articulation **A6**. (**A6** is still an articulation in *Supella*). The hook-curvature at the median end of **R1t** has been elaborated as the **cwe**-thickening. At its lateral end, **R1t** has been separated from the **R1c**-region: resulting sclerites **R1P** and **R1S**. (In *Supella* **R1c** and **R1t** are still connected with each other. In *Blaberus, Nauphoeta, Blaptica*, and *Byrsotria* **R1t** and **R1c** are also connected: sclerite **R1T'**; this situation is interpreted as a secondary fusion of these regions and as a synapomorphy of these species, which view is suggested by the assumed autapomorphies of the subgroups 2.2.3.2.2.2.2. and 2.2.3.2.2.2.2.2.).

Subgroup 2.2.3.2.2.2.1.: *Euphyllodromia*

No derived features restricted to this species have so far been found in the phallomere complex. According to the phylogenetic hypothesis presented here, the following derived features appear as autapomorphies: The **L2**-sclerotisations of the **via**-process and of the **lve**-pouch have fused secondarily (i.e. articulation **A10** has been lost). Muscle **l10** has been lost. (Both features also in some other species of subgroup 2.2.3.2.2.2.; compare (**Q**), (**R**) in 7.5.). The membranous left wall of the **lve**-pouch has deeply invaginated to the left (also in *Loboptera*; 6.2.4.).

Subgroup 2.2.3.2.2.2.2.: *Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria))*

Only two possible autapomorphies are present in the phallomere complex: First, the presence of a **dla**-lobe (6.7.6.). **dla** is clearly missing in *Supella* and *Euphyllodromia*. **dla** is also missing in *Nauphoeta*, but in this species the whole right phallomere has been strongly reduced. Second, the presence of a **tve**-tendon (6.2.4.). **tve** is absent in *Supella* and *Euphyllodromia* and present in all members of this subgroup except *Blaberus* (*Byrsotria* not investigated). The absence in *Blaberus* is regarded as a secondary loss. The holophyly of this subgroup is strongly supported by a clearly derived feature of the females: They perform a rotation of the ootheca within the vestibulum (into a horizontal orientation; McKittrick 1964; termed advanced rotation by Roth 1967). In *Supella* and *Euphyllodromia* the ootheca retains a vertical orientation till it is dropped (Roth 1967).

Subgroup 2.2.3.2.2.2.2.1.: *Parcoblatta*

Features of *Parcoblatta* which are derived as compared with all other investigated species are the **vge**-groove on the **via**-process (fig.273) and the rotation of the **via**-process and of some adjacent elements, which includes a ventrad shift of the genital opening (6.2.4.). Some other features of *Parcoblatta* are derived at least as compared with *Blaberus* (characters mostly not investigated in the other species of subgroup 2.2.3.2.2.): Sclerite **L4U** has been lost (6.3.4.). Sclerite **R2** has become distinctly curved (6.7.4.). The muscles **l39** and **l40** have developed (fig.277, 278). Muscle **s14** has divided into two bundles **s14a** and **s14b** (6.9.). The ventral insertion of muscle **l6a** and the dorsal and ventral insertions of muscles **s5a** and **s6a** have shifted very far posteriad (6.2.4., 6.9.). Further derived features are the fusion of the **L2**-sclerotisations of the **via**-process and of the **lve**-pouch and the loss of muscle **l10** (6.2.4.; both like in *Euphyllodromia* and *Blaberus*: compare (**Q**), (**R**) in 7.5.).

Subgroup 2.2.3.2.2.2.2.2.: *Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)*

This subgroup has some probably derived features on the right phallomere: There are two new sclerites, **R5** in the ventral part of the right phallomere (6.7.4.) and **R4** in the dorsal wall of the **dla**-lobe (6.7.6.). A new muscle **r11** runs from the dorsal **dla**-wall to the ventral **fda**-wall (6.7.6.).

Subgroup 2.2.3.2.2.2.2.2.1.: *Nyctibora*

No certain autapomorphies have so far been found in the phallomere complex.

Subgroup 2.2.3.2.2.2.2.2.2.: *Blaberus + Nauphoeta + Blaptica + Byrsotria*

In all listed members of this subgroup, which corresponds to the Blaberidae sensu McKittrick (1964), the **R1t'**-region (sclerite **R1S'**) and the rest of **R1'** (sclerite **R1P'**) have fused secondarily to form sclerite **R1T'**. Only in *Blaberus, Blaptica*, and *Byrsotria* the **ate**-tendon has shortened and broadened (6.3.4.; **ate** has remained long and thin in *Nauphoeta*), the **L10'**-sclerotisation has evolved (one sclerite in *Blaberus*, fig.299; many small sclerites in *Blaptica*, fig.291, and *Byrsotria*), and the **via**-process and some adjacent elements have rotated (6.2.4.; this rotation, which includes a dorsad shift of the genital opening, is most advanced in *Blaberus*).

At least *Blaberus* has developed the muscles **l41** to **l46** and **r12** to **r18** (not investigated in *Nauphoeta, Blaptica*, and *Byrsotria*) and lost muscle **s7** (6.9.; **s7** is present at least in *Nauphoeta*; not investigated in *Byrsotria* and *Blaptica*).

7.4. Survey of phylogeny and aut/synapomorphies

In this section, the character states assumed to be autapomorphies of subgroups are listed, and a phylogenetic tree is given (diagram 1). The autapomorphies are termed by bold printed numbers put in brackets. Some symbols give additional information: **!**: The same apomorphic character state has evolved in at least one other subgroup, too, and homology is not contradicted by morphological data or functional arguments but only by the distribution of the apomorphic states of other characters (i.e. by parsimony). The apomorphic state has the same number in all subgroups concerned. **?**: The position of the autapomorphy in the tree is questionable, due either to lack of investigations or to not definitely interpretable morphology. (**?** element): The homology of the named element and hence that of the respective apomorphic state in the various species included in the subgroup is questionable. // separates different conceivable morphological interpretations of character states. In the tree bold print, the brackets, and the symbols except for **?** are omitted.

The plesiomorphic character states are given in brackets, and for each state the taxon or subgroup is named within the range of which it is plesiomorphic: (1) In most cases one character state is listed which is plesiomorphic within Blattaria and Mantodea as a whole (i.e. which is present in the common ground-plan of Blattaria and Mantodea). Such a character state is preceded by "BM:" = Blattaria + Mantodea. (2) In some cases one character state is listed whose categorisation as plesiomorphic is related to the range of Blattaria, of Mantodea, or of a subgroup of Blattaria or Mantodea which is superordinate to the subgroup under consideration and includes it. Such a character state is preceded by the name of the respective superordinate subgroup or taxon, e.g. "SG2.2.:" = subgroup 2.2., "SG1.:" = Mantodea, "SG2.:" = Blattaria. This is practised if the character concerns a property of an element whose presence in the common ground-plan of Blattaria and Mantodea is uncertain, if the character is for any reason not assessable in the species outside the named subgroup or taxon, or if an exact description of the character is only possible within the named subgroup (e.g. if a sclerotisation has divided and changed its shape previously, and the character concerns a further derivation of such a sclerotisation). (3) If several states of a character form a transformation series, all states which are more plesiomorphic than the named apomorphic state are listed, and for each of them the respective subgroup is given as in (1) and (2).

Subgroup 1.2.: **(1)** Region L4b between L4-regions L4l, L4v, and L4n present (BM: L4b absent) **(2)** Apodeme swe vestigial or absent (BM: swe present along most of L4l) **(3)** Region L4l in dorsal wall extending far to the right (BM: L4l restricted to left margin of dorsal wall) **(4)** Region L4d not prominent from outline of region L4l // L4d absent (BM: L4d prominent from outline of L4l // L4d present) **(5)** Membranous part of pne-wall on right side (BM: Membranous part of pne-wall dorsal or right-dorsal) **(6)** Distal part of region L1m curving into dorsal wall of pouch lve (BM: Distal part of L1m not curving into dorsal wall of lve) **(7)** Pouch lve narrow (BM: lve moderately broad) **(8)** Sclerite L2 ribbon- or plate-like (BM: L2 arch-shaped) **(9)** Process paa long (BM: paa very short) **(10)** Sclerotisations of processes pda and paa = regions L4l and L2d separated (BM: L4l and L2d connected) **(11)** Region R1c divided by stripe 4: sclerites R1A, R1B, or R1A, R1C (BM: R1c undivided, stripe 4 absent).

Subgroup 1.2.2.: **(12)** Region L4l divided by articulation A1: sclerites L4A, L4B (BM: L4l undivided, A1 absent) **(13)** Region L4b as heavily sclerotised as L4-regions L4l, L4v, and L4n (SG1.2.: L4b weaker than L4-regions L4l, L4v, and L4n; BM: L4b absent) **(14)** Region L1m rather broad (BM: L1m very narrow) **(15)(?** afa) Region L1m occupying process afa (SG1.: afa membranous) **(16)** Region L1m divided in its posterior part by membranous stripe 2 (BM: L1m completely undivided, stripe 2 absent) **(17)** Left part of apodeme age abruptly deepened (BM: Left part of age not or gradually deepened).

Subgroup 2.1.: **(18)** Pouch lve: anteroventral part deeply invaginated to the left, posteroventral part receded to the right (BM: anterior or anteroventral part of lve not deeper invaginated to the left than posterior part, posterior or posteroventral part not receded to the right) **(19)** Process paa far on the right and far to the right of process pda (BM: paa on the left and immediately to the right of pda) **(20)** Sclerotisations of processes pda and paa = regions L4l and L2d separated (BM: L4l and L2d connected) **(21)** Sclerite L4F present (BM: L4F absent) **(22)** Ventral insertion of muscle l5 far posteriorly and on sclerite L4F // Muscle l5 present, not homologous with l5 of other subgroups (BM: Ventral insertion of l5 far anteriorly // This l5 absent) **(23)** Left insertion of muscle b4b on top of pouch pne (BM: Left insertion of muscle b4b in dorsal wall outside pouch pne) **(24)!** Region L1a level (BM: L1a hood-shaped) **(25)!** Muscle l1 absent (BM: l1 present) **(26)** Region R1t rather large, occupying entire dorsal and anterior walls of invagination cbe (BM: R1t narrow, occupying only part of dorsal wall of cbe).

Subgroup 2.2.: **(27)** Region L4l divided by articulation A5 or by a farther separation homologous with A5: sclerites L4K, L4N (BM: L4l undivided, A5 absent) **(28)** Apodeme swe absent (BM: swe present along most of L4l) **(29)?** Muscle l10 present // Muscle l4 divided into anterior and posterior (= l10) bundle and posterior bundle shifted posteriad to common sclerotisation of pda and paa (BM: l10 absent // l4 undivided and inserted on L4l left-anterior to sclerotisation of paa and pda) **(30)** Region L4d directed anteriad (BM: L4d directed to the right or right-anteriad) **(31)** Tooth pia absent (BM: pia present) **(32)** Regions R1d and R1v broadly connected posterior to membrane 17: sclerite R1J (BM: R1d and R1v not or narrowly connected posterior to membrane 17) **(33)?** Muscle s2 extremely reduced (SG2.: s2 moderately reduced; BM: s2 not reduced and as strong as s1) **(34)** Posterior part of sclerite L1 forming a ring (BM: L1 not forming a ring).

? Subgroups 2.2.1. + 2.2.3.: (35) Membranous basal part 30 of hook hla extensive, hla rather deeply retractable (SG2.: 30 very narrow, hla hardly retractable) **(36)** Base of hla in middle part of left ventral wall of left complex (SG2.: Base of hla in anterior left ventral

? Subgroups 2.2.2. + 2.2.3.: (37) Anterior and posterior parts of region L4l far separated (SG2.2.: Anterior and posterior parts of L4l separated but articulated in A5; BM: L4l undivided) **(38)** Utmost right-anterior part of region L4l absent (BM: Utmost right-anterior part of L4l present) **(39)** Region L4d directed to the left (SG2.2.: L4d directed anteriad; BM: L4d directed to the right or right-anteriad) **(29)?** Muscle l10 present // Muscle l4 divided into anterior and posterior (= l10) bundle and posterior bundle shifted posteriad to common sclerotisation of pda and paa (BM: l10 absent // l4 undivided and inserted on L4l left-anterior to sclerotisation of paa and pda) **(33)?** Muscle s2 extremely reduced (SG2.: s2 moderately reduced; BM: s2 not reduced and as strong as s1).

Subgroup 2.2.1.: (40) Membranous part of pne-wall on left side (BM: Membranous part of pne-wall dorsal or right-dorsal) **(41)** Region L1m plate-like, articulation A2 very broad (BM: L1m ribbon-like, A2 narrow) **(24)!** Region L1a level (BM: L1a hood-shaped).

Subgroup 2.2.2.: (42) Right-ventral part of sclerite L4K missing (SG2.2.: Right-ventral part of L4K present) **(43)** Process nla absent (SG2.: nla present) **(44)** Right insertion of muscle l2 on top of pouch pne (BM: Right insertion of l2 in left wall of pne) **(45)** Left insertion of muscle l2 on anterior left edge of left complex, on sclerite L4K and region L4l (BM: Left insertion of l2 in posterior two thirds of left edge of left complex, on region L4l) **(46)** Anterior face of pouch pne and sclerite L1 plateau-like (BM: Anterior face of pouch pne and of sclerite L1 pointed or ridge-like) **(47)?!** Muscle s2 absent (SG2.2.: s2 extremely reduced; SG2.: s2 moderately reduced; BM: s2 not reduced and as strong as s1).

Subgroup 2.2.2.2.: (48) Sclerite L8 present (BM: L8 absent) **(49)** Sclerite L7 present (BM: L7 absent) **(50)** Muscle l11 present (BM: l11 absent) **(51)** Muscle l12 present (BM: l12 absent) **(52)** Muscle s12 present (BM: s12 absent) **(53)** Region L4a bearing dorsal s3-insertion present (BM: L4a absent, dorsal s3-insertion on membrane) **(54)** Left insertion of muscle l2 on anterior left edge of left complex, anterior to sclerite L4K and region L4l (SG2.2.2.: Left insertion of l2 on anterior left edge of left complex, on L4K and L4l; BM: Left insertion of l2 in posterior two thirds of left edge of left complex, on L4l) **(55)** Pouch lve almost reaching left edge of left complex (BM: lve by far not reaching left edge of left complex) **(56)** Muscle s7 absent (SG2.: s7 present) **(25)!** Muscle l1 absent (BM: l1 present) **(47)?!** Muscle s2 absent (SG2.2.: s2 extremely reduced; SG2.: s2 moderately reduced; BM: s2 not reduced and as strong as s1).

Subgroup 2.2.2.2.2.: (57) (Dorsal part of) Sclerite L4K in posteroventral part of hla-base (SG2.2.2.: L4K in dorsal part of hla-base; SG2.2.: Dorsal part of L4K left-dorsal to hla-base) **(58)** Muscle l14 absent (SG2.: l14 present) **(59)** Region L4x bearing left l2-insertion present (BM: L4x absent) **(60)** Left insertion of muscle l2 in left anterior ventral wall of left complex, on region L4x (SG2.2.2.2.: Left insertion of l2 on anterior left edge of left complex, anterior to L4K and L4l; SG2.2.2.: Left insertion of l2 on anterior left edge of left complex, on L4K and L4l; BM: Left insertion of l2 in posterior two thirds of left edge of left complex, on L4l) **(61)** Lobe lba present (BM: lba absent) **(62)** Sclerites R2 and R3 fused, articulation A7 absent (SG2.: R2 and R3 separated, articulated in A7) **(63)** Regions R1t and R1c reaching far posteriad and probably fused with parts of the broadly interconnected regions R1d and R1v: articulations A8 and A9 and membranous area 17 absent; sclerite R1M (SG2.2.: R1t and R1c restricted to a more anterior area and separated from the broadly interconnected R1d and R1v: A8, A9, and 17 present; SG2.: R1t and R1c restricted to a more anterior area and separated from the narrowly interconnected R1d and R1v: A8, A9, and 17 present; BM: R1t restricted to a more anterior area and not connected with R1d or R1v; R1c restricted to a more anterior area ventrally but possibly extending more posteriad dorsally, connected with both R1d and R1v which are separated from each other: A8 and A9 absent but 17 present) **(64)!** Muscle r3 absent (BM: r3 present) **(65)** Ridge pva longitudinally orientated (BM: pva transversely or obliquely orientated) **(66)** Sclerite R2 occupying left-ventral and anterior walls of invagination cbe, broadly connected with R1t (SG2.: R2 restricted to left-ventral base of cbe, separated from R1t) **(67)** Articulation A6 absent (SG2.: A6 present).

Subgroup 2.2.3.: **(68)** Membranous basal part 30 of hook hla very extensive, hla very deeply retractable (SGs2.2.1.+2.2.3.: 30 extensive, hla rather deeply retractable; SG2.: 30 very narrow, hla hardly retractable) **(69)** Base of hook hla at left posterior edge of left complex (SGs2.2.1.+2.2.3.: Base of hla in middle part of left ventral wall; SG2.: Base of hla in anterior left ventral wall) **(70)** Infolding fpe present (BM: fpe absent) **(71)** lve-apodeme present (BM: lve-apodeme absent) **(72)** Common sclerotisation of processes paa and pda with stout basal ring (BM: Common sclerotisation of paa and pda not with stout basal ring) **(73)!** Tendon tre and muscles s8 and b4a,b absent (SG2.: tre, s8, and b4a,b present; BM: presence of tre and s8 unclear, b4a,b present) **(74)** Region R1c fused with the broadly interconnected regions R1d and R1v: articulations A8 and A9 and membranous area 17 absent; sclerite R1N (SG2.2.: R1c separated from the broadly interconnected R1d and R1v: A8, A9, and 17 present; SG2.: R1c separated from the narrowly interconnected R1d and R1v: A8, A9, and 17 present; BM: R1c connected with both R1d and R1v which are separated from each other: A8 and A9 absent but 17 present) **(64)!** Muscle r3 absent (BM: r3 present) **(75)** Groove rge absent (SG2.: rge present) **(76)** Hook-curvature on median end of region R1t present (BM: Hook-curvature on R1t absent) **(77)** Muscle s1 absent (BM: s1 present) **(78)** Ventral insertion of muscle l5 on region L4n near process nla // Muscle l5 present, not homologous with l5 of other subgroups (SG2: Ventral insertion of l5 not on L4n // This l5 absent).

Subgroup 2.2.3.2.: **(79)** Anterior insertion of muscle l14 on region L2a (SG2.: Anterior insertion of l14 on L4n) **(80)** Lobe vla small (BM: vla large) **(81)** Process via present (BM: via absent) **(82)** Right posterior dorsal part of left complex small (SG2.: Right posterior dorsal part of left complex large) **(83)** Sclerite L2 divided by articulation A10: sclerites L2D, L2E (BM: L2 undivided, A10 absent) **(84)** Sclerite L4K divided: sclerites L4U, L4V (SG2.2.: L4K undivided) **(85)** Region L4v absent (BM: L4v present) **(86)** Right insertion of muscle l2 on basal part 30 of hook hla (BM: Right insertion of l2 in left wall of pouch pne on L1) **(87)** Muscle l30 present (BM: l30 absent) **(47)!** Muscle s2 absent (SG2.2.: s2 extremely reduced; SG2.: s2 moderately reduced; BM: s2 not reduced and as strong as s1) **(88)** Muscles s5 and s6 divided into s5a,b and s6a,b (BM: s5 and s6 undivided) (**89**) Insertions of muscles p4 median to lateral margin of subgenital plate (BM: Insertions of p4 on lateral margin of subgenital plate).

Subgroup 2.2.3.2.2.: (90) Groove hge and notch 45 on hook hla present (SG2.: hge and 45 absent) **(91)** Tendon ate very long and narrow, including region L4n or the membranous area corresponding to L4n (SG2.2.3.: tendon ate short and broad, not including L4n) **(92)** Region L4n = sclerite L4V very small or absent, not forming a process nla // Region L4n and process nla absent, new sclerite L4V present (SG2.: L4n large, forming a process nla // L4n and nla present, sclerite L4V absent) **(93)** Process via unbranched, subordinate processes paa and pda not distinct (SG2.2.3.2.: via branching into distinct paa and pda; BM: via absent, paa and pda distinct) **(94)** Right posterior branch of sclerite L2 or L2D = right arm of L2-arch absent (BM: Right posterior branch of L2 = right arm of L2-arch present) **(95)!** Region L4d absent (BM: L4d present) **(96)** Extension 28 on sclerite L2 absent (SG2.2.3.: 28 present; BM: 28 or sclerite L5 possibly present).

Subgroup 2.2.3.2.2., or 2.2.3.2.2.2., or 2.2.3.2.2.2.2.: (97) That part of apodeme age along posterior right margin of sclerite R3 absent, age by far not reaching articulation A3 (BM: That part of age along posterior right margin of R3 present, age reaching A3) **(98)** Muscle l14 divided into two bundles l14a and b (SG2.: l14 undivided) **(99)** Muscle l3 absent (BM: l3 present) **(100)** Muscle l36 present (BM: l36 absent) **(101)** Muscle l37 present (BM: l37 absent) **(102)** Muscle l38 present (BM: l38 absent) **(103)** Muscle l5 absent // Muscle l5 integrated into muscle l6b (BM or SG2.2.3.: l5 present // l5 not integrated into l6b) **(104)** Muscle l6a very large (SG2.: l6a of moderate size) **(105)** Muscle s3 divided into two bundles s3a and b (BM: s3 undivided) **(106)** Muscle s14 present (BM: s14 absent) **(107)** Dorsal insertion of muscle s6b on entire right margin of sclerite R3 (SG2.2.3.2.: Dorsal insertion of s6b restricted to anterior right margin of R3; SG2.2.: Dorsal insertion of s6 restricted to anterior right margin of R3; BM: Dorsal insertion of s6 in ventral wall of genital pouch, possibly extending to anterior margin of R3) **(108)** Ventral insertions of muscles s5a and, less distinctly, s6a more posteriorly (SG2.2.3.2.: Ventral insertions of s5a and s6a more anteriorly; BM: Ventral insertions of s5 and s6 more anteriorly) **(109)!** Sclerite L1 absent (BM: L1 present) **(110)!** Process(es) dca absent (SG2.: dca present) **(25)!** Muscle l1 absent (BM: l1 present) **(111)** Pouch pne absent (BM: pne present).

Subgroup 2.2.3.2.2.2.: (112) Median ends of region R1t and sclerite R2 connected: articulation A6 absent (SG2.: Median ends of R1t and R2 separated and articulated in A6) **(113)** Thickening cwe present (BM: cwe absent) **(114)** Region R1t separated from region R1c: sclerites R1P, R1S (BM: R1t connected with R1c).

Subgroup 2.2.3.2.2.2.2.: (115) Lobe dla present (BM: dla absent) **(116)** Tendon tve present (BM: tve absent) **(117)** Females: Advanced rotation of ootheca present (BM: Advanced rotation absent).

Subgroup 2.2.3.2.2.2.2.2.: (118) Sclerite R5 present (BM: R5 absent) **(119)** Sclerite R4 present (BM: R4 absent) **(120)** Muscle r11 present (BM: r11 absent).

Subgroup 2.2.3.2.2.2.2.2.2.: (121) Region R1t connected with region R1c: sclerite R1T (SG2.2.3.2.2.2.: R1t separated from R1c; BM: R1t connected with R1c).

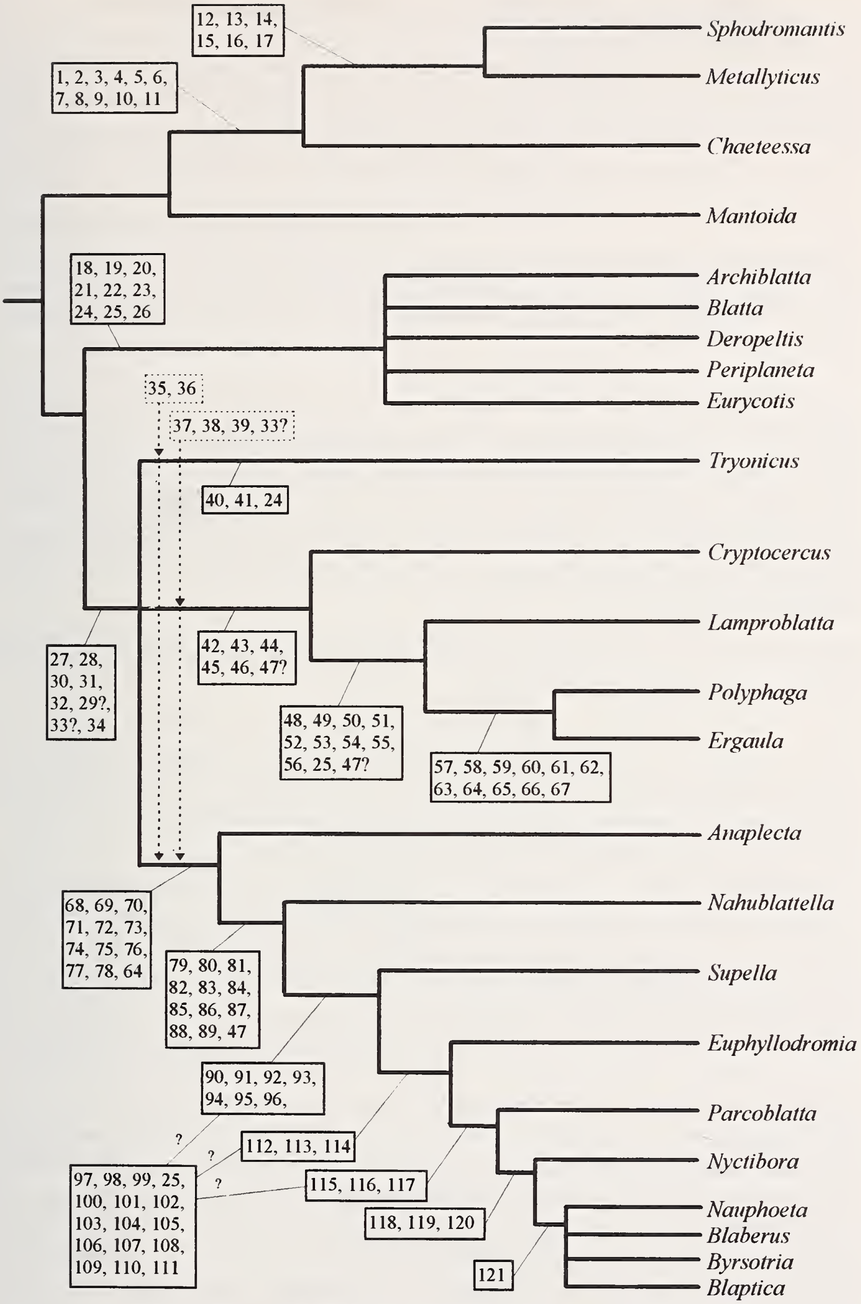


Diagram 1: Phylogenetic tree of the investigated representatives of Blattaria and Mantodea, with the assumed aut/synapomorphies

7.5. Remarks on the polarity and evolution of some characters

For some characters the polarity assumptions in 7.1.-7.4. are not yet sufficiently substantiated. In some cases the polarity question can be settled by a detailed discussion of morphology, homology, or functional intercorrelations. The respective discussions will be largely independent of the phylogenetic hypothesis in 7.4. In other cases a solution of the polarity question can only be approached by a reciprocal consideration of the various arguments or possibilities in terms of parsimony, i.e. a weighing of the various possible polarity assumptions against the assumed autapomorphies of the subgroups defined in 7.2. and 7.3. and against the outgroup comparison between Blattaria and Mantodea. The respective discussions will be done in interdependence with the phylogenetic hypothesis in 7.4.

The following discussions under **(A)**-**(C)** are concerned with the polarity of three characters for which the outgroup comparison between Blattaria and Mantodea is somewhat conflicting since the same two character states are present in Blattaria as well as in Mantodea. The question arises whether **that** character state represents the ground-plan condition which in 7.1. has been assumed to do this. (A similar conflict is also present in (**G**), which will be discussed below.) These discussions will be independent of the phylogenetic hypothesis in 7.4.

(**A**) The connection or separation of the sclerotisations **L2d** and **L4l** of the processes **paa** and **pda** and the length of **paa** and **pda**

The area bearing the **paa**- and **pda**-processes is very similar in *Mantoida* (fig.44) and *Tryonicus* (fig.91): The sclerotisations of **paa** (**L2d**-region) and **pda** (**L4l**-region) are connected; **paa** and **pda** are completely sclerotised, are bulge-like and short, **paa** being somewhat upcurved, and are close to each other. This has been regarded as the condition of the common ground-plan of Blattaria and Mantodea (6.2.1., 7.1.).

In other Blattaria (6.2.1., 6.2.4.) as well as in other Mantodea (6.2.3.) **paa** and **pda** can be longer, and their sclerotisations can be separated from each other. Alternatively, these two states could be regarded as the ground-plan states of the respective characters, but there are some arguments against this view: Within Blattaria the sclerotisations are separated in *Eurycotis* (fig.66), *Archiblatta* (fig.53), and *Cryptocercus* (fig.150). This separation is accompanied (1) by a reduction of the sclerotisation of one of the processes in *Cryptocercus* (**pda**) and in *Archiblatta* (**paa**), and (2) by a far separation of the processes themselves in *Eurycotis* and *Archiblatta*, which feature is correlated with the recess of the posterior part of the **lve**-pouch to the right (6.2.1.). These accompanying conditions in *Eurycotis, Archiblatta*, and *Cryptocercus* are clearly derived features, and the separation of the **paa**- and **pda**-sclerotisations can easily be explained as correlated with these and as being derived, too. In *Chaeteessa* (fig.34), *Metallyticus* (fig.25), and *Sphodromantis* (fig.11) the sclerotisations of **paa** and **pda** are separated from each other without being reduced (with the exception that in *Chaeteessa* the whole **pda** has been lost), and the close vicinity of **paa** and **pda** has been retained. According to these very different concomitant circumstances in *Cryptocercus*, in *Archiblatta* + *Eurycotis*, and in the respective Mantodea, the separation of the sclerotisations of **paa** and **pda** is clearly suggested to have been achieved three times independently. As regards the length of **paa** and **pda**, there are no peculiar similarities in the shape of **paa** and **pda** in the Blattaria and Mantodea with these processes being long. On the other hand, both **paa** and **pda** of *Tryonicus* and *Mantoida* are rather similar, and in my view it is the most parsimonious solution to regard this similarity as homologous and as representing the ground-plan condition.

(**B**) Sclerite **L2** arch-shaped or plate-like

In *Mantoida, Archiblatta*, and *Polyphaga* **L2** extends like an arch along the margins of the **lve**-pouch, and this has been regarded as the condition of the common ground-plan of Blattaria and Mantodea (6.2.1., 7.1.; fig.324d,f,k). A plate-like **L2**, with the arms of the arch (regions **L2p** and **L2m**) probably fused to each other, is present in *Chaeteessa, Metallyticus*, and *Sphodromantis* (6.2.3.), but also in *Eurycotis* (6.2.1.) and, more or less, in *Cryptocercus* (6.2.4.) (fig.324a,b,c,e,h). However, in *Cryptocercus* the indistinctness of the arch-shape of **L2** is due to a reduction of the right part of the **L2**-arch (**L2m**-region, area of articulation **A2**) and to a broadening of the **L2a**-region; vestiges of the arch-shape are still recognisable in this **L2**. *Eurycotis* has the posterior left-ventral part of **L2** extremely reduced. In the respective Mantodea **L2** is only narrowed, with none of its parts reduced. Thus, the morphology of **L2** and the concomitant circumstances of its plate-like condition are very different in *Eurycotis*, in *Cryptocercus*, and in the respective Mantodea, and this supports the assumption that the plate-like shape of **L2** has arisen several times by parallel evolution. Additionally, the plate-like condition is in my opinion more liable to homoplasy than the more complicated arch-shape.

(**C**) Sclerite **L5** present or absent and in various positions

As discussed in 6.5., the presence of **L5** – somewhere in the dorsal wall of the **vla**-lobe – might be the plesiomorphic state for Blattaria or even Blattaria + Mantodea, but a definite decision is not possible. The extension **28** (a ventral part of sclerite **L2**) of *Anaplecta* and *Nahublattella* is possibly homologous with **L5** (6.5.). The position of **L5** or **28** is very similar in *Polyphaga, Anaplecta*, and *Nahublattella*, but since it is not clear which position of **L5** or **28** has to be regarded as primitive, this similarity could also represent the plesiomorphic state of Blattaria or Blattaria + Mantodea. At the present state of knowledge, the characters of these sclerotisations are not yet suitable for a phylogenetic analysis since the polarity of their states remain uncertain.

The following discussions will be concerned with the polarity of some characters, termed (**D**)-(**K**) and (**L**), for which the reciprocal outgroup comparison between Blattaria and Mantodea suggests another polarity as it has been assumed in 7.1.-7.4. (or, in the case of (**G**), this outgroup comparison is conflicting in the same way as in the characters discussed under (**A**)-(**C**)). The question is whether some features present in some Blattaria but not in the other Blattaria and in Mantodea are either ground-plan features of Blattaria as stated in 7.3. or autapomorphies of Blattarian subgroups as it is suggested by the outgroup comparison. If the polarity assumptions are based on the latter alternative, then (1) the distribution of the states of the characters (**D**)-(**K**) would suggest a phylogenetic hypothesis which is roughly the reverse of the hypothesis in 7.4., and (2) the distribution of the states of character (**L**) would suggest a grouping which is inconsistent with the phylogenetic hypothesis in 7.4. as well as with the hypothesis discussed in the context of the characters (**D**)-(**K**). These possibilities have to be tested.

(**D**) The presence or absence of the curvature of the right parts of sclerite **L2** and of the **lve**-pouch

That the right parts of **L2** and of **lve** curve dorsad and back to the left (6.2.1., 6.2.4.) has been assumed to be a ground-plan feature of Blattaria. This curvature is present in *Archiblatta, Eurycotis, Tryonicus, Lamproblatta, Polyphaga, Ergaula*, and *Anaplecta* but absent in the remaining Blattaria (*Cryptocercus* and subgroup 2.2.3.2.) and in Mantodea.

(**E**) The presence or absence of the **nla**-process

The **nla**-process (6.3.1., 6.3.4.) has been assumed to be a ground-plan element of Blattaria. **nla** is present in *Eurycotis, Archiblatta, Tryonicus, Anaplecta*, and probably *Nahublattella* but absent in the remaining Blattaria (subgroups 2.2.2. and 2.2.3.2.2.) and in Mantodea.

(**F**) The presence or absence of the **dca**-processes

The **dca**-processes (6.1.1., 6.1.4.) have been assumed to be ground-plan elements of Blattaria. **dca** are present in *Eurycotis, Archiblatta, Tryonicus, Cryptocercus, Polyphaga, Ergaula, Nahublattella*, and possibly *Lamproblatta* but absent in the remaining Blattaria (*Anaplecta* and subgroup 2.2.3.2.2.) and in Mantodea.

(**G**) The connection or separation of the regions **R1t** and **R1c**

In most Blattaria and in the Mantodea *Chaeteessa* and *Sphodromantis* the regions **R1t** and **R1c** are firmly connected, and several Blattaria and *Chaeteessa* have a distinct edge **16**, which has been defined as the border between **R1t** and **R1c**. This has been regarded as the condition of the common ground-plan of Blattaria and Mantodea (6.7.1., 7.1.). In most Blattaria of subgroup 2.2.3.2.2.2. (6.7.6.) as well as in the Mantodea *Mantoida* and *Metallyticus* (6.7.3.) **R1t** and **R1c** are separated from each other.

(**H**) The connection or separation of the regions **R1c, R1d,** and **R1v** (= the absence or presence of the articulations **A8** and **A9**)

That **R1d** as well as **R1v** are separated from **R1c** by the articulations **A8** and **A9** (6.7.1., 6.7.6.), respectively, has been regarded as a ground-plan feature of Blattaria (7.3.). This separation is present in *Eurycotis, Archiblatta, Tryonicus, Lamproblatta*, and *Cryptocercus*, but in the Blattarian subgroups 2.2.2.2.2. and 2.2.3. (6.7.6.) and in the ground-plan of Mantodea (6.7.1.) the regions **R1c**, **R1d**, and **R1v** are contained in one sclerite.

(**I**) The presence or absence of the **tre**-tendon and of muscle **s8**

The **tre**-tendon (6.7.1., 6.7.5.) and the **s8**-muscle (6.9.) have been assumed to be ground-plan elements of Blattaria. **tre** and **s8** are present in *Eurycotis, Archiblatta, Tryonicus, Cryptocercus, Polyphaga*, and *Ergaula* (**s8** not studied in *Archiblatta* and *Tryonicus*) but absent in the remaining Blattaria (*Lamproblatta* and subgroup 2.2.3.) and in Mantodea.

(J) The presence or absence of the **rge**-groove

The **rge**-groove (6.7.1., 6.7.6.) has been assumed to be a ground-plan element of Blattaria. **rge** is present in *Archiblatta, Eurycotis, Tryonicus, Cryptocercus, Lamproblatta, Polyphaga*, and *Ergaula* but absent in the remaining Blattaria (subgroup 2.2.3.) and in Mantodea.

(K) The presence or absence of muscle **r6**

The **r6**-muscle (6.7.1., 6.7.6.) has been assumed to be a ground-plan element of Blattaria. **r6** is present in *Eurycotis, Lamproblatta, Polyphaga*, and *Ergaula* but absent in the remaining Blattaria (*Cryptocercus* and subgroup 2.2.3.) and in Mantodea. (*Archiblatta* and *Tryonicus* not investigated.)

A comparison between Blattaria and their outgroup Mantodea could hence lead to the view that in the ground-plan of Blattaria **nla, dca, rge, tre, s8, r6**, and the curvature of **L2** and **lve** are missing; **R1t** is separated from **R1c**, and **R1c** is connected with both **R1v** and **R1d** (no articulations **A8** and **A9**). The counterparts of these character states would then have developed within Blattaria and would have to be regarded as possible autapomorphies of Blattarian subgroups. From this view the following phylogenetic hypothesis could arise:

1. Part of subgroup 2.2.3.2.2.2. (*Euphyllodromia* + *Parcoblatta* + *Nyctibora*) is the sistergroup of the other Blattaria. All remaining Blattaria have connected **R1t** and **R1c**.
2. The next offshoots are *Supella* and *Blaberus* + *Nauphoeta* + *Blaptica* + *Byrsotria*. All remaining Blattaria have developed the **nla**-process (lost again in *Lamproblatta, Ergaula, Polyphaga*, and *Cryptocercus*) and the **dca**-processes (lost again in *Anaplecta*), and they have also developed, for example, sclerite **L1** and region **L4d** (both lost again in *Anaplecta*), the posterior branching of sclerite **L2** (the first hint of the arch-shape), and the division of the **via**-process into **paa** and **pda**.
3. The next offshoot is *Nahublattella*. All remaining Blattaria have developed the curvature of **L2** and **lve** (lost again in *Cryptocercus*), and they have also translocated the anterior insertion of **l14** from the **lve**-apodeme to **nla** (**L4n**-region).
4. The next offshoot is *Anaplecta*. All the remaining Blattaria have developed the **rge**-groove, and they have also lost the **lve**-apodeme and developed the contact between **L1** and **L2** (articulation **A2**).
5. The next dichotomy would be questionable: *Polyphaga* + *Ergaula* could be the next offshoot, with the remaining species having separated **R1c+R1t** and **R1d+R1v** (new articulations **A8** and **A9**). Alternatively, *Lamproblatta* could be the next offshoot, with the remaining species having developed the **tre**-tendon and the **s8**-muscle. Alternatively, *Cryptocercus* could be the next offshoot, with the remaining species having developed the **r6**-muscle.
6. *Eurycotis* + *Archiblatta* and *Tryonicus* would represent a holophyletic group which has, for example, developed a close contact between the anterior and posterior parts of the **L4l**-region and rotated the **L4d**-region anteriad (from a formerly leftward orientation).
7. In *Eurycotis* + *Archiblatta* the anterior and the posterior parts of the **L4l**-region have

fused, **L4l** has developed an **swe**-apodeme, and the right phallomere has evolved the **pia**-tooth.

This phylogenetic hypothesis as a whole is for several reasons extremely improbable: (1) If accepting it, one would have to suppose that many of the features assumed for the common ground-plan of Blattaria and Mantodea (listed in 7.1.) are not ground-plan features but similarities born by parallel evolution. Some of the most important have been mentioned in the steps 1.-7. Concerned are, for example: the detailed similarities of the **L4l**- and **L4d**-regions and of the **swe**-apodeme in *Mantoida* and *Archiblatta*; the arch-shape of **L2** and articulation **A2** in e.g. *Mantoida, Archiblatta*, and *Polyphaga*; the similar morphology of **paa** and **pda** in *Mantoida* and *Tryonicus*; the **pia**-teeth of Mantodea and e.g. *Archiblatta*. (2) In addition, some elements present in subgroup 2.2.3. or its subordinate subgroups but not in the other Blattaria and in Mantodea would have to be regarded as ground-plan elements of Blattaria, e.g. the hook-like curvature of the median end of the **R1t**-region, inclusive of its **cwe**-thickening, and the **lve**-apodeme. Features of the females could be added to this "ground-plan" list, e.g. the advanced rotation of the ootheca. Hence, as regards (1) and (2), this hypothesis would be extremely conflicting with the outgroup comparison of Blattaria with Mantodea – much more than the hypothesis proposed in 7.4. (3) This hypothesis is rather inconsistent in itself: In several cases secondary reductions (e.g. **nla**-process in 2.) or parallel evolution (situation in 5.) have to be assumed. If the developments contained in the steps 1.-5. are arranged in another way, some of these assumptions could be avoided, but they would only unavoidably be replaced by other assumptions of secondary loss or parallel evolution.

If only some or even only one of the polarity statements of this alternative hypothesis are accepted, this would still cause extensive inconsistencies either with the ground-plan hypothesis given in 7.1. or with the clusters of assumed autapomorphies given in 7.4. If it is, for example, supposed that **rge (J)** is an autapomorphy of a Blattarian subgroup comprising *Archiblatta, Eurycotis* (and the other species assigned to subgroup 2.1.), *Tryonicus, Lamproblatta, Cryptocercus, Polyphaga*, and *Ergaula*, and that the lack of **rge** in subgroup 2.2.3. is the plesiomorphic state, one would have to accept many cases of parallel evolution. Which features would have to be regarded as having evolved several times depends on which type of phallomere complex is regarded as plesiomorphic for this hypothetical grouping: (1) If the basic phallomere morphology is supposed to resemble *Archiblatta*, all the assumed autapomorphies of subgroup 2.2. must have developed two times independently. (2) If the basic phallomere morphology is supposed to resemble either *Tryonicus, Lamproblatta, Cryptocercus, Polyphaga*, or *Ergaula*, most of the similarities in the morphology of the **L4l**- and **L4d**-regions (including the similar insertions of **l2** and **l4**; 6.3.1.) and in the posterior part of the right phallomere (with the **fda**-lobe and the **pia**-tooth; 6.7.1.), which have revealed in the comparison between *Mantoida, Chaeteessa, Archiblatta*, and *Eurycotis*, would have to be regarded as cases of parallel evolution. (3) If any combination or mixture of these types is supposed to represent the basic phallomere morphology, the extent of parallel evolution having to be accepted could not be decreased, but only the assumptions of parallel evolution necessary for (1) and (2) would mingle.

If it is assumed that either **tre** and **s8**, or **r6**, or the **L2**-curvature, or **nla**, or **dca**, or the separation of **R1d** and **R1v** from **R1c**, or the connection of **R1c** and **R1t** is an autapomorphy of the respective Blattarian grouping, one would likewise have to accept extensive parallel evolution – in an analogous way as described for **rge**. It is thus certainly by far most parsimonious to regard all these elements or properties as ground-plan features of Blattaria (like in 7.3.) and to assume secondary loss or change when any of these elements or properties is missing in any of the Blattarian species investigated in this paper. As regards **(E)** and **(I)**, this view is additionally supported by arguments concerning the functional intercorrelation of phallomere elements. **(E)**: compare discussion in 7.5. **(M)**, **(N)**. **(I)**: The **b4**-muscles, which in Blattaria insert with **s8** on **tre**, are probably elements of the common ground-plan of Blattaria and Mantodea (6.7.1., 7.1.). When present all together, **tre**, **b4**, and **s8** are certainly functionally intercorrelated elements (and in this case the function of the **b4**-muscles is certainly different from that of the **b4**-muscles of *Mantoida*). If reduction occurs in such a situation, all three elements can be expected to be concerned. Hence, the lack of **b4** in *Lamproblatta* and subgroup 2.2.3. (there are no muscles in a similar position as **b4a** and **b4b** are in *Mantoida*) might indicate that **tre** and **s8** were present in former times.

(L) The presence or absence of muscle s7

s7 (6.9.) has been assumed to be a ground-plan element of Blattaria (7.3.). **s7** is present in the subgroups 2.1. and 2.2.3., and vestiges are probably present in subgroup 2.2.2.1. (*Cryptocercus*). In subgroup 2.2.2.2. and in Mantodea **s7** is absent. Subgroup 2.2.1. (*Tryonicus*) has not been investigated. Hence, **s7** could be a synapomorphy of the subgroups 2.1. and 2.2.3. and possibly *Cryptocercus*. However, since this assumption would be inconsistent with the assumed autapomorphies of the subgroups 2.2. and 2.2.2., it is assumed that **s7** has been lost secondarily in *Lamproblatta, Polyphaga*, and *Ergaula*. The lack of **s7** in *Blaberus* (6.9.) is certainly a secondary loss since **s7** is present in all other investigated species of subgroup 2.2.3. (inclusive of *Nauphoeta*).

The following discussions under **(M)** + **(N)** and **(O)** will be concerned with the polarity of some characters of Blattaria for which an outgroup comparison with Mantodea is not possible since the respective elements (**hla**-hook or **dca**-processes) are present in all Blattaria (**hla**) or at least in the Blattarian ground-plan (**dca**, compare **(F)**) but not in Mantodea. A result can be achieved in interdependence with the phylogenetic hypothesis in 7.4., but, mainly in the case of **(M)** and **(N)**, also independently of this hypothesis, if correlations with other elements for which an outgroup comparison with Mantodea is possible are considered.

(M) The position of the hla-base

(N) The extension of the membranous basal part 30 of hla

The **hla**-hook and the **L3**-sclerite are present in all Blattaria (6.4.3.). In 7.3. it has been stated that in the ground-plan of Blattaria the **hla**-base takes a position in the left anterior ventral wall of the left complex, and that the introversible membranous basal part **30** of **hla** is narrow (and **hla** is therefore – almost – non-retractable). These statements have to be substantiated.

In dependence on the phylogenetic hypothesis in 7.4. the following view results: A far anterior position of the **hla**-base and a narrow membrane **30** (and a non-retractable **hla**) are present in the subgroups 2.1. and 2.2.2.2. Thus, the more posterior position of the **hla**-base and the expansion of membrane **30** (and the retractility of **hla**) can be regarded as apomorphic states developed in the Blattarian subgroups 2.2.1. and 2.2.3. (These are possibly synapomorphies of these two subgroups: **(35)** and **(36)** in 7.4.) The more posterior position of the **hla**-base in subgroup 2.2.2.1. (*Cryptocercus*, fig.151), which is, however, not accompanied by an expansion of membrane **30** and by a retractility of **hla**, is also derived.

There are some functional intercorrelations between the various characters of **hla** and between these and some other elements of the left complex. Consequently, the species with a completely retractable **hla** (subgroup 2.2.3.) show some concomitant morphological and functional differences to the species with a non-retractable **hla**. Since for some of these correlated elements or properties an outgroup comparison with Mantodea and hence a polarisation of the respective character states is possible, these intercorrelations permit assessing the polarity of the characters of **hla** independently of the phylogenetic hypothesis in 7.4. The following intercorrelations and evolutionary changes are assumed:

- The extension of membrane **30**, the retractility of **hla**, and the position of the **hla**-base are intercorrelated: If membrane **30** is more extensive, **hla** can be retracted more deeply, and then its base can be more posteriorly without having **hla** exceeding the subgenital plate or protruding from the genital pouch during its inactive state. From a functional point of view, the more posterior position of the **hla**-base and the retractility of **hla** might have the advantage that in its active state (during copulation) **hla** protrudes farther from the genital pouch and is more flexible. In *Cryptocercus* the more posterior position of the **hla**-base is not accompanied by an extension of membrane **30** but by a shortening of **hla** (fig.151).

- The retractility of **hla**, the length of **l14**, and the positions of the **l14**-insertions are intercorrelated: In the species with a non-retractable **hla**, muscle **l14** has only the function to move **hla**; to accomplish this function **l14** has to be contracted for a short distance only and can be rather short (fig.72). In the species retracting **hla** (subgroup 2.2.3.) the contraction distance of **l14** has to be much longer, and thus **l14** itself has to be longer. This requirement is in part fulfilled by the posteriad shift of the posterior **l14**-insertion together with the **hla**-base. Additionally, the anterior insertion of **l14** has shifted anteriad. At a first stage, this latter shift has evidently been achieved by an anteriad shift of the **L4n**-region and of the **nla**-process, the primary anterior insertion area of **l14**; this stage is represented by *Anaplecta* (fig.222; compare *Eurycotis*, fig.68, 72, where **nla** and the **l14**-insertion are by far more posteriorly). At a later stage, in subgroup 2.2.3.2., the anterior **l14**-insertion has been translocated to the top of the **lve**-pouch (**lve**-apodeme), and the **l14**-insertion is shifted further anteriad by a lengthening of this **lve**-apodeme (compare *Anaplecta*, fig.222, and *Nahublattella* and *Parcoblatta*, fig.249, 276).
- The position of the anterior **l14**-insertion and the condition of the **swe**- and **lve**-apodemes and of the **nla**-process are intercorrelated: A lot of force seems to be needed in operating

the **hla**-hook, and there are various supporting mechanisms present to give the contraction of **l14** the proper effect, which is the movement or retraction of **hla**, and to prevent a distortion of the areas (1) between the anterior **l14**-insertion and the **hla**-base and (2) immediately around the anterior **l14**-insertion. (1) In *Archiblatta* and *Eurycotis* the **swe**-apodeme might fulfil the former function (fig.53, 65), and since the morphology of the **L4l**-region and **swe** is the same in *Mantoida* (6.3.1.), this mechanism is certainly the most primitive within Blattaria. In subgroup 2.2.3. **swe** is missing, and the anterior part of the **lve**-pouch has been elaborated as a long and stiff **lve**-apodeme. In *Anaplecta* (subgroup 2.2.3.1.) the anterior **l14**-insertion on **nla** is stabilised by **nla** being firmly rested upon the top of the **lve**-apodeme (fig.209, 210). The stabilisation of **nla** might be the primary function of the **lve**-apodeme. In the further evolution (in subgroup 2.2.3.2.) the anterior **l14**-insertion has shifted even further anteriad, and it has apparently been preferred to make more directly use of the supporting function of the **lve**-apodeme and to translocate the **l14**-insertion to the top of **lve**. (2) The **nla**-process itself assumedly has the function to stiffen the immediate vicinity of the anterior **l14**-insertion – as long as this insertion is on the **L4n**-region – and is therefore bulge-like (*Archiblatta, Eurycotis, Anaplecta*). In species having this insertion translocated to the **lve**-apodeme, **nla** is either modified in its shape (*Nahublattella*: whip-like) or has been lost (*Parcoblatta, Blaberus*).

- The position of the anterior **l14**-insertion and the condition of the phallomero-sternal muscles **s1** and **s7** are intercorrelated: Additional stabilisation preventing a distortion of the area around the anterior **l14**-insertion is probably achieved by muscles conducting much of the force which **l14** exerts to this area to the left apophysis of the subgenital plate. These phallomero-sternal muscles insert immediately anterior to the anterior **l14**-insertion. In *Eurycotis* this function is accomplished by muscle **s1**, which inserts between **nla** and the anterior end of **swe** (fig.70). In the species of subgroup 2.2.3., where the supporting function has been transferred from **swe** to **lve** and where, except for *Anaplecta*, the muscle-insertion for which the support is needed (**l14**) has been transferred from **nla** to **lve**, the function of the "conductor"-muscle has consequently been transferred from **s1** to **s7**, which inserts anteriorly on the **lve**-apodeme. Muscle **s1** has been lost in all species using a **lve**-apodeme for support (subgroup 2.2.3.; 6.9.).

The reciprocal outgroup comparison between Blattaria and Mantodea clearly suggests that **swe** (6.3.1.) and **s1** (6.9.) are ground-plan elements, that the primitive position of the **L4n**-region is like in *Eurycotis* (6.3.1.; compare fig.325c and e), and that there is no tube-shaped **lve**-apodeme. The lack of **swe** and **s1**, the extremely far anterior position of the **L4n**-region (or its lack), and the **lve**-apodeme – the features of subgroup 2.2.3. – are certainly derivations within Blattaria. Especially the assumedly primitive position of the **L4n**-region (like in *Eurycotis*) is clearly correlated with a short **l14** inserted on **L4n**, with the non-retractility of **hla**, and with a narrow basal membrane **30**, and a non-retractable **hla** can be expected to have its base far anteriorly. Thus, the non-retractable **hla** with its base in the anterior ventral wall can be assumed to represent the plesiomorphic condition within Blattaria. A bulge-shaped **nla**-process can also be regarded as a ground-plan element of Blattaria, since it is present in all species showing the primitive condition that the anterior **l14**-insertion is on a well-developed **L4n**-region.

In subgroup 2.2.2. the anterior **l14**-insertion (**l14** present in *Lamproblatta* and *Cryptocercus* only) is not stabilised by cuticular elements (no **swe**- or **lve**-apodemes, **L4n**-region highly reduced, no **nla**-process), and the force acting on the anterior **l14**-insertion seems to be completely conducted to the subgenital plate by the **s1**-muscles, which insert immediately anterior to **l14** (fig.157, 158, 184, 185). Also in subgroup 2.2.1. (*Tryonicus*) neither an **swe**- nor an **lve**-apodeme are present, and the stabilisation by cuticular elements does not seem to be very effective. The mechanism cannot be assessed here since the muscles are not known.

(**O**) The shape and sclerotisation of the **dca**-processes

dca-processes are restricted to Blattaria (6.1.1.) and are probably ground-plan elements of this taxon (7.5. (**F**)). In 7.3. it has been stated that in the Blattarian ground-plan the **dca** are two cushion-like processes posterior to **L1**; this statement has to be substantiated. Two membranous cushion-like **dca** are present in representatives of both of the basic Blattarian subgroups 2.1. (*Archiblatta*, fig.54) and 2.2. (*Tryonicus angustus*, fig.107, *Cryptocercus*, fig.153, *Polyphaga*, fig.120). More or less completely sclerotised (by **L1**) **dca** are also present in both the subgroups 2.1. (*Eurycotis*, fig.67) and 2.2. (*Tryonicus parvus*, fig.94, *Nahublattella*, fig.243, 244), but since the **L1m**-region is a ribbon-like extension in the common ground-plan of Blattaria and Mantodea, and since **L1m** is expanded posteriad in the species with sclerotised **dca**-processes (to contribute to this sclerotisation), this is assumed to be a derived state.

In those species of subgroup 2.2. having two membranous **dca**, these **dca** are very similar (fig.107, 120, 153; these are the members of the subgroups 2.2.1. and 2.2.2. except *Ergaula*, fig.105, and *Lamproblatta*, fig.177, but no member of subgroup 2.2.3. is concerned). This peculiar shape of the **dca** is assumed to represent the plesiomorphic state within subgroup 2.2. It is not regarded as a synapomorphy of the respective species since this assumption would be inconsistent with the many assumed autapomorphies of the subgroups 2.2.2. and 2.2.2.2. It also cannot be regarded as a synapomorphy of the subgroups 2.2.1. and 2.2.2. (assuming a secondary change in *Lamproblatta* and, less drastic, in *Ergaula*) since the shape of the **dca** in their primitive membranous condition is not assessable in subgroup 2.2.3.: Here the **dca** are either completely sclerotised (*Nahublattella*) or missing (remaining species), situations which are both derived.

A sclerotised peak **18** in between the **dca**-processes is present only in *Tryonicus angustus* and *Cryptocercus* (fig.107, 153). To regard this as a synapomorphy (assuming secondary loss in *Tryonicus parvus*) would be inconsistent with the autapomorphies of subgroup 2.2.2. only, but in my view the latter are much more conclusive. The peaks **18** are possibly non-homologous in the two species, or they are again an element of the ground-plan of subgroup 2.2.

The following discussions under (**P**) and (**Q**) + (**R**) will be concerned with the evolution of three characters for which the polarity is essentially clear, but for which the distribution of the character states within Blattaria is somewhat in conflict with the phylogenetic hypothesis in 7.4.; reversals of apomorphic character states seem to have taken place.

These discussions will be dependent on the phylogenetic hypothesis in 7.4., and the soundness of the results depends on the soundness of this hypothesis.

(P) The presence or absence of a sclerite-ring formed by the regions **L1m, L1l,** and **L1r**

A distinct extension **L1m** and possibly also a less distinct extension **L1l** are elements of the common ground-plan of Blattaria and Mantodea (6.1.1.). However, only in species of the Blattarian subgroup 2.2. **L1l** and **L1m** curve ventrad (**L1m** does this in a different way as in the Mantodean subgroup 1.2.) and approach each other again (6.1.4.); this is certainly a derived feature. The sclerite ring is either complete (*Ergaula, Cryptocercus*), and in this case it sometimes additionally expands onto the **dca**-processes (*Tryonicus parvus, Nahublattella*), or the ring has a short gap (ventrally in *Polyphaga*, dorsally in *Tryonicus angustus*). In all other species of subgroup 2.2. the feature is not assessable since **L1** has been completely lost. The only exception is *Lamproblatta*, which shows no trace of a ring though **L1** is present; this is assumed to be a secondary loss because of the many assumed autapomorphies of the subgroups 2.2.2. and 2.2.2.2. A complete sclerite-ring is assumed to be a ground-plan feature of subgroup 2.2.

(Q) The connection or separation of the sclerotisations of the **lve**-pouch (**L2** or **L2D**) and of the **paa-** and **pda-** (or **via-**) processes (**L2+L4N** or **L2E+L4N**)
(R) The absence or presence of muscle **l10**

In the common ground-plan of Blattaria and Mantodea the sclerotisation of the **lve**-pouch is connected with the common sclerotisation of the **paa**- and **pda**-processes (6.2.1., 7.1.), and the same is true of the ground- plan of the Blattarian subgroup 2.2. Muscle **l10** connecting these two sclerotisations is certainly also a ground-plan element of subgroup 2.2. (or at least of 2.2.2. + 2.2.3. since *Tryonicus* = 2.2.1. has not been investigated; 7.3.). Within subgroup 2.2.3. (fig.328) the sclerotisations concerned can be connected with (*Anaplecta, Euphyllodromia, Parcoblatta, Blaberus*) or separated from each other (*Nahublattella, Supella, Nyctibora, Nauphoeta*), and muscle **l10** is present in the species showing a separation (and in *Anaplecta*) but absent in the species showing a connection (except for *Anaplecta*).

Anaplecta is the first offshoot within subgroup 2.2.3. The outgroup comparison with the subgroups 2.2.1. and 2.2.2. clearly suggests that the connection of the sclerotisations in *Anaplecta* corresponds to the plesiomorphic state. *Nahublattella* is the next offshoot, and *Supella* follows. Both species show an (probably homologous) apomorphic separation of these sclerotisations. In the remaining species, which together form subgroup 2.2.3.2.2.2., both conditions – connection and separation – are represented. The outgroup comparison with the subgroups 2.2.3.2.1. (*Nahublattella*) and 2.2.3.2.2.1. (*Supella*) clearly suggests that within subgroup 2.2.3.2.2.2. the connected condition is an apomorphic state. This view is supported by the additional lack of **l10**, which is certainly a derived feature, and which is probably correlated with this secondary fusion of the sclerotisations.

The fusion of the sclerotisations and the concomitant loss of **l10** have certainly happened several times within subgroup 2.2.3.2.2.2. since the distribution of these two derived features is completely inconsistent with some other well-founded groupings: (1) *Blaberus* and *Nauphoeta* are (together with *Blaptica* and *Byrsotria*) members of the certainly holophyletic taxon Blaberidae (McKittrick 1964). (2) *Parcoblatta, Nyctibora, Blaberus*, and *Nauphoeta* are (together with *Blaptica* and *Byrsotria*) members of a probably holophyletic taxon characterised by the autapomorphies **(115)-(117)** in 7.4. Hence, the fusion and the loss of **l10** can be assumed to have been achieved independently in *Euphyllodromia, Parcoblatta*, and *Blaberus*.

7.6. Conflicts in the distribution of character states

In some characters whose polarity is rather clear, the distribution of the apomorphic state(s) over the taxa is inconsistent with the phylogenetic hypothesis in 7.4.; these inconsistencies can only be resolved by the assumption of either parallel evolution in the one or reversal in the other species. In some other characters, mainly in those discussed in 7.5., the polarity might be supposed to be the reverse of that assumed in 7.4. or resulting from the discussions in 7.5. The discussions have shown that this is highly improbable, but some doubt may remain. If the reverse polarity is supposed, the distribution of the surmisedly apomorphic character states would also be inconsistent with the hypothesis in 7.4.

The (clearly or possibly) apomorphic character states concerned and the groupings they might support will be listed here, and the respective plesiomorphic states are given in brackets. This will be done in the same manner as in 7.4. The conclusiveness of many of these "apomorphic" states is in terms of their value as possible autapomorphies decreased by uncertain homology relations, uncertain or even improbable polarity assumptions, or other circumstances. Some of these states, however, could really be autapomorphies and could hazard the phylogenetic hypothesis in 7.4., but only in very few points.

In the species provided with "?" some or all of the respective characters have not been investigated. For muscles the two insertion areas are given.

Arguments for alternative groupings within Mantodea

Grouping A: *Metallyticus* + *(Mantoida* + *Sphodromantis)*

(122) Groove on region R1c behind articulation A3 and anterodorsal to right insertion of muscle r3 present (BM: Groove on R1c behind A3 and anterodorsal to left r3-insertion absent).

This groove on the **R1c**-region (fig.6, 20, 41), not homologous with the **rge**-groove of Blattaria (6.7.1.), is very distinct in *Mantoida* and *Sphodromantis*, hardly recognisable in *Metallyticus*, and missing in *Chaeteessa* (6.7.3.). To interpret the groove as an autapomorphy of this grouping would be in conflict with the many assumed autapomorphies of the subgroups 1.2. and, since the groove is more distinct in *Mantoida* and *Sphodromantis*, 1.2.2. It is assumed that this groove is a ground-plan element of Mantodea and has been reduced in *Metallyticus* and lost in *Chaeteessa*. The following fact supports this interpretation: The **age**-apodeme on **R3** probably reaches articulation **A3** in the common ground-plan of Blattaria and Mantodea (6.7.1., 7.1.), but in *Chaeteessa* **age** does not reach **A3**, and the right posterior part of **age** has evidently been reduced. A concomitant reduction of the groove posterior to **A3** would be plausible.

Grouping B: *Mantoida* + *Metallyticus*

(123) Region R1t separated from region R1c: sclerites R1D, R1E or R1D, R1C (BM: R1t connected with R1c).

To regard this certainly apomorphic state (6.7.1., 6.7.3.; compare **(G)** in 7.5.) as a synapomorphy of *Metallyticus* and *Mantoida* would be in conflict with the assumed autapomorphies of the Mantodean subgroups 1.2. and 1.2.2. Parallelism is thus highly suggested. Support for this assumption comes from the fact that some other taxa have also achieved this state independently: According to LaGreca (1955), at least *Amorphoscelis abyssinica* (Amorphoscelididae), *Tarachodes insidiator* (Mantidae), and *Polyspilota* sp. (Mantidae) (fig.13, 15, 16 in LaGreca) show the separation of **R1t** from **R1c**, and this is certainly not a synapomorphy of these distantly related species. The Blattarian subgroup 2.2.3.2.2.2. also shows the separation of **R1t** and **R1c**.

Arguments for alternative groupings within the Blattarian subgroup 2.2.

Grouping C: *Tryonicus* + *Cryptocercus* + *(Anaplecta* + *(Nahublattella* + *(Supella* + *(Euphyllodromia* + *(Parcoblatta* + *(Nyctibora* + *(Blaberus* + *Nauphoeta* + *Blaptica* + *Byrsotria)))))))*

(124) Left edge 61 of lobe vla extending far anteriad (BM: 61 ending far posteriorly).

This certainly apomorphic state (6.2.1., 6.2.4.) is distinct in *Tryonicus, Cryptocercus, Anaplecta*, and *Nahublattella*, and the character is hardly assessable in the other species listed. Hence, it might be an autapomorphy of this grouping. This character is inconsistent with the assumed autapomorphies of subgroup 2.2.2.

Grouping D: *Cryptocercus* + *(Anaplecta* + *(Nahublattella* + *(Supella?* + *(Euphyllodromia?* + *(Parcoblatta* + *(Nyctibora?* + *(Blaberus* + *Nauphoeta?* + *Blaptica?* + *Byrsotria?)))))))*

(125) Muscle s10 present: from subgenital plate to ejaculatory duct (BM: s10 absent) **(126)** Muscle r6 absent: from region R1c to region R1d (SG2.: r6 present) **(127)** Sclerites L1 and L2 far separated: articulation A2 absent (BM: L1 and L2 articulated in A2).

(127) is certainly the apomorphic state (6.2.4.), and the same is probably true of **(125)** (6.9.) and **(126)** (6.7.6., **(K)** in 7.5.). These characters are inconsistent with the assumed autapomorphies of subgroup 2.2.2. but consistent with **(124)** of grouping C. (**s10** and **r6** not investigated in *Supella, Euphyllodromia, Nyctibora, Nauphoeta, Blaptica*, and *Byrsotria*.) As regards **(127)**, however, non-homology is suggested for *Cryptocercus, Anaplecta*, and the other species: *Cryptocercus* and *Nahublattella* have lost the right part of **L2**, which curves upwards and bears articulation **A2** distally in the Blattarian groundplan, but have retained **L1**. *Anaplecta* has retained the upcurved right part of **L2** but has lost **L1**. Hence, **A2** has possibly been lost in different ways. If this is true, **A2** has been lost three times since *Anaplecta* and *Nahublattella* are clearly more closely related (autapomorphies of subgroup 2.2.3. in 7.4.).

Grouping E: *Lamproblatta + (Anaplecta + (Nahublattella + (Supella + (Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)))))))*

(73) Tendon tre and muscles s8 and b4a,b absent (SG2.: tre, s8, and b4a,b present; BM: Presence of tre and s8 unclear, b4a,b present).

This is probably the apomorphic state (compare **(I)** in 7.5.; 6.7.5., 6.9.). To regard it as an autapomorphy of this grouping would be inconsistent with the many assumed autapomorphies of the subgroups 2.2.2. and 2.2.2.2.

Grouping F: (*Polyphaga + Ergaula) + (Anaplecta + (Nahublattella + (Supella + (Euphyllodromia + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica + Byrsotria)))))))*

(128) Region R1c probably fused with at least part of the broadly interconnected regions R1d and R1v: articulations A8 and A9 and membranous area 17 absent; sclerites R1M or R1N (SG2.2.: R1c separated from the broadly interconnected R1d and R1v: A8, A9, and 17 present; SG.2.: R1c separated from the narrowly interconnected R1d and R1v: A8, A9, and 17 present; BM: R1c connected with both R1d and R1v which are separated from each other: A8 and A9 absent but 17 present) **(64)** Muscle r3 absent: from region R1c to region R1v (BM: r3 present).

(128) is a less specific formulation of **(63)** as well as **(74)** (compare list in 7.4.) and is true of both the subgroups 2.2.2.2.2. and 2.2.3. **(128)** and **(64)** are certainly apomorphic – and the characters are probably intercorrelated (6.7.6.; compare **(H)** in 7.5.). The special kind of fusion, however, is rather different in *Polyphaga + Ergaula* (subgroup 2.2.2.2.2.) and in the other species (subgroup 2.2.3.); consequently, it is highly questionable whether the fusion, the resulting sclerites **R1M** and **R1N**, and the loss of **r3** are each homologous. If these states are still regarded as autapomorphies of this grouping, these characters would be inconsistent with the many assumed autapomorphies of the subgroups 2.2.2. and 2.2.2.2.

Grouping G: *Tryonicus + Lamproblatta*

(129) Apodeme age absent (BM: age present) **(130)** Extension R2m present (SG2.: R2m absent).

Both states are certainly apomorphic (6.7.4.). To regard them as autapomorphies of this grouping would be inconsistent with the many assumed autapomorphies of the subgroups 2.2.2. and 2.2.2.2.

Grouping H: *Cryptocercus + (Polyphaga + Ergaula)*

(131) Muscle s5 absent: from subgenital plate to left wall of genital pouch (BM: s5 present).

This state is certainly apomorphic (6.9.). To regard it as an autapomorphy of this grouping would be inconsistent with the assumed autapomorphies of subgroup 2.2.2.2.

Grouping J: *Cryptocercus + Polyphaga*

(132) Sclerite R1K present (BM: R1K absent).

The presence of a separate **R1K** is certainly apomorphic. However, the homology of the

R1K of these two species is uncertain since it is only indicated by a roughly similar position (6.7.6.). If this state is still regarded as an autapomorphy of this grouping, the character would be inconsistent with the many assumed autapomorphies of the Blattarian subgroups 2.2.2.2. and, if **R1K** is not assumed to have been lost secondarily in *Ergaula*, 2.2.2.2.2.

Grouping K: *Cryptocercus* + *(Lamproblatta* + *Anaplecta)*

(133) Muscle l4 reduced or absent: from sclerite L2 to region L4l (BM: l4 present and stout).

l4 is certainly stout in the common ground-plan of Blattaria and Mantodea (6.2.1., 6.3.1.). Its reduction in *Cryptocercus* and its loss in *Lamproblatta* and *Anaplecta* are certainly apomorphic states (6.3.4.). To regard them as autapomorphies of the respective groupings would be inconsistent with the many assumed autapomorphies of the subgroups 2.2.2., 2.2.2.2., and 2.2.3. To regard the reduction of **l4** as a synapomorphy of *Lamproblatta* and *Cryptocercus* (assuming parallel loss in *Anaplecta*) would be inconsistent with the assumed autapomorphies of subgroup 2.2.2.2. However, the possibility must be considered that **l4** was strongly reduced in the ground-plan of subgroup 2.2.2. and has enlarged secondarily at the base of subgroup 2.2.2.2.2. (*Polyphaga* + *Ergaula*) where the **hla**-muscle **l14** has been lost and **l4** has acquired a new function in moving the **hla**-hook (6.3.4.). In this case the reduction in *Cryptocercus* and *Lamproblatta* would at least be homologous.

Grouping L: *Anaplecta* + *(Supella?* + *(Euphyllodromia?* + *(Parcoblatta* + *(Nyctibora?* + *(Blaberus* + *Nauphoeta?* + *Blaptica?* + *Byrsotria?)))))*

(109) Sclerite L1 absent (BM: L1 present) **(110)** Process(es) dca absent (SG2.: dca present) **(134)** Pouch pne indistinct (BM: pne distinct) **(25)** Muscle l1 absent: from pouch pne to region L4d (BM: l1 present) **(95)** Region L4d absent (BM: L4d present).

These states are certainly all apomorphic (6.1.4., 6.3.4.), and they are probably all intercorrelated since **(109)**, **(110)**, **(134)**, and **(25)** relate to reductions in the same area, and **(95)** relates to the opposite insertion area of muscle **l1**. **L1**, **dca**, a distinct **pne**, **l1**, and **L4d** are all clearly present in *Nahublattella*. In *Supella* and *Euphyllodromia* **(109)**, **(110)**, **(134)**, and **(25)** have not been investigated. In *Nyctibora, Nauphoeta, Blaptica*, and *Byrsotria* **(25)** has not been investigated.

If these character states are regarded as autapomorphies of this grouping, the characters would be inconsistent with the assumed autapomorphies of subgroup 2.2.3.2. Since all states relate to the reduction of elements and are intercorrelated, the assumed autapomorphies of subgroup 2.2.3.2. are regarded as much more convincing: These include more complicated features, e.g. the **l14**-translocation **(79)**, the **L4K**-division **(84)**, and the **l2**-shift **(86)**. Moreover, the presence of **L1** in another species of *Anaplecta* (McKittrick 1964) might suggest that **(109)** is not an autapomorphy of this grouping; however, since the phylogenetic position of this species within subgroup 2.2.3. is not known (the genus *Anaplecta* is not necessarily holophyletic), this argument is not of high value.

Arguments for other alternative groupings within Blattaria

Grouping M: (*Archiblatta? + Periplaneta + Blatta + Deropeltis + Eurycotis) + Tryonicus? + (Anaplecta + (Nahublattella + (Supella? + (Euphyllodromia? + (Parcoblatta + (Nyctibora + (Blaberus + Nauphoeta + Blaptica? + Byrsotria?)))))))*

(135) Muscle s7 present: from subgenital plate to L2 (SG2. and BM: s7 absent) (**24**) Region L1a level (BM: L1a hood-shaped).

s7 (6.9.) has been regarded as a ground-plan muscle of Blattaria (7.3.) which has been lost in subgroup 2.2.2.2. (compare (**56**) in 7.4., with the reverse polarity assumption, and (**L**) in 7.5.). The anterior part of **L1** (**L1a**) is hood-shaped in the common ground-plan of Blattaria and Mantodea (6.1.1.). In *Archiblatta, Periplaneta, Blatta, Deropeltis*, and *Eurycotis*, in both species of *Tryonicus*, and in *Nahublattella* **L1a** has become level (6.1.4.). In the other species listed this character has not been investigated (*Supella, Euphyllodromia*) or is not assessable for the complete loss of **L1** (remaining species). *Lamproblatta* does not reveal (**24**) since it has a distinct vestige of the hood- or even of the plateau-shape (**L1** bends into the dorsal **pne**-wall; 6.1.4.).

To regard (**24**) and (**135**) as autapomorphies of this grouping would be inconsistent with the assumed autapomorphies of subgroup 2.2. If *Cryptocercus* really has vestiges of **s7**, (**135**) would moreover be inconsistent with the assumed autapomorphies of subgroup 2.2.2.

Grouping N: (*Archiblatta? + Periplaneta + Blatta + Deropeltis + Eurycotis) + (Tryonicus? + (Cryptocercus + (Polyphaga + Ergaula)))*

(**136**) Tendon tre and muscle s8 present (SG2. and BM: tre and s8 absent).

The presence of **tre** (6.7.1., 6.7.5.) and **s8** (6.9.) has been regarded as a ground-plan feature of Blattaria (7.3.; compare (**73**) in 7.4., with the reverse polarity assumption, and (**I**) in 7.5.). (**s8** not investigated in *Archiblatta* and *Tryonicus*). If this state is regarded as an autapomorphy of this grouping, the character would be inconsistent with the assumed autapomorphies of the subgroups 2.2. and, if **tre** and **s8** are not assumed to have been lost secondarily in *Lamproblatta*, 2.2.2. and 2.2.2.2.

Grouping O: (*Archiblatta? + Periplaneta + Blatta + Deropeltis + Eurycotis) + (Tryonicus? + (Lamproblatta + (Polyphaga + Ergaula)))*

(**137**) Muscle r6 present: from region R1c to region R1d (SG2. and BM: r6 absent).

The presence of **r6** (6.7.6.) has been regarded as a ground-plan feature of Blattaria (7.3.; compare (**126**) of grouping D, with the reverse polarity assumption, and (**K**) in 7.5.). If this state is regarded as an autapomorphy of this grouping, the character would be inconsistent with the assumed autapomorphies of the subgroups 2.2. and 2.2.2.

Grouping P: (*Archiblatta + Periplaneta + Blatta + Deropeltis + Eurycotis) + (Tryonicus + (Cryptocercus + (Lamproblatta + (Polyphaga + Ergaula))))*

(**138**) Groove rge present (SG2. and BM: rge absent).

The presence of **rge** (6.7.1., 6.7.6.) has been regarded as a ground-plan feature of Blattaria (7.3.; compare (**75**) in 7.4., with the reverse polarity assumption, and (**J**) in 7.5.). If this state is regarded as an autapomorphy of this grouping, the character would be inconsistent with the assumed autapomorphies of subgroup 2.2.

Grouping Q: (*Archiblatta* + *Periplaneta* + *Blatta* + *Deropeltis* + *Eurycotis)* + *(Lamproblatta* + *Cryptocercus)*

(139) Region R1c separated from regions R1d and R1v: articulations A8 and A9 present (SG2. and BM: R1c connected with R1d and R1v: A8 and A9 absent).

The presence of this separation and of **A8** and **A9** (6.7.1., 6.7.6.) has been regarded as a ground-plan feature of Blattaria (7.3.; compare **(128)** of grouping F, with the reverse polarity assumption, and **(H)** in 7.5.). If this state is regarded as an autapomorphy of this grouping, the character would be inconsistent with the many assumed autapomorphies of the subgroups 2.2., 2.2.2., and 2.2.2.2.

Grouping R: (*Archiblatta?* + *Periplaneta* + *Blatta* + *Deropeltis* + *Eurycotis)* + *(Tryonicus?* + *(Lamproblatta* + *(Polyphaga* + *Ergaula))* + *(Anaplecta* + *(Supella?* + *(Euphyllodromia?* + *(Parcoblatta* + *(Nyctibora?* + *(Blaberus* + *Nauphoeta?* + *Blaptica?* + *Byrsotria?)))))))*

(25) Muscle l1 absent: from pouch pne to region L4d (BM: l1 present).

Muscle **l1** has been found only in *Mantoida, Sphodromantis, Cryptocercus*, and *Nahublattella*, and since it is in the same relative position in all these species it has been regarded as homologous and as a muscle of the common ground-plan of Blattaria and Mantodea (6.1.1., 6.1.3., 6.1.4.). To regard the loss of **l1** as an autapomorphy of this grouping would be inconsistent with the many assumed autapomorphies of the subgroups 2.2., 2.2.2. (since *Cryptocercus* is excluded), 2.2.3., and 2.2.3.2. (since *Nahublattella* is excluded). It is thus clearly suggested that **l1** has been lost several times (or that the **l1** of Mantodea, *Cryptocercus*, and *Nahublattella* are not homologous despite their similar positions).

7.7. Conclusions in terms of phylogeny

The phylogenetic ideas presented in 7.2.-7.4. are highly supported by many autapomorphies for the various subgroups. The inconsistent characters supporting the groupings listed in 7.6. can in most cases not compete with the clusters of autapomorphies given in 7.4., and this is due to various reasons:

- The (certainly) apomorphic character state relates to the loss or reduction of an element (such derivations are not as convincing in their role as possible autapomorphies as those relating to the presence of new elements): **(126), (127), (73), (64), (129), (131), (133), (109), (110), (134), (25), (95).**
- The (certainly or surmisedly) apomorphic character state is, if related as an autapomorphy to one of the groupings in 7.6., the only one suggesting the respective grouping, not supported by the distribution pattern of any other character and inconsistent with the distribution pattern of many other characters: **(25)** as related to grouping R, **(122), (123), (124), (73), (131), (132), (133), (136), (137), (138), (139).**

- For the (certainly) apomorphic character state the homology in the species concerned is questionable since the possibility of parallel evolution is revealed by other species having achieved the same apomorphic character state independently: **(123)**.
- For the (certainly) apomorphic character state the homology in the species concerned is questionable since except for a formal correspondence the morphology of the respective elements is rather different: **(127), (128), (132)**.
- The polarity of the character is unresolved or even suggested to be the reverse: **(122), (135), (136), (137), (138), (139)**.
- The polarity of the character is suggested to be the reverse in a certain part of the phylogenetic tree, (i.e. the apomorphic character state has been secondarily reduced in the crucial species excluded): **(133)**.

In my view, the only conceivable alternative resulting from the list in 7.6. is that supported by **(124), (125), (126)**, and possibly **(127)**: *Cryptocercus* might be the sister-group of subgroup 2.2.3. (Blattellidae and Blaberidae) and not of subgroup 2.2.2.2. *(Polyphaga, Ergaula, Lamproblatta)*. And *Tryonicus* could well be the sister-group of *Cryptocercus* + subgroup 2.2.3.: The possibility of a close relation between *Tryonicus* and subgroup 2.2.3. has already been considered in 7.3., based on the similar morphology of the **hla**-hook (**(35)** and **(36)** in 7.4.). In *Cryptocercus* the **hla**-base has also shifted posteriad (fig.151), and the retractility and the large extension of the membranous base **30** of **hla** present in *Tryonicus* and subgroup 2.2.3. could well have been reduced in this species – in correlation with the shortening of **hla** (compare **(M)**, **(N)** in 7.5.). However, in my view, the very similar reduction of sclerite **L4K** and of the **nla**-process and the shift of **l2** in correlation with the plateau-like shape of the anterior face of the **pne**-pouch, the arguments suggesting that *Cryptocercus* belongs to subgroup 2.2.2., are somewhat more convincing (**(42)-(46)** in 7.4.).

Another problematical issue is the assumed phylogeny of subgroup 2.2.3.2.2. Apart from the fact that more species will have to be investigated in detail to get a really reliable result, some character states of members of the genus *Blattella* are somewhat in conflict with the hypothesis in 7.4. According to Mizukubo & Hirashima (1987), fig.41, there are a **dla**-lobe and a **R4**-sclerite (= **RD1d**) and possibly also a **R5**-sclerite (= **RD2v**) present in *Blattella karnyi*. (A muscle corresponding to **r11** has not been found by these writers.) In *Blattella germanica* (Linné, 1767) I could also find sclerites which are certainly **R4** and **R5.** According to McKittrick (1964), the females of *Blattella germanica* rotate their oothecae. These features suggest that *Blattella* belongs to subgroup 2.2.3.2.2.2.2.2. or, at least (if **R4** and **R5** are assumed to be secondarily reduced in *Parcoblatta*), to subgroup 2.2.3.2.2.2.2. (compare **(115)** and **(117)-(120)** in 7.4.). On the other hand, *Blattella karnyi* (not *B. germanica*) resembles *Nahublattella* in that the posterior part of sclerite **L2** is branched, and each branch occupies a process. (The two branches of *B. karnyi* are **LD2d** and **LD2v** in Mizukubo & Hirashima, fig.41; those of *Nahublattella* are the sclerotisations of **via** and **psa** in fig.244, 245.) The morphology of this area would in *B. karnyi* be more primitive than in all species included in subgroup 2.2.3.2.2. (compare **(94)** in 7.4.). This might indicate that some of the apomorphic character states regarded as autapomorphies of the subgroups 2.2.3.2.2., 2.2.3.2.2.2., and 2.2.3.2.2.2.2. are cases of parallel evolution, or that **R4**, **R5**, and the rotation of the ootheca have developed earlier and have been reduced again in various taxa belonging to subgroup 2.2.3.2.2. However, details of morphology of the *Blattella*-species are not yet investigated. Thus, there is compelling need for further investigations on the phallomeres of the various subgroups of Blattellidae to resolve these problems in terms of the evolution and polarity of characters.

The most parsimonious phylogenetic hypothesis resulting from the discussions in chapter 7 is shown in diagram 1 in 7.4. If the species investigated in this paper are true representatives of the Mantodean and Blattarian families and subfamilies they are usually assigned to (compare the systems of McKittrick 1964 and Beier 1968 given in chapter 2), the overall phylogeny of Mantodea and Blattaria is as follows:

In Mantodea, the basal dichotomy is between Mantoididae and all other families. The second dichotomy is between Chaeteessidae and the remaining families. In Blattaria, the basal dichotomy is between Blattinae + Polyzosteriinae and all other Blattaria. These remaining Blattaria form three groups: The first consists only of the rather isolated Tryonicinae. The second contains Cryptocercidae, Lamproblattinae, and Polyphaginae, the two latter taxa being especially closely related. The third group corresponds to Blattellidae + Blaberidae. Blattellidae are clearly paraphyletic, with Blaberidae being a rather subordinate subgroup. The earliest offshoot within Blattellidae (+ Blaberidae) are the Anaplectinae; the three subsequent offshoots are various taxa previously comprised in Plectopterinae. Blaberidae, Nyctiborinae, Blattellinae, and Ectobiinae form together a holophyletic group. Nyctiborinae and Blaberidae are possibly sister-groups.

As regards Blattaria, this phylogenetic hypothesis is in several repects very different from the system of McKittrick (1964):

- Tryonicinae are not related to Blattinae + Polyzosteriinae.
- Lamproblattinae are also not related to Blattinae + Polyzosteriinae but to Polyphaginae.
- Cryptocercidae are not the sister-group of Blattidae but probably of Polyphaginae + Lamproblattinae (or possibly of Blattellidae + Blaberidae).
- Blattellidae are paraphyletic since Blaberidae are one of their subgroups. (McKittrick has also expressed this idea in her phylogenetic trees – text figure 3 – but not in her system).
- Plectopterinae are paraphyletic.

This hypothesis is based almost exclusively on male postabdominal and genital morphology. Of course, there are still other character complexes which have proved to be useful in analysing Dictyopteran phylogeny, e.g. the morphology of the female genitalia, of the proventriculus (McKittrick 1964), or of the wings. The present knowledge on these character complexes has been revised in a phylogenetic approach in Klass (1995), and a study on the evolution of the ovipositor containing many new results has been completed more recently (Klass, in press). The many characters which are now reliably interpretable are consistent with the phylogenetic hypothesis presented here. Some characters, however, are still problematic, due to insufficent (in quantity and quality) data. To improve the data base for these character complexes, and also for the male genitalia, by detailed morphological investigations should be the major task of future work on Dictyopteran phylogeny.

7.8. Conclusions in terms of the side-reversal of the phallomere complex

Of the species discussed in this paper, *Nahublattella, Supella, Euphyllodromia* (Plectopterinae), *Blaberus, Byrsotria, Blaptica*, and *Nauphoeta* (Blaberidae) have side-reversed phallomeres, and this is certainly an apomorphic feature. According to Bohn (1987), side-reversal also occurs in some species of *Ectobius*. All these species belong to subgroup 2.2.3.2. If projected on the phylogenetic tree in 7.4., the distribution pattern of this feature is as follows:

The three basal offshoots within subgroup 2.2.3.2. give rise to species with side-reversed phallomeres (*Nahublattella, Supella, Euphyllodromia*). Subgroup 2.2.3.2.2.2.2., the sister-group of *Euphyllodromia*, contains both normally orientated (*Parcoblatta, Nyctibora*, part of *Ectobius*) and side-reversed (*Blaberus, Byrsotria, Blaptica, Nauphoeta*, part of *Ectobius*) species. (*Ectobius* can be assigned to this subgroup since the females show the advanced rotation of the oothecae, (**117**) in 7.4.).

This distribution can be interpreted in two ways: (1) Side-reversal is a ground-plan feature of subgroup 2.2.3.2. *Nahublattella, Supella, Euphyllodromia*, the Blaberidae, and the respective species of *Ectobius* have retained this orientation. *Parcoblatta, Nyctibora*, and the other species of *Ectobius* have achieved their normal orientation by a second side-reversal (independently in the various taxa concerned). (2) In the ground-plan of subgroup 2.2.3.2. the phallomere complex is still normally orientated. The basal offshoots *Nahublattella, Supella*, and *Euphyllodromia*, and also the Blaberidae and the respective species of *Ectobius* have independently reversed the phallomere complex.

Alternative (1) is highly supported by the fact that the three basal offshoots of subgroup 2.2.3.2. are side-reversed. However, a definitive decision, whether (1) or (2) or any combination of these possibilities is true, is not possible at the present state of knowledge, and more species will have to be investigated. At least, it is strongly suggested that the orientation of the phallomere complex, side-reversed or normal, is not a very good criterion for phylogenetic conclusions.

7.9. Remarks on the procedure in the phylogenetic analysis and on character lists and character state matrices

Character lists, describing the characters, their states, and the assumed polarities, and character state matrices, describing the distribution of the character states over the taxa, have the function to present all the character states used and their distribution independently of any previous assumptions on phylogeny – as an objective basis for the phylogenetic analysis or as a starting-point for a computer-based cladistic analysis. The applicability of this method of presentation in the frame of an analysis concerned with a very complex type of character evolution, as it has been found in the male genitalia of Blattaria and Mantodea, is discussed here.

The procedure in the present phylogenetic analysis is mainly hierarchical: Mantodea and Blattaria have been, in the frame of the species investigated, regarded as sister-groups (Isoptera disregarded); this basic assumption is well-founded (Hennig 1969, Klass 1995).

Blattaria and Mantodea have then been reciprocally used as outgroups, and many features of the common ground-plan of Blattaria and Mantodea could be reconstructed. Then, in the discussions of phallomere evolution in 7.2. and 7.3., holophyletic subgroups have been established according to their hierarchy. It was begun with the search for apomorphic character states common to several species, permitting the delimitation of higher-ranked subgroups (subgroups 1.2., 2.1., and 2.2.). On this level, "apomorphic" relates to a comparison with features well-ascertained for the common ground-plan of Blattaria and Mantodea. These higher-ranked subgroups, if their holophyly could be well ascertained, were then split into more subordinate subgroups, again by searching apomorphic character states common to part of the species. At this level, "apomorphic" relates, if e.g. a Blattarian subgroup is under consideration, to a comparison either with the common ground-plan of Blattaria and Mantodea, or with the ground-plan of Blattaria, or with the ground-plan of any Blattarian subgroup superordinate to and including the subgroup under consideration. At last, in 7.6., the distribution of the states of the characters inconsistent with the majority has been discussed in terms of parsimony.

This hierarchical analysis has to be continuously accomplished with a procedure of reciprocal illumination: There has to be a mutual feedback between the characters used, also concerning their evidence in terms of phylogeny. This includes a continuous feedback to the delimitation of superordinate subgroups when working on subordinate subgroups, since an autapomorphy of a superordinate subgroup might be absent within a subgroup suggested to be subordinate to it, and whether a reversal has ocurred or whether the range of the superordinate subgroup has to be modified by removing the subordinate subgroup from it has to be discussed in terms of parsimony.

The feedback between characters and also the resulting preliminary assumptions on phylogenetic relationships can be necessary at various levels of the phylogenetic analysis: for the interpretation of morphology in terms of homology relations, for the assignment of a certain morphological condition present in certain species to a certain character state, as well as for recognising the polarity of character states within a certain subgroup (and, consequently, for the definition and formulation of characters and character states, too). Hence, in the present analysis, the assumptions and conclusions related to these issues and concerning certain subgroups are in many characters dependent on the distribution of apomorphic states of other characters regarded as autapomorphies of a subgroup superordinate to that under consideration. A character list and a matrix independent of previous reciprocal illumination and preliminary assumptions on phylogeny do not include this kind of feedback between characters (and their evidence) and are consequently incomplete or even highly misleading in some characters. The following examples shall illustrate this topic.

(1) Concern: Interpretation of morphology in terms of homology relations.

As discussed in 6.3.4., the fused sclerites **L3** and **L4K** and the muscle **l4** of *Ergaula capucina* resemble **L3** and **l14** of Blattellidae and Blaberidae, *Anaplecta* excluded. These **l4** and **l14** have been regarded as non-homologous, and the similar position of the anterior insertion of the muscle moving **hla** – **l4** or **l14** – is not a synapomorphy of these taxa. This hypothesis is only in part based on a homology analysis – using the criteria of relative position and special structure – since it is not possible to identify the muscle of *Ergaula* reliably as the **l4** by a morphological comparison alone. This identification also depends on a preliminary assumption of phylogenetic relationships between *Polyphaga* and *Ergaula* on the one hand and *Anaplecta* and the remainder of Blattellidae and Blaberidae on the other, and this assumption results from the distribution of the apomorphic states of other characters (autapomorphies of the subgroups 2.2.2.2.2. and 2.2.3. in 7.4.). Hence, many characters referring to the properties of **l4** and **l14** (e.g. (**58**) and (**79**) in 7.4.) would have to be regarded as not (reliably) assessable in *Ergaula* without preliminary assumptions on phylogeny.

(2) Concern: Assignment of a certain morphology to a certain character state.

The description of autapomorphy (**27**) of subgroup 2.2. (division of region **L4l**, see in 7.4.) is not valid for *Parcoblatta* since this species has the anterior part of region **L4l** completely lost (fig.268; compare sclerite **L4U'** of *Blaberus*, fig.299), and it is not a priori decidable if this loss was preceded by a division of **L4l** or not. That the condition in *Parcoblatta* has to be assigned to character state (**27**), or is derived from it, can only be recognised by regarding the evidence from the distribution of apomorphic states of other characters revealing the close relationship between *Parcoblatta* and *Anaplecta* and especially *Blaberus* (e.g. most autapomorphies of the superordinate subgroups 2.2.3. or 2.2.3.2. in 7.4.) – i.e. by practising reciprocal illumination between characters and after having made preliminary assumptions on phylogenetic relationships.

(3) Combination of concerns: Assignment of a certain morphology to a certain character state and recognition of the polarity.

In the common ground-plan of Blattaria and Mantodea the **L2**-sclerotisation within the **lve**-pouch (regions **L2m, L2a, L2p**), the **paa**-sclerotisation (region **L2d**), the **pda**-sclerotisation (posterior part of region **L4l**), and the region **L4d** are all firmly connected within one sclerite (e.g. *Mantoida*, fig.44-47). The apomorphic division of the left part of **L2** and the named parts of **L4** (= sclerite **L4N** in the ground-plan of subgroup 2.2.) is clearly different, and non-homologous, in *Lamproblatta* (resulting sclerites **L2A+L4S** and **L2C+L4T**, fig.178-180) and in *Nahublattella* (resulting sclerites **L2D** and **L2E+L4N**, fig.242-245; discussions in 6.2.4. and 6.3.4.). Non-homology can be recognised only by the different position of the **L4d**-region: In *Lamproblatta* **L4d** is connected with the **L2**-sclerotisation within **lve** (fig.178, 186); in *Nahublattella* **L4d** is connected with the sclerotisation of the insertion area of muscle **l10**, fig.244, 250); this is also the only property that can serve for a description of the difference in the formulation of the respective characters:

Character 1: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** from the **L2**-sclerotisation within **lve** but does not separate **L4d** from the sclerotisation of the posterior insertion area of muscle **l10** (division = articulation **A10**). Character states: (0) absent; (1) present (in *Nahublattella*); Polarity: 0>1.

Character 2: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** from the sclerotisation of the posterior insertion area of muscle **l10** but does not separate **L4d** from the **L2**-sclerotisation within **lve**. Character states: (0) absent; (1) present (in *Lamproblatta*); Polarity: 0>1.

Nahublattella and the members of subgroup 2.2.3.2.2. (e.g. *Blaberus, Parcoblatta*) reveal many apomorphic features in common, and together they form the certainly holophyletic subgroup 2.2.3.2.: **(79)-(89)** in 7.4. The morphology near the left posterior end of **L2** is in some species of subgroup 2.2.3.2.2. (e.g. *Nyctibora*) rather similar to *Nahublattella* and can easily be derived from it, and the division of **L2** (articulation **A10**) is certainly homologous (fig.328b,h). However, in all members of subgroup 2.2.3.2.2. the **L4d**-region, and thus the only element yielding a criterion by which this special division of **L2** can be recognised or charcterised, is absent: **(95)** in 7.4. (In the **L2**-division as present in subgroup 2.2.3.2., **L4d** has primitively also retained the connection with the common sclerotisation of **paa** and **pda**, and this would be a second criterion for recognising the difference to *Lamproblatta*, whose **L2**- and **L4**-division separates **L4d** from the sclerotisation of **paa** and **pda**; fig.329f,g, 6.3.4. However, this criterion can be applied neither to *Nahublattella* – this species shows a certainly autapomorphic division of sclerite **L2E+L4N** into a basal and a distal sclerite by the membranous ring **39**, fig.244, which separates **L4d** from the sclerotisation of **paa** and **pda** – nor to subgroup 2.2.3.2.2. for the loss of **L4d**).

Hence, there is a first problem in the **L2**-division of subgroup 2.2.3.2.2. concerning the assignment of a certain morphology to a certain apomorphic character state: Without having used reciprocal illumination between characters previously, i.e. without having the preliminary assumption of the holophyly of the superordinate subgroup 2.2.3.2. resulting from the consideration of other characters, the characters 1 and 2 would have to be regarded as not assessable in those members of the subordinate subgroup 2.2.3.2.2. which show a **L2**-division (Table 1a). The assessment and the matrix entries of the characters 1 and 2 can only be proper if these two characters are considered in interdependence with other characters having apomorphic states common to *Nahublattella* and subgroup 2.2.3.2.2., i.e. if the probable holophyly of the superordinate subgroup 2.2.3.2. has been recognised previously (Table 1b).

Moreover, some members of subgroup 2.2.3.2.2. reveal a secondary fusion of **L2D** and **L2E+L4N** and a secondary loss of muscle **l10**. That these are reversals results clearly from the hierarchical analysis. Concerning the sclerotisations, the highly apomorphic character state achieved by this reversal conforms exactly with the state present in e.g. *Polyphaga* (all parts of **L2** and **L4N** form together one sclerite), and it also conforms with the most plesiomorphic state within Blattaria and Mantodea (all parts of **L2** and the posterior part of region **L4l** – **L4N** not yet differentiated as a separate sclerite – are contained in one sclerite). As regards **l10**, its absence does likewise correspond with the most plesiomorphic state within Blattaria and Mantodea.

Hence, there is a second problem in the **L2**-division of subgroup 2.2.3.2.2. concerning the recognition of the polarity and the definition of character states: In elaborating a character state matrix without having used reciprocal illumination between characters previously, the morphology of the sclerotisation and of **l10** would have to be regarded as representing rather or most plesiomorphic states of the respective characters (Table 1a). Only the distribution of the states of other characters and their evidence in terms of phylogeny reveals

Table 1a,b: Character lists and character state matrices of the characters 1, 2, and 3; a) without regarding evidence of other characters in terms of phylogeny; b) under consideration of evidence of other characters in terms of phylogeny.

Matrices: 0 = most plesiomorphic state; 1 = apomorphic state derived from 0; 2 = apomorphic state derived from 1; / = character not investigated; ? = character not assessable; C = Character; Sp = *Sphodromantis*; Me = *Metallyticus*; Ch = *Chaeteessa*; Ma = *Mantoida*; Ar = *Archiblatta*; Eu = *Eurycotis*; Tp = *Tryonicus parvus*; Po = *Polyphaga*; Er = *Ergaula capucina*; Cr = *Cryptocercus*; La = *Lamproblatta*; An = *Anaplecta*; Na = *Nahublattella*; Su = *Supella*; Ep = *Euphyllodromia*; Pa = *Parcoblatta*; Ny = *Nyctibora*; Np = *Nauphoeta*; Bb = *Blaberus*; Bp = *Blaptica*; By = *Byrsotria*.

To the characters 1 and 2 the criterion of the connection of the **paa**-sclerotisation (region **L2d**) has been added in order to distinguish the described divisions from the division between the **paa**- and **pda**-sclerotisations as present in some Blattaria and Mantodea (compare (**A**) in 7.5.).

a)

Character 1: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** as well as the sclerotisation of **paa** from the **L2**-sclerotisation within **lve** but does not separate **L4d** from the sclerotisation of the posterior insertion area of muscle **l10** (= articulation **A10**). Character states: (0) absent; (1) present; Polarity: 0>1.

Character 2: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** from the sclerotisation of **paa** and from sclerotisation of posterior insertion area of muscle **l10** but does not separate **L4d** from the **L2**-sclerotisation within **lve**. Character states: (0) absent; (1) present; Polarity: 0>1.

Character 3: Presence of muscle **l10**. Character states: (0) absent; (1) present; Polarity: 0>1.

C	Sp	Me	Ch	Ma	Ar	Eu	Tp	Po	Er	Cr	La	An	Na	Su	Ep	Pa	Ny	Np	Bb	Bp	By
1	0	0	0	0	0	0	0	0	0	0	0	0	1	?	0	0	?	?	0	0	0
2	0	0	0	0	0	0	0	0	0	0	1	0	0	?	0	0	?	?	0	0	0
3	0	/	/	0	/	0	/	1	1	1	1	1	1	1	0	0	1	1	0	0	0

subgroup 2.2.3.2.2.

b)

Character 1: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** as well as the sclerotisation of **paa** from the **L2**-sclerotisation within **lve** but does not separate **L4d** from the sclerotisation of the posterior insertion area of muscle **l10** (= articulation **A10**). Character states: (0) absent; (1) present; (2) secondarily absent; Polarity: 0>1>2.

Character 2: Division in the left posterior part of main sclerite **L2** and the associated parts of **L4** which separates region **L4d** from the sclerotisation of **paa** and from the sclerotisation of the posterior insertion area of muscle **l10** but does not separate **L4d** from the **L2**-sclerotisation within **lve**. Character states: (0) absent; (1) present; Polarity: 0>1.

Character 3: Presence of muscle **l10**. Character states: (0) absent; (1) present; (2) secondarily absent; Polarity: 0>1>2.

C	Sp	Me	Ch	Ma	Ar	Eu	Tp	Po	Er	Cr	La	An	Na	Su	Ep	Pa	Ny	Np	Bb	Bp	By
1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	2	2	1	1	2	2	2
2	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
3	0	/	/	0	/	0	/	1	1	1	1	1	1	1	2	2	1	1	2	2	2

subgroup 2.2.3.2.2.

that the absence of the division described in character 1 and the absence of **l10** are plesiomorphic for Blattaria and Mantodea as a whole but apomorphic within subgroup 2.2.3.2. (discussion in 7.5. **(Q)**, **(R)**). The character states achieved by these reversals can then be properly defined as highly apomorphic states (Table 1b).

As a consequence of the combined presence of the first and the second problem, in the character state matrix in Table 1a the items relating to the **L2**-divisions would suggest that these **L2**-divisions have originated independently in *Nahublattella* and in subgroup 2.2.3.2.2. and are non-homologous. In a computer-based cladistic analysis this would cause a misleading trend away from a holophyly of *Nahublattella* + subgroup 2.2.3.2.2. In the matrix in Table 1b this misleading impression is eliminated.

As a result, the assessment of homology relations, the definition of character states, the assignment of morphological conditions to certain character states, and the polarity assumptions, and hence also the respective entries of items into the matrix, can in some cases only be proper in dependence on a previous hierarchical analysis with reciprocal illumination and on the resulting preliminary assumptions in terms of phylogeny. It is, at least in the frame of the analysis presented here, not suitable to give a character list and a character state matrix with the characters considered independently of each other and of preliminary assumptions on phylogeny.

8. HOMOLOGY RELATIONS ACCORDING TO MIZUKUBO & HIRASHIMA (1987) AND GENERAL REMARKS ON THE ANALYSIS OF HOMOLOGY RELATIONS

The assumptions and procedures of Mizukubo & Hirashima

Mizukubo & Hirashima (1987) investigate the sclerites and the muscles of the phallomeres of *Periplaneta fuliginosa* (Blattidae / Blattinae), of 3 species of *Blattella* (Blattellidae / Blattellinae), and of *Opisthoplatia orientalis* (Blaberidae). Additionally, they use data from other writers concerning various species of Blattinae. The phallomeres of Blattinae are regarded as the most primitive. The results of the authors comprise: (1) Homologies of the phallomere elements of the different species. (2) Side-homologies of the elements of the left and the right halves of the phallomere complex. (3) A ground-plan for the sclerotisations of the phallomere complex of Blattaria, which is mainly based on the morphology of Blattinae.

As regards (1), the supposed homology relations are fundamentally different from those I assume for the respective close relatives *Eurycotis* (Blattidae), *Parcoblatta* (Blattellinae), and *Blaberus* (Blaberidae). For example, Mizukubo & Hirashima suppose that the hooks designated here as **hla** have developed from completely different elements in the three groups. (In my view these **hla** are strictly homologous.) Their opinions concerning the ground-plan of the Blattarian phallomeres are also completely contradictory of my results. The paper of Mizukubo & Hirashima must therefore be discussed in detail.

Mizukubo & Hirashima procede as follows:

- They divide both the left and the right side of the phallomere complex into 11 "subregions". The definition of "subregion" is: "The smallest and indivisible unit which is a part of the bordered region in a plane and, in this entire region, possesses its own relative position determined by its relations with other surrounding subregions." (p.251). The relationships between sclerites and subregions are characterised on p.251: **(A)** Principally a single sclerite (often inclusive of the surrounding membrane) corresponds with a single subregion. **(B)** A single sclerite can spread over two or more subregions, or two or more subregions can participate in a single sclerite. **(C)** A subregion can be completely membranous.

- They do not explicitly say whether **(B)** and **(C)** are exclusively regarded as derived states, or if they can be already realised in the hypothetical ground-plan of Blattaria. However, the definition of the subregions makes sense only if the demarcation of "smallest indivisible units" obeys a uniform principle – and this can only be the possession of an own sclerite according to **(A)**. Hence, I interpret Mizukubo & Hirashima in the following way: A set of 11 subregions on each side, each subregion with one sclerite of its own, is regarded as the ground-plan pattern of Blattaria. (According to **(A)**; **(B)** and **(C)** realised in derived states only.)
- They deduce the basic pattern of 11 subregions per side from the morphology of the various Blattinae: By considering several Blattinae and by combining their features, the dividing of the phallomere complex into subregions can be accomplished in a way that the relative positions of the subregions of the left side are a mirror-image of the relative positions of the subregions of the right side.
- In both *Blattella* and *Opisthoplatia* the dividing into subregions can be accomplished in a way that the subregions of the left side as well as those of the right side have the same relative positions as they have in Blattinae and in the hypothetical basic pattern. In their dividing procedure the authors assume losses or fusions for some sclerites (according to **(B)** and **(C)**).
- From these equal relative positions of the subregions they deduce homology relations between the subregions of the left and of the right side of the phallomere complex as well as between the subregions of the phallomeres of different species. Side-homologous subregions get the same names – except for **L** (left) or **R** (right) in the first position.
- Concerning the closeness of the relations between neighboring subregions, they distinguish four categories which describe the closeness or intensity of the mutual relations between the respective sclerites: weak adjacency – adjacency – articulation – fusion. All the relations between all neighboring subregions together are the association pattern of the phallomere complex.
- They investigate the muscle insertions on the various subregions.
- In their homology analysis the authors largely neglect the musculature. If the course of a muscle is consistent with the homology assumptions deduced from the relative positions of the subregions, this is regarded as a confirmation. If there is inconsistency, the authors do not regard this as a matter of conflict.

The statements of Mizukubo & Hirashima include, or result in, the following assumptions regarding the ground-plan of Blattaria:

- The left as well as the right side of the phallomere complex are provided with (exactly) 11 separate sclerites. (This results from the definition and characterisation of "subregion", compare above).

- The whole phallomere complex is bilaterally symmetrical (p.256). Consequently, all side-homologous subregions would have to be regarded as completely symmetrical, too.

The procedure and the argumentation of Mizukubo & Hirashima have some weak points, and many of their statements are in contradiction to my results. My critique concerns the topics discussed subsequently.

The negligence of the musculature as a reference frame for the homology analysis

Mizukubo & Hirashima base their homology analysis on the relative positions of the cuticular subregions to each other but largely neglect the musculature. Regarding their results, the courses of most muscles are inconsistent with the homology assumptions deduced from cuticular morphology. Referring to Matsuda (1976), they assume that, since the muscles develop independently of the exoskeleton, the insertions of muscles generally have a too large shifting potential in their evolution to be reliable landmarks in the analysis of homology relations. Matsuda (1976) regards the musculature as a valuable supplementary criterion only "when the structures within a relatively narrow range of species – within a family, or perhaps an order – are under study" (p.36). The question arises, therefore, how valuable the muscles are in homologising the phallomere elements of Blattaria and Mantodea and to what extent they deserve to be considered.

In *Eurycotis* and *Mantoida*, which are only distantly related, the cuticular elements of the phallomeres are quite similar in their principal arrangement. The arrangement of the musculature is to a large extent consistent with the homology relations resulting from the relative positions and special features of the cuticular elements: The main muscles of the phallomere complex have the same course (**l2, l3, l4, l6, r1, r2, r3**). In many cases the musculature can help in confirming homology assumptions. This is not inconsistent with the views of Mizukubo & Hirashima, but in my opinion it also suggests that one should not a priori regard the musculature as highly variable as these authors do.

In my view, (1) to regard the insertions a priori as conservative and (2) to assume shifts of insertions only if inconsistencies arise is the better approach. (1) In the comparison between *Mantoida* and *Sphodromantis*, the evolution of some sclerotisations could be reconstructed in detail, because the musculature was taken as an integral instrument of the homology analysis (compare **L4** in 6.3.3.). In the comparison of distantly related species in which homologous cuticular elements show, apart from a somewhat similar position, hardly any similarities, the insertions of muscles can in my opinion be extremely valuable landmarks. For example, the insertions of **l4**, **l2**, and **l14** suggest that sclerite **L4K** of *Cryptocercus* is homologous with a part of sclerite **L4H** of *Eurycotis* (**L4n**-region and anterior **L4l**-region). The insertion of **l4** suggests (partial) homology for **L4K** of *Ergaula* and **L4K** of *Cryptocercus*, though **L4K** of *Ergaula* has shifted to the ventral **hla**-base and fused to sclerite **L3** (compare in 6.3.4.). (2) On the other hand, of course, the muscle insertions **have** a certain shifting potential. By studying enough species, however, these shifts can often be "observed" step by step, and in many cases it becomes obvious whether the insertions of the muscles or the similarities in cuticular morphology are the better basis for homology assumptions. Drastic shifts of muscle insertions are e.g. that of **l14** from the **L4n**-region (*Eurycotis*) to the **L2a**-region (*Nahublattella*) and that of **l2** from sclerite

L1 (*Mantoida*) to the base of the **hla**-hook (*Nahublattella*). In these two cases, the morphology of *Anaplecta* reveals how these shifts have taken place (and that with high probability the insertions **have** shifted).

In my view the arrangement of the musculature is a very important element of the homology analysis. A simultaneous consideration and a mutual weighing of similarities in the cuticular elements and in the musculature – combined with the investigation of a larger sample of species – has proved most useful in this work. Moreover, in this kind of proceding, the consideration of the musculature has the advantage that the information about the shifts of insertions, the losses, divisions, fusions, or de-novo-formations of muscles can provide many autapomorphies – in addition to those gathered from cuticular morphology. In my view, a homology hypothesis on the Blattarian phallomere elements which accepts extensive inconsistencies in the arrangement of the musculature is not very convincing.

The division into 11 subregions per side

Mizukubo & Hirashima deduce the presence of a natural division into 11 subregions on each side of the phallomere complex from the morphology of various Blattinae. However, in my view their special kind of procedure is debatable. (The subsequently used terms of Mizukubo & Hirashima can be distinguished from mine by D or V in the second position.) Mizukubo & Hirashima assume that the sclerotisations comprised in **R1** in my terminology represent 7 subregions (compare *Eurycotis*, fig.74-78, 330g, 331e, 332e, and *Archiblatta*, fig.330f):

1. **RD1d**	essentially region **R1d** (sclerite **R1H**)
2. **RD1l**	sclerotisation of process **pra**, part of region **R1d**
3. **RD1m**	sclerotisation of spine **sra**, part of region **R1d**
4. **RD1v**	essentially region **R1v** (sclerite **R1G**)
5. **RD1vm**	a ribbon-like sclerotisation connecting **R1H** and **R1G**; missing in *Eurycotis* but present in *Archiblatta* in the ventral wall of lobe **fda** (compare fig.330f and g)
6. **RD2l**	essentially region **R1c**
7. **RD2d**	essentially region **R1t** (with ridge **pva**)

The remaining subregions of the right phallomere are:

8. **RD2v**	sclerite **R2**
9. **RD3**	sclerite **R3**
10. **RVv**	sclerite **L4G** (region **L4v** on lobe **vla**)
11. **RVd**	right part of sclerite **L5** of *Periplaneta* (within ejaculatory duct, compare in 6.5.); **RVd** is supposed to have fused with its left counterpart **LVd** = left part of sclerite **L5**.

In my view, **R1** is in the common ground-plan of Blattaria and Mantodea either one undivided sclerite (more probable) or composed of three sclerites (**R1F**, **R1G**, **R1H**; separated by the articulations **A8** and **A9**; 6.7.1.). For the ground-plan of Blattaria I assumed the latter condition, which is still present in *Eurycotis*. For the subregions **RD1l**, **RD1m**, **RD1vm**, **RD2d**, and **RD2l** there is no indication that they have been separate sclerites in the ground-plan of Blattaria. (The separation of **RD2d** and **RD2l** = **R1t** and **R1c** is realised as an apomorphic feature in some Mantodea and Blattellidae only, compare in 6.7.3., 6.7.4., 7.5.(G). **RD1l** and **RD1m** are separate sclerites in some Blattinae, but the outgroup comparison with Mantodea suggests that this is not a ground-plan feature of Blattaria.) As regards the ventral sclerotisation of the **vla**-lobe (**RVv** = **L4G**), it is not impossible that this is an element of the right half of the phallomere complex (according to Quadri 1940), but in my view this is not very probable (discussion in 3.1.).

The left complex is divided into the following subregions (compare *Eurycotis*, fig.65-69, 323e, 324e, 325e, and *Archiblatta*, fig.53-57, 323f, 324f, 325f):

1. LD1d	left part of sclerite **L1** (part of region **L1a**)
2. LD1l	right part of sclerite **L1** (parts of regions **L1a** and **L1m**)
3. LD1m	rightmost part of sclerite **L1**, near articulation **A2** (part of region **L1m**)
4. LD1v	sclerite **L4F** (posterior part of region **L4c**) + sclerotisation of **paa** (region **L2d**)
5. LD1vm	essentially sclerite **L2** (except region **L2d**)
6. LD2l	posterior part of sclerite **L4C** of *Archiblatta* (posterior part of region **L4l**)
7. LD2d	sclerite **L3** (on hook **hla**)
8. LD2v	sclerite **L4D** of *Archiblatta* (region **L4n**)
9. LD3	anterior part of sclerite **L4C** of *Archiblatta* (anterior part of region **L4l**)
10. LVv	sclerite **L4E** of *Archiblatta* (anterior part of region **L4c**)
11. LVd	left part of sclerite **L5** of *Periplaneta*

In 6.3.1. it has been shown that the sclerotisation of the **L4l**-region (**LD2l** and **LD3**) is undivided in the common ground-plan of Blattaria and Mantodea as well as in the ground-plan of Blattaria, and that this situation is retained in *Archiblatta* (sclerite **L4C**) and *Eurycotis* (sclerite **L4H**). And there is no indication that **L4l** was present as two separate sclerites in still earlier times.

In some cases the division into subregions is based on apomorphic features of Blattinae (and Polyzosteriinae): **L4F** is a sclerite peculiar to these groups and certainly not a ground-plan element of Blattaria. The **L4n**-region is only in Blattinae an isolated sclerite (**L4D**), not in *Eurycotis*, *Tryonicus*, or *Anaplecta*; the ground-plan situation of Blattaria, however, is unclear in this respect. The branching of the posterior part of **L1** into several lobe-like extensions (**LD1d**, **LD1m**, **LD1l**) is a consequence of the posteriad expansion of **L1** onto the **dca**-processes, and in this distinct form it is certainly an apomorphic state; that **L1** is a fusion product of several previously isolated sclerites cannot be deduced fom this situation.

As a result, there are two principal reasons to refute (1) the division into 11 subregions in Blattinae as well as (2) the ascription of this division to the ground-plan of Blattaria:

- Neither the left nor the right side of the phallomere complex of *Periplaneta* (or other Blattinae or Polyzosteriinae) shows a priori a composition of exactly 11 subregions, nor does the Blattarian ground-plan show such a pattern. Most of the dividing into subregions is based either on apomorphic situations in a subgroup of Blattaria (Blattinae) or on arbitrary – and in my view wrong – assumptions on which sclerotisations were isolated from each other in the Blattarian ground-plan.

- Though the demarcation or identification of a ground-plan subregion has a clear theoretical background (indivisible unit = 1 sclerite), no uniform principle can be recognised in the practical application to extant species (analysis of Blattinae), let alone the attempt to come close to the definition or to explain discrepancies. It is not comprehensible why Mizukubo & Hirashima assume for some sclerites of Blattinae a contribution of several subregions and why for other sclerites they do not. The dividing procedure seems to aim to have subregions with corresponding relative positions on the left and on the right side. So the division of the **L4l**-region (into **LD2l** and **LD3**) results in having – like on the right side (**RD2l** and **RD3**) – one subregion for the sclerotisation in the anterior ventral wall (**LD3** and **RD3**) and one for the sclerotisation in the lateral edge of the phallomere (**LD2l** and **RD2l**). (According to my results, only the division on the right side is a ground-plan feature: articulation **A3**.)

The argumentation concerning homology assumptions

Mizukubo & Hirashima mainly make use of the first criterion of homology (relative positions). However, the specific procedure of the dividing into subregions described above makes the homology assumptions questionable: From the fact that the left as well as the right side **can** be (in a largely arbitrary way) divided into 11 areas having the same relative positions cannot be decuced that these areas are side-homologous because of their equal relative positions (circular argumentation). Assumptions of homology would only be justified, if (1) these areas have specific features in common (i.e. if there are **similar structures** in the same relative positions, e.g. similar sclerites, muscle insertions, processes, apodemes, etc.), or if (2) an equal arrangement on both sides results from a uniform principle of dividing. The same critique applies to the homology assumptions that concern the comparison of different species: Again, the surface of the phallomeres is divided largely arbitrarily into subregions with equal relative positions, and the subregions are then supposed to be homologous because their relative positions are equal.

Moreover, the reliability of the homology hypothesis becomes further diminished by the fact that neither the side-homologies nor the homologies between different species are supported by similarities in the arrangement of the musculature or in the intensities of the mutual relations between the subregions / sclerites:

- Side-homologies: Related to the side-homologies assumed by Mizukubo & Hirashima, the musculature of *Periplaneta* is completely different in the left and in the right half of the phallomere complex (of 20 phallomere muscles only two are a pair, Mizukubo & Hirashima, fig.6). As regards the principal relative positions of the subregions, the association patterns of the left and of the right side of *Periplaneta* are very similar. This simply results from the fact that the two halves of the phallomere complex have been arbitrarily divided into subregions which are in the same relative positions. However, the subregions of the left and of the right side supposed to be homologous hardly have any intensity of the mutual relations in common (Mizukubo & Hirashima, fig.2).
- Homologies between species: In *Periplaneta* and *Blattella germanica*, of 14 or 7, respectively, intrinsic muscles of the left half of the phallomere complex only 2 have

the same course (Mizukubo & Hirashima, fig.6, 8). The intensities of the mutual relations between the subregions are almost never the same in the two species.

The special morphology of the supposedly homologous subregions (e.g. position in a pouch, formation of a process) is not considered at all.

The symmetry of the phallomere complex in the Blattarian ground-plan

The investigations and conclusions of Mizukubo & Hirashima are restricted to Blattaria; Mantodea are not mentioned at all. With their statement "We cannot detect proto-types of the genitalia .... indirectly on evidence obtained from other insect groups." (p.250) the authors deprive the phallomeres of Mantodea of any value to contribute to the reconstruction of the ground-plan of the Blattarian phallomeres. However, in the reconstruction of the ground-plan of any group an outgroup comparison can be very useful. In the case of the Blattarian phallomeres the consideration of the Mantodean phallomeres was of great value for the determination of the polarities of characters within Blattaria (and within Mantodea). Since Mizukubo & Hirashima neglect Mantodea, the statement "We believe that, at the period of the formation of the order, the early Blattaria had symmetrical genitalia" has no foundation at all. According to this statement, the asymmetry of the Blattarian and the Mantodean phallomeres is a case of parallel evolution. However, my results clearly suggest that the very special kind of asymmetry present in Blattaria and Mantodea is homologous and a feature of their common ground-plan.

Mizukubo & Hirashima recognise the side-reversed similarities in the phallomeres of Blattellidae (*Blattella*) and Blaberidae (*Opisthoplatia*). However, they do not assume homology for these similarities but parallel evolution due to similar selective pressure. Hence, they assume completely symmetrical phallomeres even for the last common ancestor of Blattellidae and Blaberidae. These opinions are refuted:

- Since extreme asymmetry had already been established in the common ground-plan of Blattaria and Mantodea, it must have been present in the common ancestors of Blattellidae and Blaberidae, too.
- The similarities of the left complexes of Blaberidae and the more derived Blattellidae (*Nyctibora*, *Parcoblatta*) are so detailed and peculiar that the probability for parallel evolution is in my view infinitely small; side-reversal is substantially ascertained by my results (compare in 6.13.).
- That a reversal of the left-right asymmetry must be considered as a possible evolutionary pathway is clearly demonstrated by those species of *Ectobius* (Ectobiinae) having side-reversed phallomeres (compare in 6.13.).

9. HOMOLOGY RELATIONS ACCORDING TO GRANDCOLAS (1994) AND THE PHYLOGENETIC POSITION OF *CRYPTOCERCUS*

Apart from other morphological studies, Grandcolas & Deleporte (1992) and Grandcolas (1994) investigate the phallomere sclerites of some Blattaria. The latter paper contains nearly all the information given in the former, and also some additional data, and will be referred to in the following discussions.

Grandcolas (1994) investigated the phallomeres of *Periplaneta americana* (Blattinae), *Cryptocercus punctulatus*, and several Polyphaginae and proposes a homology hypothesis for the phallomere sclerites. He finds many synapomorphies suggesting *Cryptocercus* to be a subordinate taxon of Polyphaginae. However, his homology hypothesis is very different from my homology assumptions for *Archiblatta* (Blattinae), *Eurycotis* (Polyzosteriinae), *Polyphaga*, *Ergaula* (Polyphaginae), and *Cryptocercus*, and these discrepancies and the resulting assignment of *Cryptocercus* have to be discussed.

9.1. Discussion of the homology relations assumed by Grandcolas

The data base of Grandcolas

Grandcolas gives data on phallomere morphology in figures showing the cuticular phallomere elements of *Periplaneta americana* (fig.1), *Heterogamodes ursina* (fig.3), *Therea petiveriana* (fig.5), and *Cryptocercus punctulatus* (fig.6), and in sketches showing the principal sclerite pattern in Blattinae (fig.2) and Polyphaginae (fig.4). He terms the sclerites in the same manner as McKittrick (1964), but due to different homology assumptions the names of the sclerites are in many cases different, too. Some differences result from Grandcolas' assumptions on side-homologies, which are expressed by giving side-homologous sclerites the same names (except for **L** or **R** in the first position to name the side). The sclerite terminology of Grandcolas is rather different from mine, and table 2 gives the synonymy and the homology assumptions. To distinguish them from mine the terms of Grandcolas will be provided throughout with *.

Table 2: Synonymy of the sclerite terms of Grandcolas (1994) and those used in this paper.
Terms of Grandcolas are provided with *. Somewhat questionable synonymies are provided with **?**. **L1** of *Periplaneta* (2nd column): In his fig.2 Grandcolas 1994 assigns **L1** to **L2***, but it is not clear whether he assigns it to **L2d*** or to **L2v***.

	Periplaneta *Archiblatta*	*Cryptocercus*	*Therea*	*Heterogamodes*
L1*	L5	L1	L1	L1
L2d*	L4C and L1?	L3	L4N?	L4N?
L2v*	L2 and L1?	L2	L2	L2
L3d*	L3	part of L4N	L4K?	L3
L3v*	L4D	part of L4N	L3?	L4K or L4M?
vp*	L4G	L4G	L7?	—
N*	—	R2	L8	L8
R2*	R2 and R1F	R1F	R2	R2
R3d*	R1G and R1H	R1J	R1M	R1M
R3v*	R3	R3	R3	R3

In Grandcolas' fig.3 and 5 showing *Heterogamodes* and *Therea* at least some of the apomorphies listed in 7.4. can be recognised, and these permit the integration of these species into my phylogenetic hypothesis. *Therea*, fig.5, shows five of these apomorphies:

(48) L8 = **N*** is present. **(55) L2** = **L2v*** and the **lve**-pouch almost reach the left edge of the left complex. **(62) R2** = **R2*** and **R3** = **R3v*** are fused. **(63) R1M** = **R3d*** is present. **R2** = **R2*** is so broad that **R3** = **R3v*** is for most of its breadth confluent with it (compare in 7.3., subgroup 2.2.2.2.2.2., and fig.330m). Hence, *Therea* can be assigned to subgroup 2.2.2.2. (*Polyphaga* + *Ergaula* + *Lamproblatta*) by **(48)** and **(55)**, to subgroup 2.2.2.2.2. (*Polyphaga* + *Ergaula*) by **(62)** and **(63)**, and to subgroup 2.2.2.2.2.2. (*Ergaula*) by the breadth of **R2**, and Grandcolas is probably right in assuming a close relation between *Ergaula* and *Therea*. *Heterogamodes*, fig.3, shows at least **(48) L8** = **N*** and **(63) R1M** = **R3d*** and can be assigned to subgroup 2.2.2.2.2. (*Polyphaga* + *Ergaula*). These assignments permit treating *Therea* and *Heterogamodes* – independently of the assumptions of Grandcolas – as true representatives of subgroup 2.2.2.2.2. ("Polyphaginae") in the following discussions and to assume that at least all autapomorphies of the subgroups 2.2., 2.2.2., and 2.2.2.2. are also present in these species (if there have not occurred secondary changes). Also, the morphology of the phallomere sclerites can be expected to be at least similar to *Polyphaga* and *Ergaula*.

The way Grandcolas uses his terminology in Polyphaginae (excluding *Cryptocercus*) and his homology assumptions between Polyphaginae and *Cryptocercus* or *Periplaneta* can only be inferred from the figures showing *Therea* and *Heterogamodes*. The terminology applied to these two species can largely be transferred to the Polyphaginae I have studied, *Polyphaga* and *Ergaula*, since for most phallomere elements the homology relations between *Therea* / *Heterogamodes* and *Polyphaga* / *Ergaula* are quite evident; in some other cases, however, problems arise. In combination with Grandcolas' figures on *Periplaneta* and *Cryptocercus*, this transfer allows the comparison and discussion of the homology relations which are assumed for Polyphaginae (in general), Blattinae, and *Cryptocercus* by Grandcolas and by me. *Polyphaga* and *Ergaula* (alone), *Periplaneta*, and *Cryptocercus* can be compared independently of this transfer, since the homology relations between these species have been discussed in chapter 6. In the following discussions **(A)**-**(F)** the phallomere morphology of *Therea*, *Heterogamodes*, *Polyphaga*, and *Ergaula* (designated as Polyphaginae) will be compared with that of *Cryptocercus* and Blattinae (and, in part, Polyzosteriinae, which are closely related to Blattinae).

Sclerite L1* sensu Grandcolas and the genital opening (A)

Grandcolas names the sclerite next to the genital opening **L1***. In *Cryptocercus* and *Therea* and probably also in *Heterogamodes* **L1*** is sclerite **L1** (compare fig.3, 5, 6 of Grandcolas and fig.151). As regards the homology of **L1** = **L1*** of these three species, I agree with Grandcolas. However, if **L1*** of *Heterogamodes* really is the homologue of the **L1** = **L1*** of *Cryptocercus*, *Polyphaga*, and *Ergaula*, the opening concerned would not be the genital but the phallomere-gland opening (compare black arrow in fig.3 of Grandcolas and **P** in fig.106, 121, 153). In *Cryptocercus*, *Polyphaga*, and *Ergaula* the genital opening is much more ventrally: the ejaculatory duct (**D** in fig.122, 151) opens into the **lve**-pouch, next to sclerite **L2** = **L2v***. This relation resulted clearly from own investigations of the internal anatomy.

In *Periplaneta* **L1*** is sclerite **L5**, which is situated inside the true ejaculatory duct (compare in 6.5.). Since the assumption of Grandcolas that this **L5** is homologous with

L1 of Polyphaginae and *Cryptocercus* is only based on the similar position next to the genital opening and since the genital opening has been misidentified in Polyphaginae and *Cryptocercus*, the homology of these sclerites is no longer supported. McKittrick (1964) assumes homology for the **L1** of Polyphaginae, *Cryptocercus*, and Blattinae (as I do), and this assumption is confirmed by the similar morphology of the sclerites, by a similar position relative to other sclerites, by similar muscle insertions, and by a position next to the phallomere-gland opening (discussion in 6.1.).

Sclerites L2d*, L3d*, and L3v* sensu Grandcolas (B)

As regards **L2d***, **L3d***, and **L3v*** of *Therea* and *Heterogamodes*, neither the muscles nor the exact morphology and relative position of the sclerites are shown in fig.3 and 5 of Grandcolas, and an exact homologisation with the sclerites of *Polyphaga*, *Ergaula*, *Cryptocercus*, and *Periplaneta* is, therefore, not possible.

L3v* of *Periplaneta* is sclerite **L4D** (**L4n**-region, fig.325f). **L3v*** of *Heterogamodes* might correspond to either **L4M** or **L4K** of *Polyphaga* and *Ergaula* (fig.325k). However, neither **L4M** nor **L4K** nor any other sclerite of *Polyphaga* and *Ergaula* is strictly homologous with **L4D** (discussion in 6.3.4.). Hence, the sclerites **L3v*** of *Heterogamodes* and *Periplaneta* are certainly not homologous. **L3v*** of *Therea* is possibly homologous with **L3** (on the **hla**-hook) of *Ergaula*, *Polyphaga*, and *Periplaneta*.

L2d* of *Periplaneta* is sclerite **L4C** (**L4l**- and **L4d**-regions, fig.325f). **L2d*** of *Therea* and *Heterogamodes* probably correspond to **L4N** (on the **pda**-process) of *Polyphaga* and *Ergaula* (fig.325k). **L4N**, however, is not strictly homologous with **L4C** but only with the posterior part of **L4C** (discussion in 6.3.4.).

L3d* of *Periplaneta* and *Heterogamodes* – I agree with this homology assumption – correspond to sclerite **L3** of Blattinae, *Polyphaga*, and *Ergaula* (on the **hla**-hook in fig.53, 117). **L3d*** of *Therea* occupies a shallow bulge (not a long hook as **hla** is), and **hla** is hence supposed to be reduced; however, the long and somewhat hook-like process, whose sclerotisation is designated **L3v***, is in my view more likely to be **hla**. I suppose that **L3d*** of *Therea* is sclerite **L4K**, which is on a shallow bulge like in *Ergaula* (fig.326d).

In *Cryptocercus* (fig.6 of Grandcolas, fig.150, 151) the sclerites are designated as follows: **L3*** (Grandcolas probably assumes a fusion of **L3v*** and **L3d***) is **L4N**. Hence, **L4N** and **pda** of *Cryptocercus* are regarded as the homologues of **L3** and **hla** of *Polyphaga* and *Ergaula* (fig.117) and Blattinae (fig.53). The **hla**-hook of the other species is thus supposed to be quite reduced in *Cryptocercus* (as Grandcolas also supposes for *Therea*, which assumption, however, is probably not true).

L2d* is **L3**. Hence, **L3** and **hla** of *Cryptocercus* are regarded as the homologues of **L4N** and **pda** of *Polyphaga* and *Ergaula* (fig.117) and of **L4C** and **pda** of Blattinae (fig.53).

In my view, **hla** and **L3** of *Cryptocercus* are homologous with **hla** and **L3** of the other species (discussion in 6.4.3.), and **pda** and **L4N** of *Cryptocercus* are homologous with **pda** and **L4N** (or the posterior part of **L4C**, respectively) of the other species (discussion in 6.3.4.). These relations are clearly demonstrated by the muscles inserting on these elements (compare e.g. **l14** in *Eurycotis* and *Cryptocercus*, fig.72, 157) and by the relative positions of the respective elements (compare the dorsoventral arrangement of the posterior part of **L4C**, **pda**, **L3**, and **hla** in *Archiblatta* and of **L4N**, **pda**, **L3**, and **hla** in *Cryptocercus*, fig.65, 150). As a result, Grandcolas has certainly misidentified **L2d*** and **L3*** in *Cryptocercus* (as compared with Blattinae, *Polyphaga*, *Ergaula*, and probably *Heterogamodes*).

As regards *Cryptocercus* and *Therea*, the sclerites **L3*** (or **L3v*** and **L3d***) as well as the **L2d*** are probably also not homologous (compare the interpretation of the *Therea*-sclerites above), since in *Therea* **L3v*** is ventral to **L2d***, whereas in *Cryptocercus* **L3*** is dorsal to **L2d***. No argument is given to explain this difference.

Sclerite R2* sensu Grandcolas (C)

As regards *Periplaneta*, Grandcolas follows McKittrick (1964) in the definition and demarcation of **R2***. This **R2*** includes sclerite **R2** but additionally the regions **R1t** and **R1c** (= sclerite **R1F**). The two sclerites of this **R2***, **R2** and **R1F**, are dorsoventrally articulated with each other in **A6** (fig.75, 76). The homology relations which Grandcolas assumes concerning the **R2***-sclerotisations are in some respects not completely clear. This is in part due to incomplete information about which sclerotisations are assigned to **R2*** and to the incompleteness of the figure showing the phallomeres of *Periplaneta*.

In fig.1 showing *Periplaneta*, Grandcolas labels that sclerite **R2*** which I designate **R2** in Blattinae / Polyzosteriinae (fig.75-77). However, **R1F** is not contained in this figure. Since in McKittrick **R1F** is assigned to **R2*** (McKittrick 1964, fig.108: the central and the right parts of the slerite termed **R2**), **R1F** is probably part of **R2*** in the terminology of Grandcolas.

For Polyphaginae and *Cryptocercus* Grandcolas evidently assumes a fusion of the two sclerites of **R2*** (**R2**, **R1F**) and a concomitant loss of articulation **A6**. This is indicated by one of the supposed synapomorphies of *Cryptocercus* and Polyphaginae: "Sclerite **R2*** with two tubercles, which are not articulated dorso-ventrally" (p.151). (The only articulation within McKittrick's **R2** is **A6** between my sclerites **R2** and **R1F**, fig.75, 76, which is a ground-plan feature of Blattaria). In fig.3 and 5 showing *Heterogamodes* and *Therea*, Grandcolas labels that sclerite **R2*** which I designate **R2** in *Polyphaga* and *Ergaula* (fig.135-137); the entire sclerite **R1M** is designated **R3d***, without any contribution of **R2***. In fig.6 showing *Cryptocercus*, Grandcolas labels that sclerite **R2*** which I designate **R1F** (fig.163); sclerite **R2** is designated **N*** (see below in (**D**)). Hence, **R1F** = **R2*** of *Cryptocercus* and **R2** = **R2*** of Polyphaginae are regarded as the results of this fusion and as strictly homologous. I cannot agree with these homology assumptions:

- That **R1F** of *Cryptocercus* has developed by a fusion of **R1F** and **R2** of *Periplaneta* is certainly wrong: In *Cryptocercus* **R1F** and **R2** take the same relative positions as **R1F** and **R2** do in *Periplaneta* (and in *Eurycotis*, compare fig.75 and 161 and in 6.7.4., 6.7.6.), and these sclerites are certainly strictly homologous. Articulation **A6** is in *Cryptocercus* as well-developed as in *Eurycotis*.
- That **R2** of Polyphaginae has developed by a fusion of **R1F** and **R2** of *Periplaneta* is, in my view, also wrong: In *Polyphaga* and *Ergaula* the sclerotisation homologous with **R1F** of *Periplaneta* (regions **R1c** and **R1t**) is contained in the anterior part of sclerite **R1M** (compare fig.332e and i), and the **R2**-sclerites of these species are strictly

homologous (fig.332e,i). Since the morphology of the respective part of the right phallomere of *Therea* and *Heterogamodes* is similar to *Polyphaga* and *Ergaula*, the same relations are assumed for these species.

- The resulting assumption that **R1F** of *Cryptocercus* is homologous with **R2** of Polyphaginae is also refuted.

Sclerite N* sensu Grandcolas (D)

Sclerite **N*** of both *Therea* and *Heterogamodes* certainly corresponds to **L8** of *Polyphaga* and *Ergaula* (fig.117), which is situated on the rightmost part of the left complex, close to the right phallomere. According to Grandcolas, a sclerite **N*** is also present in *Cryptocercus*. From its relative position shown in Grandcolas' fig.6 results that this **N*** is **R2** (fig.161-163): it articulates with both **R1F = R2*** and the left posterior end of **R3 = R3v*** (articulations **A6** and **A7**), and its general shape and position also fit. However, in my opinion (compare in (**C**)) this **R2 = N*** of *Cryptocercus* is not homologous with **L8** of *Polyphaga* and *Ergaula* but with **R2** of *Polyphaga*, *Ergaula*, *Periplaneta*, and *Eurycotis* (fig.75, 135, 161; compare in 6.7.4.), and **L8** is missing in *Cryptocercus*.

The vp*-lobe (ventral phallomere) sensu Grandcolas and its sclerotisation (E)

In *Periplaneta*, *Therea*, and *Cryptocercus* Grandcolas (fig.1, 5, 6) designates a sclerotised lobe in the median ventral wall of the phallomere complex as the ventral phallomere **vp*** (**vla**-lobe in my terminology). As regards *Cryptocercus* and *Periplaneta* I agree with him: The lobe is the true **vla** with sclerite **L4G** in its ventral wall (fig.63, 148). In *Therea*, however, since this species is closely related to *Ergaula*, the lobe concerned can be regarded as homologous with the **lba**-lobe of *Polyphaga* and *Ergaula*, which bears sclerite **L7** in its ventral wall (fig.115).

The figures showing the general phallomere structure of Blattinae and Polyphaginae (Grandcolas' fig.2, 4) furthermore reveal that Grandcolas assumes homology for **L7** of Polyphaginae (including *Polyphaga*, *Ergaula*, and *Therea*) and **L4G** of *Cryptocercus* and Blattinae / Polyzosteriinae (the white posteromedian sclerites in these figures). In my opinion this assumption is wrong: In 6.2. and 6.3. the area belonging to the ventral phallomere or **vla**-lobe of *Polyphaga* has been identified, and the sclerotisation homologous with **L4G** of the other species has proved to be contained in **L4M** (fig.325e,f,h,k); the position of the ventral insertion of muscle **l6a**, the position of the **vla**-lobe relative to the **lve**-pouch, and the position of the genital opening are the main arguments. In 6.5. it has been shown that the **lba**-lobe corresponds only to the rightmost part of the **vla**-lobe of the other species, and that **L7** is a new sclerite of *Lamproblatta* + *Polyphaga* + *Ergaula* (and probably of at least some other Polyphaginae).

Side-homologies according to Grandcolas (F)

In *Cryptocercus*, Polyphaginae, and Blattinae Grandcolas assumes side-homologies for the sclerites of the left half and of the right half of the phallomere complex. The only argument is that an identical number of sclerites with similar form and position were recognisable on each side of the ejaculatory duct opening (p.146).

I cannot agree with these assumptions: The number of sclerites is not identical on both sides (compare in Grandcolas' fig.2, 4), and the shapes and relative positions of the sclerites supposed to be side-homologous are far from being similar on both sides (compare e.g. **L2v*/L2d*** and **R2*** in fig.1, 3, 5, 6 of Grandcolas). Furthermore, the position of the genital opening, defined as the center of symmetry of these supposed side-homologies, has been identified incorrectly in Polyphaginae and *Cryptocercus* (compare **(A)**).

Generally, a superficial correspondence in the number, arrangement, and shapes of the sclerites on the left and on the right side could well indicate side-homologies, but the muscles should be investigated in terms of confirmation or contradiction. The musculature, however, does not at all support the side-homologies assumed by Grandcolas.

9.2. The phylogenetic position of *Cryptocercus*

Cryptocercus punctulatus, *Polyphaga aegyptiaca*, and *Ergaula capensis* are, apart from Blattinae, the only species investigated in both Grandcolas (1994) and this paper. According to my results *Ergaula* and *Polyphaga* are more closely related, according to Grandcolas *Ergaula* and *Cryptocercus* are more closely related.

Grandcolas lists many autapomorphies suggesting the holophyly of various groupings of Polyphagidae. The autapomorphies of all groupings containing *Cryptocercus* will be discussed subsequently according to their hierarchy, focused on the question whether the features listed provide arguments to include *Cryptocercus* in the respective grouping. The first three groupings include *Cryptocercus*, *Ergaula*, and *Polyphaga* and are not contradictory of my results. The fourth grouping includes *Cryptocercus* and *Ergaula* but not *Polyphaga* and is directly in conflict with my results. If this latter grouping – with or without *Crytocercus* – proves to be holophyletic, the last two groupings subordinate to it are also in conflict with my results.

Many of these autapomorphies relate to those phallomere sclerites for which Grandcolas' homology assumptions for *Cryptocercus* and Polyphaginae have been refuted in 9.1. **(A)-(E)**, and they are in my opinion not valid; they will be commented with "misidentification", and the letter of the respective discussion in 9.1. will be added for reference. The autapomorphies are numbered like in Grandcolas (no numbers used in the first two groupings). From the quotations references like "in male genitalia" will be omitted. The autapomorphies concerned with tibial, head, "paraproct" (= subanal lobe), or female genital morphology have been reinvestigated. The autapomorphies 10, 16, and 17 of Grandcolas have been omitted since they refer to characters of the wings, which are completely absent in *Cryptocercus*.

Polyphagidae (including *Cryptocercus*)

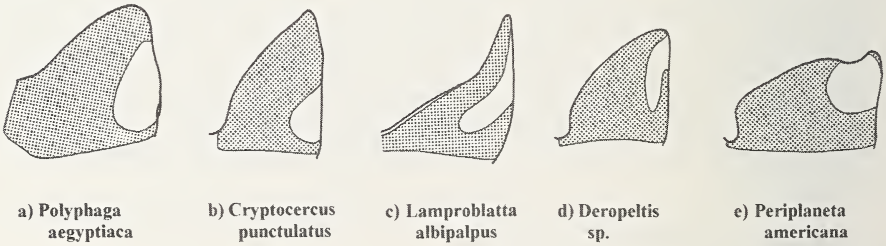
- "Sclerite **L2v*** with the form of an arch invaginated in ventro-posterior direction." An arch-shaped **L2** = **L2v*** extending along an invagination (**lve**-pouch) is a feature of the common ground-plan of Blattaria and Mantodea (6.2.1., 7.1.).
- "Sclerite **L1*** with thick-lipped edges." This probably refers to the plateau-like anterior face of the **pne**-pouch and of **L1**, and this is probably a synapomorphy of the respective

species (compare in 7.3., subgroup 2.2.2.; secondary reduction has been assumed for *Lamproblatta*).

- "Sclerite **L1*** turned on the ejaculatory duct and its opening."
- "Apical apodema of sclerite **L1*** curved around the ejaculatory duct opening."

These two features probably refer to the hood-like shape of sclerite **L1** and to its close relation to the opening of the phallomere-gland (= "ejaculatory duct": compare in **(A)**). Both features, however, are present in the common ground-plan of Blattaria and Mantodea (6.1.1., 7.1.).

- "Sclerite **R2*** with two tubercles, which are not articulated dorso-ventrally." Misidentification **(C)**.
- "Female paraprocts with a membranous area in their sub-basal and internal parts." According to fig.13 of Grandcolas (= fig.334a in this paper) this refers to a membranous area at the median base of the subanal lobes (similar to **Y** in fig.321c). However, a membranous area taking the same position is also present in the females of e.g. *Periplaneta* (fig.334e), *Deropeltis* (fig.334d), and *Lamproblatta* (fig.334c) and is certainly not an autapomorphy of Polyphagidae or Polyphagidae + *Cryptocercus*.
- "Straight, long and narrow paratergites." According to my own investigations (Klass, in press: te and tg in fig.15, 16), the fused paratergites of the abdominal segments 8 and 9 of the females are, as compared with *Periplaneta*, somewhat lengthened and narrowed in *Cryptocercus* but not in *Polyphaga*. Apart from this, a slight change of the proportions of sclerite elements is in my view not very convincing as an autapomorphy.
- "**L1*** pourvu d'une dilatation basale" (Grandcolas & Deleporte 1992). This feature probably relates to the transverse expansion of **L1** at its posterior margin, which continues towards both sides into the extensions **L1l** and **L1m** (fig.120, 153, 323i,l). However, a similar expansion, with at least one extension **L1m**, is also present in e.g. *Mantoida* (fig.49, 323d), and this is certainly a feature of the common ground-plan of Blattaria and Mantodea (6.1.1.). The extensions or regions **L1l** and **L1r** are also not restricted to *Cryptocercus* and Polyphagidae (compare e.g. *Tryonicus angustus*, fig.107, 323h, and *Nahublattella*, fig.243, 244, 323n).



334

Fig.334: Paraprocts of female Blattaria. – Ventral view of left subanal lobe; posterior↑, anterior↓, median→. Sclerotised areas (paraproct) are stippled, membranous areas are white. Fig.334a according to Grandcolas (1994).

Polyphaginae (including *Cryptocercus*)

- "Hook sclerite **L3d*** directed internally and posteriorly." Misidentification (**B**).
- "Tubercles of the sclerite **R2*** fused together." Misidentification (**C**).
- "Sclerite **L3v*** plate-like." Misidentification (**B**).
- "Spermatheque des femelles nettement bifide" (Grandcolas & Deleporte 1992). The polarity of this character (spermatheca bifid or unbranched) is unclear, but the bifid condition is certainly not a synapomorphy of *Cryptocercus* und Polyphaginae since it is also present in e.g. Blattinae, Polyzosteriinae, *Lamproblatta*, and *Mastotermes* (McKittrick 1964).

Cryptocercus* + *Therea* + *Eucorydia* + *Ergaula* + *Polyphaga* + *Eupolyphaga* + *Anisogamia

1 "Sclerite **R2*** with the fore tubercle showing a sharp outer apophysis." Misidentification (**C**).

2 "Neoformation **N***, right to **L1***, presenting a ventral loop." Misidentification (**D**).

Cryptocercus* + *Therea* + *Eucorydia* + *Ergaula

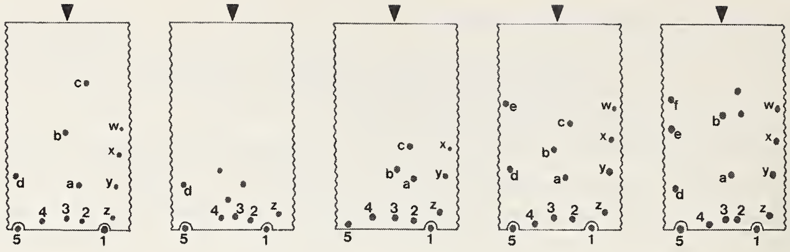
9 "Inner apophysis of sclerite **L2d*** less sharp." Misidentification (**B**).

11 "Presence of an expanded and warty area on the inner basal part of the anterior arch." In the female genitalia, the left and right second valvifers are narrowly connected with each other at their anterior margins by a median transverse bridge (anterior arch of McKittrick 1964). Grandcolas probably refers to a posteriad expansion of the sclerotisation of the second valvifers towards the bases of the second and third valves, which is lateral to this transverse bridge (compare Klass, in press: fig.2, 3). "warty" might refer to the small and thick setae in this area. The expansions as well as the bristles are present in *Cryptocercus*, but also in e.g. *Sphodromantis*, *Lamproblatta*, and *Eurycotis* (own investigations). If I have understood this autapomorphy correctly, it has to be refuted.

12 "Apical spur lacking on the outer caudal margin of the fore tibiae." I have investigated the spurs of the fore tibiae in *Polyphaga*, *Ergaula capucina*, *Cryptocercus*, *Lamproblatta*, and *Deropeltis* (fig.335a-e). All these species have 5 apical spurs, whose bases are either outside or inside the sclerotisation of the tibia. These apical spurs can be homologised one by one, if the slightly curved row of spurs **z**, **y**, **x** .... is taken as a landmark. The apical spur at the distal end of this row, which is always outside the tibial sclerotisation, has been arbitrarily termed **1**. *Ergaula*, *Polyphaga*, *Lamproblatta*, and *Deropeltis* correspond in their sets of apical spurs: Two adjacent spurs at the inner caudal margin of the fore tibiae are outside the tibial sclerotisation (**1**,**5**), three other spurs at the outer caudal margin are inside the tibial sclerotisation (**2**,**3**,**4**). Only in *Cryptocercus* spur **5** is inside the tibial sclerotisation. Hence, the apical spurs of *Cryptocercus* and *Ergaula* do not show any special situation in common differing from the other species. The autapomorphy is refuted.

13 "Neoformation **N*** adjacent to **L1** horizontal." Misidentification (**D**).

14 "Spermatheca sclerite vertical." Grandcolas probably refers to the orientation of the spermathecal plate of the female genitalia (McKittrick 1964). This sclerite, which is



a) Polyphaga aegyptiaca
b) Ergaula capucina
c) Cryptocercus punctulatus
d) Lamproblatta albipalpus
e) Deropeltis sp.

335

Fig.335: Spurs on fore-tibiae of Blattaria. – The sclerotisation and the spurs of the left fore-tibia are shown; basal↑, distal↓. The area bordered by straight or undulate lines is the sclerotisation of the tibia. This sclerotisation is cut lengthwise along the ventral = inner edge of the tibia (undulate lines) and unfolded. Black arrows mark the dorsal = outer edge of the tibia. Black dots represent the bases of spurs. Most spurs are labelled with numbers (apical spurs) or small letters – according to the homology relations assumed. Some apical spurs have their base outside the tibial sclerotisation.

vestigial in *Cryptocercus*, has a vertical orientation also in *Lamproblatta* and *Sphodromantis*, and the posterior main part of the sclerite of Blattinae and Polyzosteriinae is vertical, too. (These sclerotisations lie within the posterior wall of the bulge containing the spermathecal opening (compare Klass, in press: fig.2, 3). Thus, the vertical orientation is certainly not an autapomorphy of this grouping.

15 ”Sclerite **R2*** with a hind tubercle large and rounded.” Misidentification (**C**).

Cryptocercus + Therea + Eucorydia

25 ”Fore tubercle of **R2*** very small.” Misidentification (**C**).

26 ”Hind tubercle of **R2*** fused with **R3v***.” Misidentification (**C**). Moreover, **R1F** (= **R2***) of *Cryptocercus* is in no place fused with **R3** (= **R3v***). (According to fig.6 of Grandcolas the articulation **A3**, fig.163, is probably regarded as the point of “fusion”).

27 ”Frontal maculae of circular outline.” These frontal maculae are more or less clearly demarcated cuticular areas median to the antennal bases. I have investigated them in the following species (from externally only): In *Ergaula capucina* they are clearly demarcated and – like in Grandcolas, fig.16 – drop-shaped. In *Deropeltis* and *Polyphaga* they are nearly circular. In *Cryptocercus* and *Lamproblatta* no maculae could be found. According to this distribution of the character states the autapomorphy is refuted.

28 ”Postclypeus little or even not rounded.” It is not clear whether this feature refers to (1) the bulging of the postclypeus or to (2) the arch-like course of its anterior margin (= sutura epistomalis). According to (1), this feature would be like in e.g. *Periplaneta*

or *Sphodromantis*, whose clypei are hardly bulged. According to (2), I could not find a sutura epistomalis in *Cryptocercus*. In both cases the autapomorphy has to be refuted.

29 ”Arch of **L2v*** horizontal.” “Arch of **L2v***” is probably the part of **L2** within the **lve**-pouch. However, the orientation of **L2** in *Cryptocercus* is not or hardly different from that in *Polyphaga* or *Mantoida*. If, however, the lack of an upcurving of the right parts of **L2** and **lve** is referred to (6.2.1., 6.2.4.), this feature, if really present in the three species, would be derived. However, according to fig.5 of Grandcolas, in *Therea* **L1** and the right end of **L2** are still in contact (articulation **A2**), whereas in *Cryptocercus* the loss of this contact **A2** and the loss of the right part of **L2** (upcurved in other Blattaria) are probably intercorrelated. Hence, the levelness of the right part of **L2** would probably not be homologous in *Therea* and *Cryptocercus*.

30 ”Basis of inner apophysis of **L2d*** widened.” Misidentification (**B**).

31 ”Neoformation **N*** protruding.” Misidentification (**D**).

32 ”**L3v*** as a narrow plate in dorso-caudal position.” Misidentification (**B**).

Cryptocercus* + *Therea

34 ”**L3d*** very shortened.” Misidentification (**B**).

35 ”Neoformation **N*** as a rod.” Misidentification (**D**).

Conclusions

All surmised synapomorphies suggesting that *Ergaula*, *Eucorydia*, or *Therea* are more closely related to *Cryptocercus* than to *Polyphaga* are not valid or at least (only 29) questionable. On the other hand, in 7.3. many apomorphies have been listed which clearly suggest that at least *Ergaula* (and *Lamproblatta*) is more closely related to *Polyphaga* than to *Cryptocercus* (autapomorphies of the subgroups 2.2.2.2. and 2.2.2.2.2. in 7.4.). That *Therea* and *Eucorydia* are true members of Polyphaginae and that they are closely related to *Ergaula* is not questioned or even confirmed in the case of *Therea*, which shares at least one synapomorphy with *Ergaula* and several synapomorphies with *Ergaula* and *Polyphaga* (compare in 9.1.).

The synapomorphies of Grandcolas suggesting *Cryptocercus* to be a member of Polyphaginae or Polyphagidae are all not valid either. The only exception is the plateau-like anterior face of sclerite **L1**. However, *Cryptocercus* is probably closely related to Polyphaginae (autapomorphies of subgroup 2.2.2. in 7.4., but compare in 7.7.), and, if *Lamproblatta* is also included, *Cryptocercus* might well be assigned to the Polyphaginae sensu Grandcolas (representing the basalmost offshoot).

As regards the various other groups usually assigned to Polyphagidae (Holocompsinae, Euthyrrhaphinae, Latindiinae, and Tiviinae in Grandcolas, and some others), hardly anything is known about the morphology of their male and female genitalia, and their phylogenetic relationships are still open to question.

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APPENDIX

Synonymy of the terminology of the phallomere elements

LaGreca: Mantodea

LaGreca (1954) has introduced special terms for the phallomere elements of Mantodea (left column, taken directly from LaGreca 1954, p.27). Some of these are used for formative elements as well as for sclerites situated inside or upon them. In the following table the synonymy with the terms used in the present paper (right column) is given.

Fallomero dorsale di sinistra (fs, not fv)	Left complex minus vla-lobe and sclerite L4A
Lamina dorsale (ld)	Sclerite L4B
Lamina ventrale (lv)	Pouch lve and sclerite L2 (mainly region L2a)
Processo apicale (pa)	Process paa and region L2d
Apofisi falloide (af)	Process afa and sclerite L1B
Processo anteriore (pn)	Pouch pne and sclerite L1 or L1A
Lobo membranoso (lo)	Process loa
Fallomero dorsale di destra (fd)	Lobe fda and region R1d
Corpo del fallomero (fd)	Lobe fda and region R1d
Braccio mediale del fallomero (bm)	Leftmost part of lobe fda and region R1d
Apodema anteriore (an)	Sclerite R3 including apodeme age
Processo ventrale sclerificato (pv)	Tooth / ridge pva and region R1t
Piastra ventrale (pi)	Tooth / ridge pia and region R1v
Area sensoria (as)	(not treated in the present paper)
Fallomero ventrale (fv)	Lobe vla and remaining ventral wall of left complex and sclerite L4A
Processo articolare (ar)	The part of sclerite L4A near articulation A1
Lobo mediale (lm)	Rightmost part of lobe vla and sclerite L4A
Processo distale (pd)	Process pda and pertaining parts of L4 or L4A
Pene (p)	Lobe(s) goa next to genital opening

McKittrick: Blattaria

Synonymy is given for the terms used in the present paper and those used in McKittrick 1964, fig.106-126. Since my results concerning the homologies of the sclerites are different from those of McKittrick, the synonymy is different in the various subgroups, and some representative groups are selected. This synonymy is also valid for many taxonomic papers in which the terminology of McKittrick has been used (e.g. Roth 1974).

Blaberidae **Supella**		**Blattellinae** **Nyctiborinae**		***Anaplecta***	
McKittrick	present paper	McKittrick	present paper	McKittrick	present paper
L1	R3, R2, R1T, R4	L2vm	L2 (inside lve: L2D)	L1	L1 (?)
L2vm	L2 (inside lve: L2D)	L2d (virga)	L2 (on via: L2E+L4N)	L2v	L4K
L2d (virga)	L2 (on via: L2E+L4N)	L2	L4U	L2vm	L2 (inside lve)
R2	L3 (on hla), L4U	L3	L3	L2d	L2 (on paa), L4N
		R2	R2, R1S, R1P	L3	L3
		R3	R3	R2	R2, R1N, L4G
				R3	R3

Nahublattella **Lophoblatta**		***Cryptocercus***		**Blattinae,** **Polyzosteriinae**	
McKittrick	present paper	McKittrick	present paper	McKittrick	present paper
L1	R2, R1N, R3	L1	L1	L1	L1
L2vm	L2 (inside lve: L2D)	L2v	L2 (inside lve)	L2v	L2
L2d	L1	L2d	L2 (on paa)	L2d	L4C,D,E; L4H
R1	L2E+L4N	L3	L3	L3	L3
R2	L3, L4U	R1	R1J	R1	R1G, R1H
R3	L4V	R2	R2, R1F	R2	R2, R1F
		R3	R3	R3	R3

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